*Alewife (*Alosa pseudoharengus*) spawning and nursery areas in a sentinel estuary: spatial and temporal patterns*

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Alewife (*Alosa pseudoharengus*) spawning and nursery areas in a sentinel estuary: spatial and temporal patterns

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Abstract Spatial and temporal distribution of anadromous alewife (*Alosa pseudoharengus* Wilson) spawning and nursery habitats were determined by sampling in the Mullica River – Great Bay watershed (New Jersey, USA) in a combination of long- and short-term observational and quantitative studies. Reproduction was confirmed by examination of developing gonads, visual observations of spawning, and egg collections. Spawning typically lasted 2–4 days in discrete waves in freshwater tributaries from late March to late April. Nursery habitats for larvae and young-of-the-year alewife included low-salinity tributaries near the freshwater-saltwater interface and high salinity waters through early fall before departure to the ocean in late fall. Predation on eggs by fish predators, especially American eel (*Anguilla rostrata* Lesueur), occurred below a dam. This predation was also observed in the laboratory on eggs and larvae. These findings point out that this dam provided for enhanced predation on alewife early life history stages, and may cause an ecological hotspot for predation-prey interactions for this anadromous species and its catadromous predator.

Keywords Alewife · Anadromous · Nursery · American eel · Dam

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Introduction

The decline in anadromous *Alosa* spp. (river herrings) along the east coast of the US (Limburg and Waldman 2009; Walters et al. 2009; Hasselman and Limburg 2012; Palkovacs et al. 2013; Twining et al. 2013; Ogburn et al. 2017) and our inability to help them recover points out the lack of understanding we have for the natural history (Able 2016) of these important species. To date, several factors are suspected of contributing to the decline of river herrings including habitat loss, offshore bycatch in pelagic fisheries (Bethoney et al. 2014; Hasselman et al. 2016), overfishing (Turner et al. 2015), or all of these factors combined (Limburg and Waldman 2009). Of certain importance to the decline of river herring is the history of dam creation since European settlement, as this has precluded spawning in many miles of upstream areas (Freeman et al. 2003; Walter and Merritts 2008; Mattocks et al. 2017). In addition, climate change-induced temperature increases may affect the population dynamics (Lynch et al. 2015; Tommasi et al. 2015; Hare et al. 2016; Alexander et al. 2017) and induce earlier spawning migrations (Ellis and Vokoun 2009).

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Anadromous populations of alewife along the east coast of the U.S. share many characteristics as seasonal occupants in freshwaters and estuaries for spawning and in young-of-the-year nurseries (Collette and Klein-MacPhee 2002; Able and Fahay 2010). Spawning, often in waves (Cooper 1961; Richkus 1975; McCartin et al. 2019), occurs in the spring, but the timing and duration can vary with latitude (Greene et al. 2009). The habitat for spawning is often in freshwater ponds (e.g., Kosa and Mather 2001) or streams (Collette and Klein-MacPhee 2002; Walsh et al. 2005; Able and Fahay 2010). After hatching, the larvae and small juveniles use freshwater streams (Kosa and Mather 2001; Iafrate and Oliveira 2008; Tommasi et al. 2015) or the vicinity of the freshwater-saltwater interface (Campfield and Houde 2011). At larger sizes the young-of-the-year move into estuaries and eventually the ocean in the summer and fall (Richkus 1975; Stokesbury and Dadswell 1989; Yako et al. 2002; Iafrate and Oliveira 2008; Gahagan et al. 2010). Some of the general patterns vary between estuaries for adult age composition (Davis and Schultz 2009) and nursery habitats (Kosa and Mather 2001; Turner and Limburg 2016).

River herring are not only an important forage food source for other fish, birds, mammals, and herptiles (Loesch 1987; Wilson and Halupka 1995), but can also act as a nutrient source for freshwater systems and stimulate microbial activity that can increase overall food production (Durbin et al. 1979; Walters et al. 2009; West et al. 2010; Hall et al. 2012; Twining et al. 2013).

Despite the ease of human access to spawning sites in freshwater streams, we still lack a thorough understanding of many aspects of river herring reproduction and early life history (e.g. McCartin et al. 2019). In New Jersey, prior surveys have attempted to determine utilization in the Mullica Valley (Hastings 1984) including spawning sites throughout the state (Zich 1978; NJDEP 2005) and the occurrence of presumed young-of-the-year in the adjacent coastal ocean waters (Milstein 1981). Our prior understanding of the life history was summarized in Able and Fahay (2010).

In this study, we combine qualitative and quantitative observations to address aspects of the temporal and spatial variation in reproduction and in larval and juvenile occurrence and abundance in the Mullica River-Great Bay estuary, a relatively unaltered estuary that can, as a result, provide insights into short-and long-term change for this species. We also develop insights, for the first time, into the role of predators on the eggs and larvae at an ecological hot spot, a dam, as it may influence survival of these early life history stages.

Materials and methods

Study site

The clean waters of the Great Bay – Mullica River estuary are embedded in the Pinelands National Reserve and state and federal management areas including part of the Jacques Cousteau National Estuarine Research Reserve. Together, these make the approximately 400,000 ha estuary one of the least impacted systems in the northeastern United States (Good and Good 1984; Kennish et al. 2004) and thus is an exceptional reference watershed for studying this and other species. This estuary is a relatively shallow (<2 m), salt marsh-fringed, drowned river valley system with numerous tributaries (Fig. 1). Atypical of other northeastern U.S. estuaries, the Mullica River – Great Bay rarely approaches hypoxic dissolved oxygen levels (<4 mg/L) (NOAA NERRS, unpublished data). Water temperature regimes follow temperate seasonal patterns (<0 °C in winter to >30 °C in summer). Salinity corresponds to an upriver gradient from polyhaline regions near Little Egg Inlet (salinity 32 ppt) to the freshwater-saltwater interface near Lower Bank, approximately 30 km upstream and into tidal freshwater habitats further upstream (Fig. 1). The upper regions of the estuary, including tributaries, are naturally acidic (pH 4–6) due to tannins leached from the surrounding natural pine/oak-dominated watershed.

The Batsto River, a tributary to the Mullica River, is 25.7 km long and drains approximately 173.5 square km of southern Burlington County (Anonymous 2003). A dam at Batsto Village divides the study area into Batsto Lake and the continuation of the river below the dam (Supplemental Fig. 1). The dam consists of a rolled earth embankment with a concrete spillway and a concrete apron extending 14.6 m from the spillway (USACE 2003). Nescochogue Creek is another tributary that enters the Mullica River a few miles above where the Batsto River enters the same river (Online Resource Fig. 2). A portion of the creek has been diverted and drains into Lake Nescochogue.

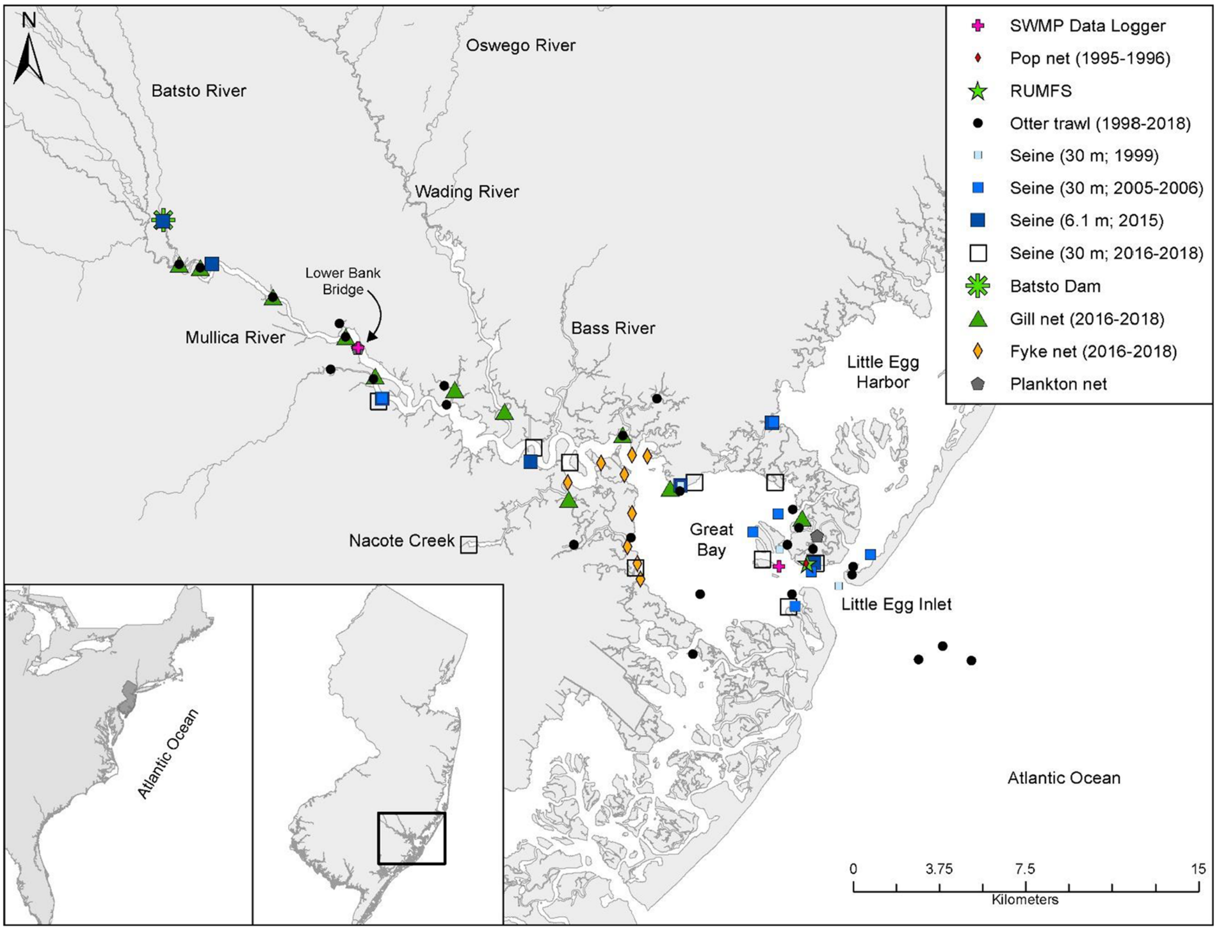

Fig. 1 Sites sampled with various gears in Mullica River – Great Bay estuary, 1989–2018. See Table 1 for additional details

Environmental data

Measures of water quality were obtained with hand-held data probes (YSI Pro Plus Professional Series, Yellow Springs Instruments, Inc., Yellow Springs, OH). In addition, a series of four water quality data loggers (YSI Model 6 series sondes) within the Mullica River – Great Bay estuary are maintained for the Jacques Cousteau National Estuarine Research Reserve by the centrally managed System-Wide Monitoring Program (SWMP) Central Data Management Office (Kennish and O'Donnell 2002). These included time stamped temperature, salinity, dissolved oxygen, and pH values.

Temporal occurrence, distribution, and abundance of larval, juvenile, and adult alewives

This work synthesizes a number of sampling events from disparate studies in the study area over many years to extract important patterns as an effect of larger temporal and spatial scales, and ties them together with additional observations intentionally made to rectify gaps identified from retrospection. The occurrence, distribution, and abundance of alewife and other alosines of all life history stages were assessed using multiple sampling gears over a large time scale. Larval alosines and alewife were assessed based on long term collections from the bridge over Little Sheepshead Creek behind Little Egg Inlet (Able and Fahay 2010; Able et al. 2017) during 1989–2015 and from Lower Bank Bridge in the Mullica River during 2005 and 2016, with identical sampling gear (Fig. 1, Table 1). Larval identification was based on at least two or more characters to confidently identify individuals to species (i.e. dorsal, anal, and pelvic fin ray counts, post-anal fin ray myomere count, myomere count between dorsal and anal fin rays, peritoneum color) (Lippson and Moran 1974; Chambers et al. 1976; Jones et al. 1978). Weekly pop net collections sampled juvenile size and abundance in the Rutgers University Marine Field Station (RUMFS) boat basin from August 1995 through December 1996 (Table 1). Juveniles were also sampled via otter trawl collections, from the ocean to the upper Mullica River, during July and September from 1998 to 2018, and bimonthly from March through October from 2016 to 2018 (Fig. 1, Table 1). Adult and additional juvenile specimens were collected via fyke, seine, and gill nets in 2016–2018 (Table 1). Additional seine samples were in 1999, 2005–2006, and 2015 (Table 1). These individuals were identified to species via peritoneum color and/or and gill raker counts.

Sex ratio, reproductive status, and behavior

To determine the timing and duration of spawning, we made frequent visual observations in the shallow, clear waters at the study sites during 2016–2017 (Table 1, Fig. 1, Online Resource Fig. 1). Between 26 March and 20 May 2016, we visually examined the areas of the Batsto River between the dam at Batsto Lake and the former USGS Gauging Station (Online Resource Fig. 2). During 2017 and 2018 we made more frequent visual observations of spawning adult alewives. In addition to these, the upper Mullica River from the Atsion Lake dam to three miles below the dam (Online Resource Fig. 1) was sampled by visual observations from a kayak for approximately 50–75 daylight hours over the alewife spawning season. The detection of reproducing river herring was augmented by audible and visual observations of splashing while they were spawning. We were also alerted to the presence of adult river herring observed by personnel at Batsto Village on several occasions. In 2016 (14 and 25 April), we sampled adult alewives with seines and dip nets at several locations in the Batsto River, including immediately below the dam, below the sawmill, and at a slag pile formed from the historical remains of the blast furnace dumping grounds at Batsto Village (Online Resource Fig. 2). Size was determined by measuring the fork length (to the nearest millimeter) from these collections. Sex was determined by expressing either milt or eggs from each individual. When neither was apparent, the assumption was that the individual was a spawned-out female. In 2016 and 2017, adult alewife collected by gill and fyke nets (Fig. 2) and seine net (Fig. 3) were dissected to determine sex and weighed to calculate gonadosomatic index (GSI). GSI for females was calculated as gonad weight/eviscerated body weight × 100. Frequent daytime visual observations of the location and behavior of spawning river herring in 2016 were aided by audio and video recordings at several locations from immediately below the dam to below the Rt. 542 bridge (Online Resource Fig. 2). Further, the location of spawning sites was verified by the presence of river herring eggs as collected with small mesh dip nets. Confirmation of the identification of the eggs was based on laboratory rearing through hatching and subsequent preservation and identification under a microscope.

Predation on alewife eggs and larvae

To determine food habits of potential predators, several fish species, with emphasis on the abundant elver and glass eel stages of American eel, were collected from March through May 2017. These individuals were preserved together, per sampling date, in jars of 10% formalin or 95% ethanol, for gut content analysis at a later date. Eels were staged based on Haro and Krueger (1988). For this study, stage seven eels were considered to be elvers at sizes ≤100 mm TL and yellow eels at larger sizes.

Observations of predation on alewife eggs and larvae were carried out in the laboratory between 1 April and 2 May 2016. American eels were collected below the dam at Batsto Village via dip net and included glass, elver, and small (101–125 mm TL) yellow eel stages. Eels were held in aerated water from the source. Food was withheld for a minimum of 24 h prior. During each trial, each eel was placed in a solitary clear glass tray (24 cm × 15 cm × 5 cm) or finger bowl (8 cm depth, 20 cm diameter) containing 0.9 L of water from the source. One piece of PVC piping (1.8 cm diameter, approx. 8 cm length) was provided for structure. One of two feeding options was also provided in each container, either five alewife eggs or five alewife larvae. To limit stress, eels were introduced to dishes after alewife eggs or larvae. Dishes were separated by opaque dividers. Dishes with eggs or larvae but no eel were prepared under the same conditions to act as a control on mortality.

Observation trials ran over 24 h under conditions replicating natural light cycles. After each trial, remaining eggs and larvae were quantified. Eels were anesthetized using MS-222 and were measured live (total length, in millimeters). A total of 235 trials were

Table 1 Sampling effort by gear for larvae, juvenile, and adult alewives and American eels

Life History Stage	Gear	Location/Habitat	Water Depth (m)	No. of Stations	Duration/Frequency	No. of Sampling Events	Abundance Metric
Larvae	Plankton net (1 m diameter, 1 mm mesh)	Little Sheepshead Creek, Great Bay – Little Egg Harbor estuary	4	1	Feb 1989 – Dec 2015, weekly	1185	Number / tow
		Lower Bank Bridge, Mullica River estuary	1.8	1	Apr – Jun 2005, weekly	29	Number / tow
					Mar – Jul 2016, biweekly	30	Number / tow
Juveniles	Pop net (5 m diameter, 6 mm mesh, 3 mm cod end mesh)	RUMFS boat basin	1	1	Aug 1995 – Dec 1996, weekly (sometimes 2x/week)	440	Number / set
Juveniles	Seine (30 × 2 m, 6 mm mesh wings, 2 mm mesh bag)	Great Bay – Little Egg Harbor estuary & adjacent ocean	0.5–1.5	11	May – Oct 1999, biweekly	413	Number / net length × distance sampled
			0.6–1.5	9	May – Oct 2005 & 2006, monthly	106	Number / net length × distance sampled
Juveniles	Seine (6.1 m, 4 mm mesh)	Mullica River – Great Bay estuary	0.2–1.5	5	May – Oct 2015, monthly	87	Number / net length × distance
Adults		Batsto River	0.7	1	April 2016	10	Total number
Juveniles & Adults	Seine (30 m, 6 mm mesh)	Mullica River – Great Bay estuary	0.2–1.8	10	May – Oct, 2016–2019, biweekly Nov – Apr, 2016–2019, monthly	485	Number / net length × distance sampled
Juveniles & Adults	Otter Trawl (4.9 m head rope, 19 mm mesh wings, 6.3 mm mesh liner)	Mullica River – Great Bay – Little Egg Harbor	0.3–16.2	27	Jul & Sep, 1998–2018, monthly	3428	Number / minute towed
			0.8–6.2	9	Mar – Nov, 2016–2018, bimonthly	377	Number / minute towed
Adults	Multi-mesh gill net (15 m × 2.4 m net with 1 panel of each mesh size: 2.5, 3.8, 5.1, 6.4, and 7.6 cm)	Mullica River – Great Bay estuary	0.7–3.0	7	Mar – Nov, 2016–2018, bimonthly	350	Number / 15 m of net / minute fished × 1000
		Mullica River	0.6–3.0	5	Mar 2017, May 2017	40	Number / 15 m of net / minute fished × 1000
Adults	Multi-mesh gill net (90 m × 2.4 m net with 2 panels of each mesh size: 1.3, 1.9 and 2.5 cm)	Mullica River – Great Bay estuary	0.7–3.6	7	Mar – Sep 2016, bimonthly	31	Number / 15 m of net / minute fished × 1000
Adults	Fyke net (45.7 m × 1.2 m × 6.4 cm mesh leader, 7.6 m × 1.2 m × 6.4 cm wings, 7.6 m × 0.8 m × 6.4 cm mesh hoops to cod end)	Mullica River – Great Bay estuary	0.9–2.5	9	Nov – Apr, 2016–2018, 3x-/month	148	Number / 48 h set
Spawning Adults	Daytime visual observations	Mullica River – Great Bay estuary and tributaries	<1	1	Mar – May 2016	29	Number / sampling event
				1	Mar – May 2017	26	
				23	Mar – May 2018	196	

See Fig. 1 for location of sampling sites. See Online Resource Fig. 1 for location of visual observations of spawning adults

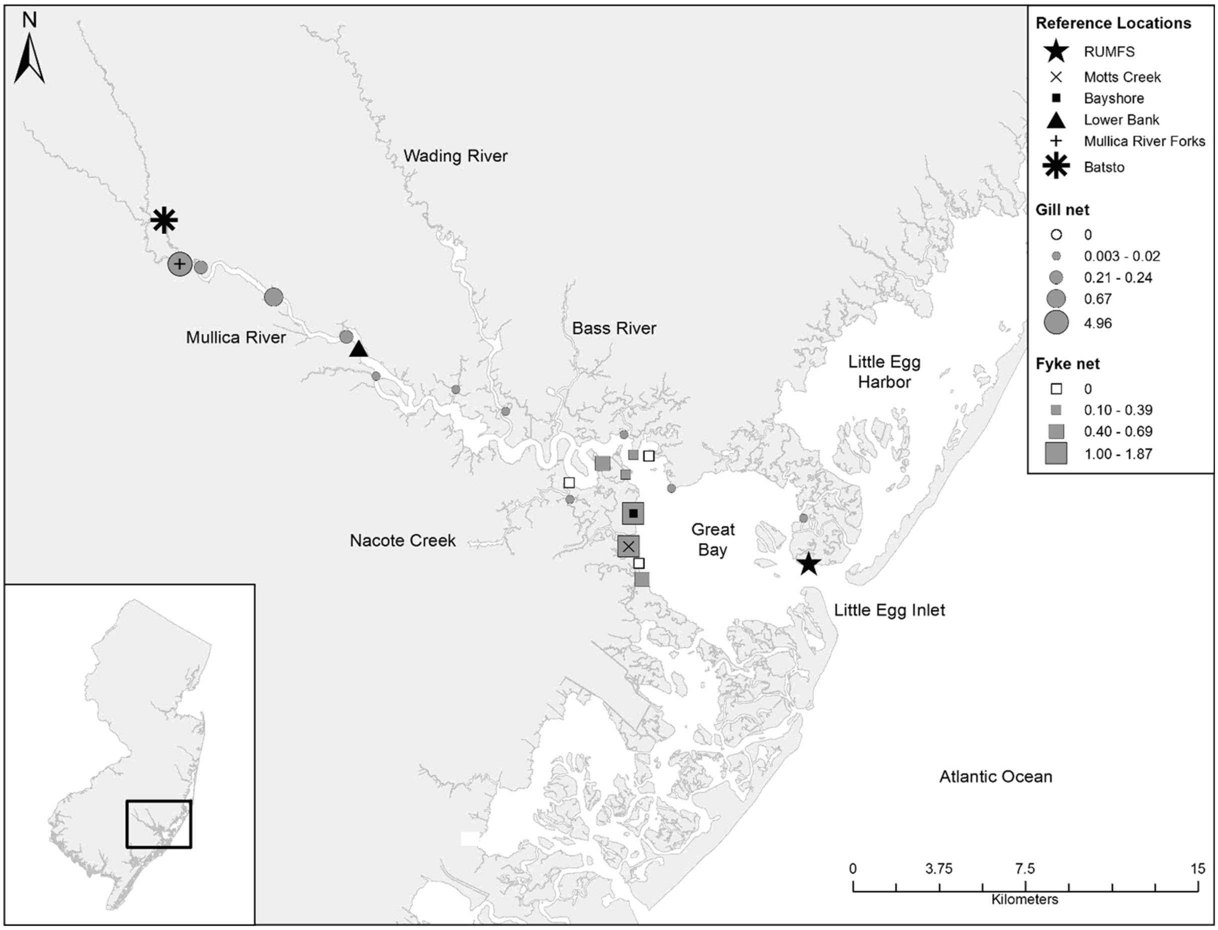

Fig. 2 Distribution and abundance (CPUE) of adult *Alosa pseudoharengus* from gill net sampling in March, May, July, and September 2016–2018 and fyke net sampling in February through April 2017–2018 in the Mullica River – Great Bay estuary. Gill net CPUE values are displayed as CPUE (fish per 15 m of net per minute) × 1000. RUMFS = Rutgers University Marine Field Station, Batsto = Batsto Village, Lower Bank Bridge = approximate location for freshwater-saltwater interface (Fig. 1)

performed using 113 glass eels, 104 elvers, and 10 yellow eels. Occasionally, non-viable eggs and dead larvae were found at the end of an observation trial. If either were discovered at the conclusion of any trial, the number of initial prey items was adjusted to reflect that the expired individuals were not available for consumption.

Results

Temporal and spatial distribution of adults

Alewife dominated the collections of juvenile and adult alosine fishes throughout the Mullica River – Great Bay estuary from spring through fall of 2016–2018 (Table 1). Fyke, seine, and gill net sampling in the study estuary found primarily alewife ($n = 634$, 96.4% of alosine catch). Other adult alosines collected were seven blueback herring (*Alosa aestivalis* Mitchill, 210–310 mm FL), ten hickory shad (*Alosa mediocris* Mitchill, 199–374 mm FL), and two American shad (*Alosa sapidissima* Wilson, 450 and 498 mm FL). Juveniles included 341 alewife (37–105 mm FL), and five blueback herring (41–105 mm FL). All other *Alosa* spp. in this study were alewife. In 2016, targeted sampling for examination of gonads and species identity occurred immediately below the dam at Batsto Village. Alewife ($n = 957$) were the only river herring captured at this location. Adult alewife (210–265 mm FL) were

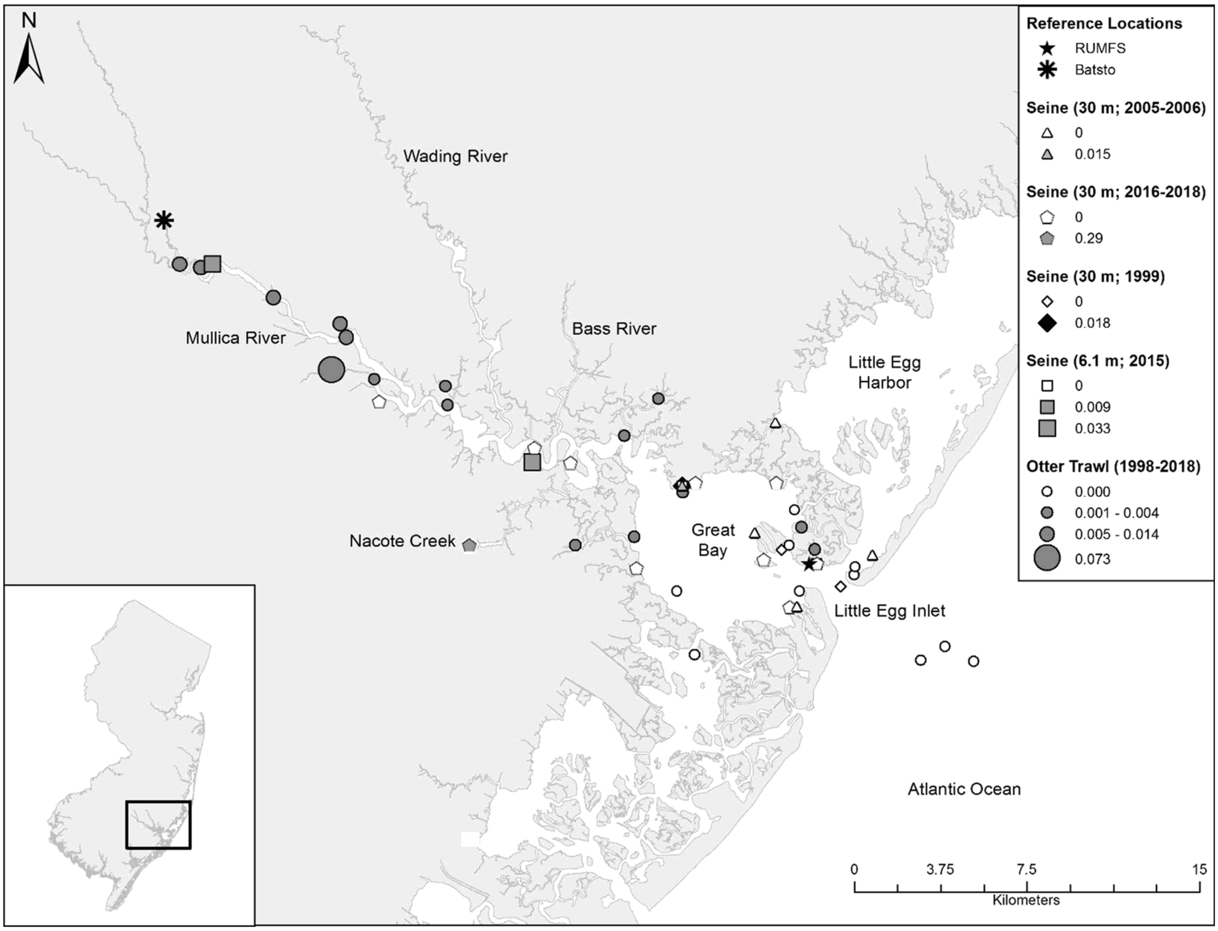

Fig. 3 Distribution and abundance (CPUE) of juvenile and adult alewife (*Alosa pseudoharengus*) from otter trawl sampling (1998–2018) and seine net sampling (1999, 2005–2006, 2015, and 2016–2018) in the Mullica River – Great Bay estuary. RUMFS = Rutgers University Marine Field Station, Batsto = Batsto Village

collected throughout the rest of the estuary during survey-structured stratified and standardized sampling. Most adult alewife were collected at Port Republic (1.65 CPUE, $n = 5$) via seine net. For 2017, sampling was expanded to include gill net sites up through The Forks of the upper Mullica River (Table 1, Fig. 2). Adult alewife (170–290 mm FL) were collected throughout this expanded range, with most collected at Bayshore (3.11 CPUE, $n = 28$) and The Forks (0.0003 CPUE, $n = 32$) by fyke net and gill net, respectively (Fig. 2). In 2018, the highest catch of adult alewife (173–287 mm FL) occurred in fyke nets at Motts Creek (1.23 CPUE, $n = 16$; Fig. 6).

The period of spawning was based on daytime visual observations (Table 2) and complimentary collections of adults. During the period of observation for spawning at Batsto Village and below the nearby Rt. 542 Bridge, from late March through mid-May 2016, there were distinct, relatively short periods when spawning alewives were visually detected in large numbers or waves (Table 2). These detections lasted several days in late March, mid-April, and late April. In the first occurrence, spawning adults were observed for the first time (no prior observations) on 26 and 27 March. Adult alewives appeared to be absent on 29 and 30 March. The second occurrence of spawning adults was on 13–14 April. No herring were present during observations made on 17, 19, and 23 April. The third occurrence was observed each day from 24 April through the morning of 27 April. No adult alewives were present during observations made at 12:00 and 18:00 h on 27 April. Alewives were absent through 20 May, after which date observations were discontinued.

Adult alewife were less abundant during the same general period in 2017. The earliest capture of alewife in fyke net samples was in Great Bay and Mullica River on February 21. About two dozen adults were visually observed below the Rt. 542 Bridge on the Batsto River on 30 March and 6 April, but were not observed upstream at the Batsto Village dam. Alewife eggs were collected below the dam on 20 April, suggesting undetected alewife spawning below the dam during prior visual checks. Adults were also observed in late March and early and late April in the Mullica River just below the Rt. 542 Bridge.

During the period between mid-March and mid-May 2018, we made 196 individual visual observations at 22 locations in the Mullica Valley to determine the spatial distribution of spawning river herring (Online Resource Fig. 1). Priority sites were visited between 17 and 24 times while other sites ranged from 2 to 14 times. In addition, the Mullica River below the Lake Atsion dam was examined by kayak for the presence of spawning river herring during the same period. We assumed that all river herring observed were alewife based on 1) visual observations of deep bodied *Alosa* spp. with large eyes relative to snout length and 2) prior extensive collecting efforts in 2016 and 2017 at the Batsto Dam which only found this species. Despite extensive visual observations at numerous locations during 2018, we only identified adult alewife at the Batsto Dam in the Batsto River and Nescochogue Creek in the Mullica River drainages (Online Resource Fig. 2). Collection of alewife eggs below the dam was used as a means to confirm spawning on multiple occasions (see Table 2). These same sites were identified during the 1970s as spawning sites (Online Resource Fig. 2). Other sites identified by Zich (1978) did not appear to support spawning in 2018 including Mullica River at Constable Bridge, Nacote Creek at Mill Pond, and Wading River above Rt. 542. Thus, the number of spawning sites may be reduced relative to the 1970s, based on these visual surveys.

During these visual observations during the springs of 2016–2018, the number of adult alewives present varied from dozens to hundreds, and perhaps thousands at the study site. These estimates were reasonably accurate because the study site contained shallow (<0.9 m), relatively clear water. The only time fewer than 100 individuals were observed was at the end of a wave.

Estuarine conditions were variable during the spawning period due to changing meteorological conditions and tidal variation. The temperature at Lower Bank, in the upper Mullica River, was variable during March and April of 2016 (4.6–29.3 °C) and 2017 (0–26.6 °C) when adult alewives were collected at several places in the Mullica River. The salinity ranged from 0 to 8.0 ppt in 2016 and 0.1–13.7 ppt in 2017. The temperature during the presumed spawning season during March to May 2017 at the Batsto Village dam ranged from 0.8–26.0 °C. This variability was, in part, due to tidal effects which were observed at the dam as well as periodic, unscheduled releases of water from Batsto Lake under high water conditions.

Table 2 Frequency of occurrence, by date, of spawning alewife adults, their eggs, and American eel glass eels and elvers in 2016 (23 March – 21 May) and 2017 (23 March – 14 May) below the dam at Batsto Village

Year		Dates Observed	Number of Dates Not Observed
2016	Adult alewife	March 26, 27 April 13, 14, 24–27	21
	Alewife eggs	March 26, 27, 29 April 14, 17, 19, 25	–
	American eel	March 29 April 11, 14, 25 May 20	–
2017	Adult alewife	March 30 April 6, 22	24
	Alewife eggs	April 20	2
	American eel	April 17, 20, 22, 23, 28 May 2	1

Size, sex ratio, and spawning behavior

The alewife collections in the Batsto River below the dam at Batsto Village (Fig. 3) on both dates in 2016 were primarily adults of >200 mm FL (Table 2). The sex ratio was dominated by males on both dates, with 72% on 14 April ($n = 89, \overline{x} = 241$ mm FL) and 85% on 25 April ($n = 47, \overline{x} = 241$ mm FL). The relatively small proportion of females in early ($n = 34, \overline{x} = 256$ mm FL) and late ($n = 8, \overline{x} = 256$ mm FL) April may be another indication of the duration of the spawning season.

Adult herring collected in gill nets and assessed for GSI in 2017 ranged from 115 to 274 mm FL, averaging 236 mm FL. Sex ratio was 45.5% female and 54.5% male, with females averaging slightly larger ($\overline{x}$ = 240.6 mm FL, range = 129–274 mm FL) than males ($\overline{x}$ = 230.8 mm FL, range = 115–265 mm FL). Alewives were primarily collected at The Forks (33% of catch, Figs. 1, 3), the most upstream sampling site on the Mullica River, and the site closest to the dam on the Batsto River. Female alewives collected in gill nets at Ed's Creek mouth ($n = 1$, 17.5%) and The Forks ($n = 9$, 17.2%) had the highest GSI. Females collected from Sweetwater ($n = 2$) had the lowest GSI (7.1%).

Alewife spawning occurred in waves. In each wave we were able to see large aggregations of adults, often split into distinct smaller groups of fish, which were obvious over several days in these shallow waters. These occurrences were often accompanied by the sounds of splashing as spawning occurred in shallow water or near the surface. We could not determine if adults were present at other times if they were in deeper water or on cloudy days when water transparency was limited. During 2016, spawning was observed in natural, shallow, riverine habitats, such as over sandy substrate with no vegetation, over sandy substrate with vegetation, at the mouth of a small rivulet leaving the river, along a section of river bank with overhanging vegetation, and on the exposed fibrous roots of river bank trees. There were several manmade sites that were also used for spawning, including the uniformly flat, algae covered, concrete apron immediately below the Batsto River dam, as well as in an area dominated by slag, a former waste product of the blast furnaces at Batsto Village. All of these spawning sites were observed to have been used on more than one day and by more than one wave. The water depth at some of these sites was <0.3 m and was so shallow that the dorsal fins of the fish were exposed. This was especially obvious at the concrete apron below the dam, which was so shallow that some fish had to swim on their sides to gain access or to leave. Other spawning sites were approximately 0.6 m deep. Typically, aggregations of up to several dozen adults gathered in one of the above locations. In many instances, following behavior, presumably of a female by one or more males, was observed. Occasionally during these observations, a single fish swam near the vent of the lead fish and used its snout to bump the vent, possibly attempting to stimulate egg release. Suddenly several fish swam in a tight circle for about one second while eggs and sperm were released. These events happened several times within 10–15 min at the same location.

Spawning during spring 2018 was infrequent but concentrated in time and space based on daytime visual observations at two of 19 sites (Table 2). At the Batsto Dam we estimated hundreds of alewife were present on 23 and 25 April. At Nescochogue Creek the number present varied from low (2 individuals on 5 April and 12 individuals on 31 March) to higher abundances (100 s on 1, 23, 25 and 26 April to 100 s to 1000 on 2 April). In the three instances in which we observed spawning, they occurred in discrete waves which lasted approximately 4–6 days at Nescochogue Creek and 3 days at Batsto Village dam.

Temporal and spatial distribution of larval and juvenile alewife

After spawning in March through April, newly hatched larvae were presumably carried downstream from below the dam in the Batsto River and elsewhere in the upper Mullica River to the main stem of the Mullica River. *Alosa* larvae (presumably *A. pseudoharengus*) first appeared at Lower Bank Bridge in plankton collections as *Alosa* spp., at sizes of 6.0–15.8 mm in May and 12.7–17.7 mm in June of 2005. Slightly larger individuals, confirmed as *A. pseudoharengus*, were 12.3–22.2 mm TL and 11.4–25.8 mm TL in the same months, respectively. In July and September of several years, *A. pseudoharengus* juveniles were collected at sizes of 37–85 mm FL. These were distributed at a number of otter trawl and seine sampling locations (Table 1, Fig. 3). Most of the juveniles, however, were captured in the lower salinities of the Mullica River, often in the spring when salinities are lower in any given year (Fig. 4). Most of these were in freshwater or at salinities less than 5 ppt. The occurrence of juveniles at the higher salinities in Great Bay were much less frequent. Almost all juveniles collected in the Mullica River were captured during the period of highest temperatures (>20 °C) as measured at Lower Bank (Fig. 4).

The timing of juvenile occurrence was observed using pop net collections from the RUMFS boat basin near Little Egg Inlet (Hagan and Able 2003), from July through October. Size mode progressed with month (July = 51–82 mm, August = 83–112 mm, September = 100–127 mm, October = 129–142 mm). These may represent those individuals that are leaving the estuary for the ocean. A few slightly smaller individuals were also collected in November ($n = 1$, 89 mm) and December ($n = 3$, 49–81 mm).

All of these composite lengths, by month, clearly depict the occurrence of adults, primarily in March – April, larvae in May – June, and juveniles in July – October (Fig. 5). Thus, our sampling captured all of the major life history stages of *A. pseudoharengus* in this estuary. The consistent pattern of growth implies survival through the time of presumed movement offshore in November – December and through the winter (Milstein 1981), where they have been captured in National Marine Fisheries Service otter trawl surveys (Able and Fahay 2010).

This pattern of annual variation in juvenile CPUE is also evident in a 1998–2016 based on otter trawling in the estuary during July (typically more abundant) and September (Fig. 6). Throughout July sampling, CPUE in Landing Creek was variable but frequently much greater than at all other sites. Throughout the duration of the July time-series,

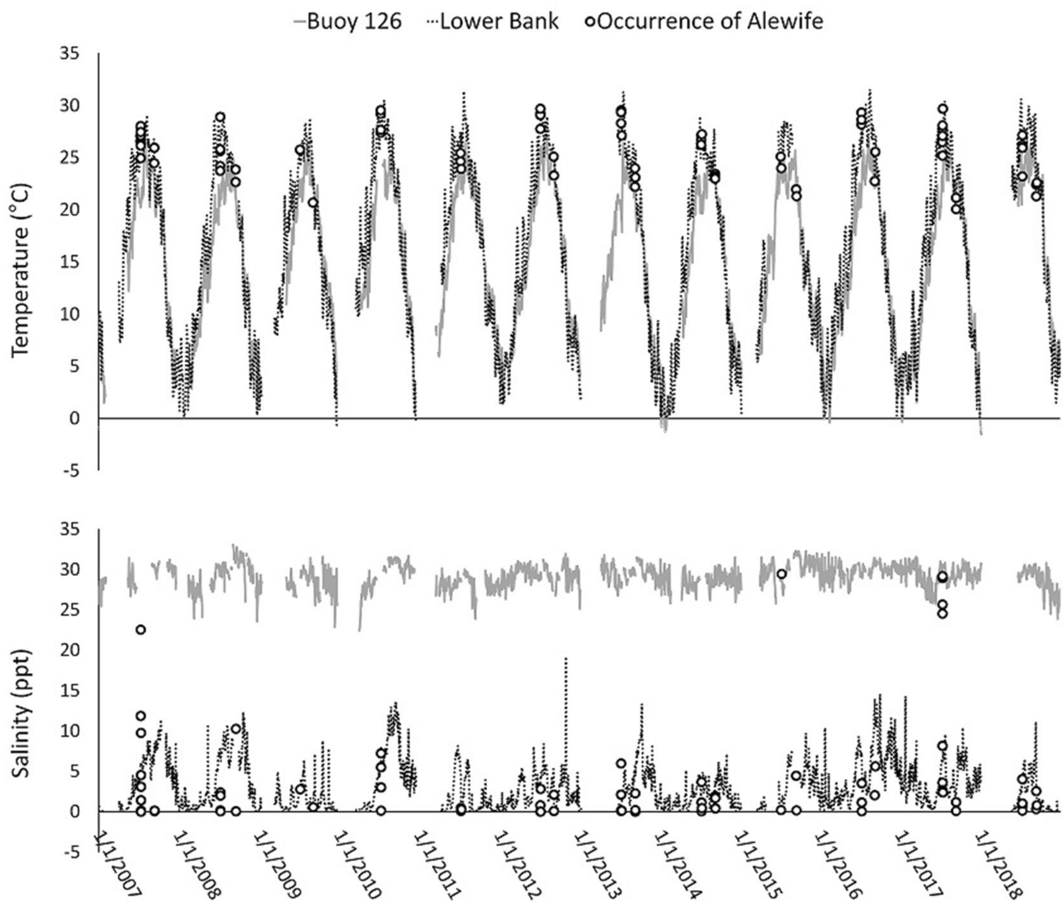

Fig. 4 Daily mean temperature (°C) and salinity (ppt) profiles from the Mullica River–Great Bay as collected by the Jacques Cousteau National Estuarine Research Reserve System-Wide Monitoring Program's Buoy 126 near Little Egg Inlet (grey continuous line) and Lower Bank (dashed line) water quality data loggers from 2007 through 2018 (NOAA NERRS 2019; see Fig. 1 for locations). Circles represent the temperature and salinity values at which juvenile *Alosa pseudoharengus* were collected during the sampling period

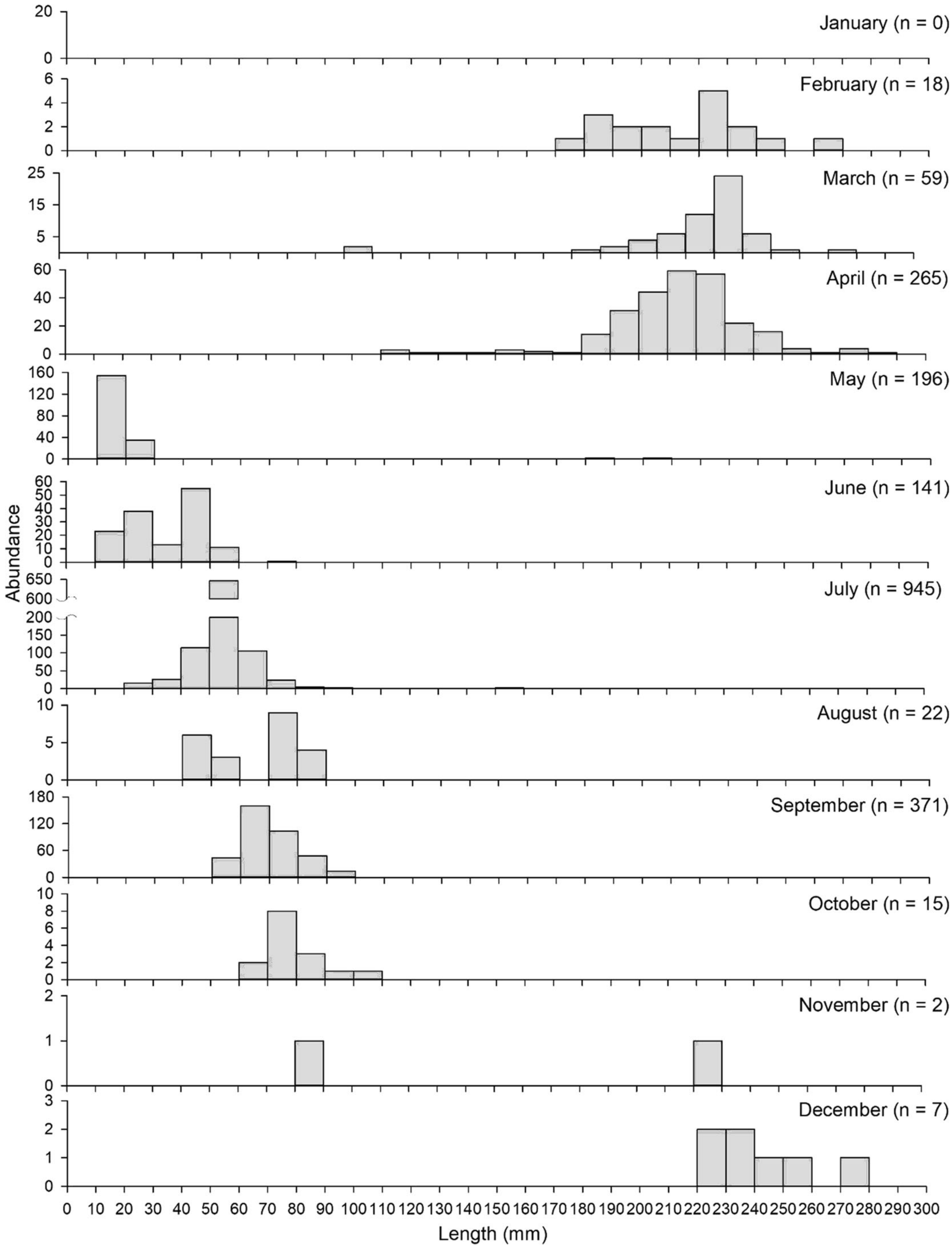

Fig. 5 Composite monthly length frequency for *Alosa pseudoharengus* ($n = 2289$) collected in the Great Bay-Mullica River estuary during 1995–2018. Data from various RUMFS and Stockton University surveys: gill net ($n = 59$), plankton net ($n = 250$), pop net ($n = 256$), seine ($n = 392$), otter trawl ($n = 1235$), and fyke net ($n = 97$). Note differences in monthly scales on the y-axis. See Table 1 for additional details

there were peaks in CPUE at Landing Creek in 2004, 2007, 2010, and 2017. By September, the abundance was overall much lower, and the catches were lower at Landing Creek relative to all the other sites indicating fall emigration from that nursery site.

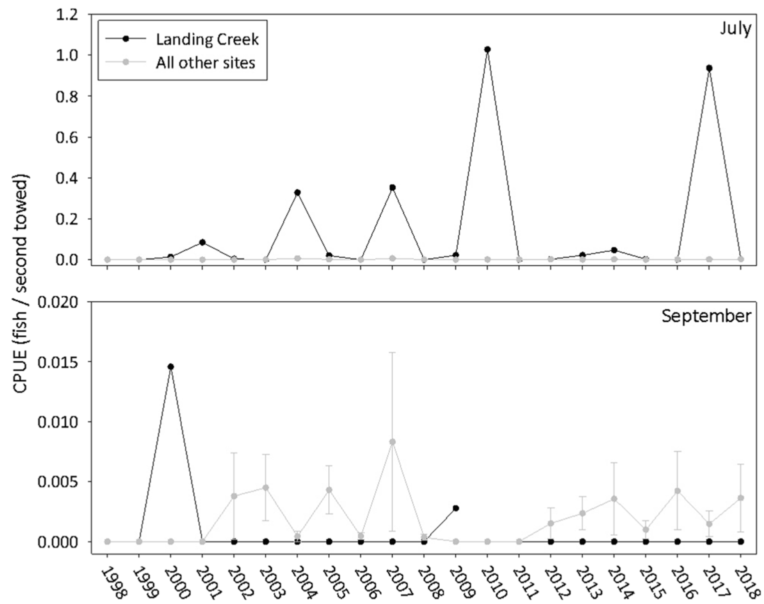

Fig. 6 Annual variation in abundance (CPUE) of juvenile alewife (*Alosa pseudoharengus*) (n = 1915) from otter trawl sampling for July (n = 1537) and September (n = 378) from 1998 to 2018 in the Mullica River – Great Bay estuary. Note that there were no collections in September 2010 in Landing Creek and that scales differ between months sampled

Predation on alewife eggs and larvae

Several species of fish fed on alewife eggs that were deposited below the dam at Batsto Village, based on stomach content analysis during March – May 2016 (Table 3, Online Resource Table 1). Glass eels and elvers were typically present in large numbers, perhaps hundreds per square meter, on the concrete apron immediately below the dam, in water depths of less than 25 cm. Here, during the day, they were often found swimming in large masses, in the algae that grew on the apron, or under rocks. The latter were typically elvers. In 2017, the glass eels and elvers were present from mid-April through early May (Table 2). In both years, these ranged from 49 to 142 mm but the vast majority were 50–70 mm.

Table 3 Stomach content analysis of American eel (*Anguilla rostrata*) (2016 and 2017) and other predator species (2016) caught in Batsto River below the dam in 2016 (see Online Resource Table 1) and 2017

Common Name	Latin Name	N Stomachs Examined	N Stomachs with Contents	N Alewife Eggs Consumed
American eel (Glass)	*Anguilla rostrata* (Glass)	129	41	24
American eel (Elver)	*Anguilla rostrata* (Elver)	101	65	1061
American eel (Yellow)	*Anguilla rostrata* (Yellow)	16	3	999
Black banded sunfish	*Enneacanthus chaetodon*	5	4	0
Banded sunfish	*Enneacanthus obesus*	3	1	0
Creek chubsucker	*Erimyzon oblongus*	9	3	0
Chain pickerel	*Esox niger*	3	3	0
Swamp darter	*Etheostoma fusiforme*	12	10	30
Tessellated darter	*Etheostoma olmstedi*	2	2	14
Pumpkinseed	*Lepomis gibbosus*	1	1	0
Largemouth bass	*Micropterus salmoides*	4	2	0
Spottail shiner	*Notropis hudsonius*	2	2	0
Bluegill	*Lepomis macrochirus*	2	2	101
Total		289	139	2229

American eels (glass eels, elvers) were collected with small mesh dip nets. Other predators and yellow eels were collected by seine

Alewife eggs were preyed upon by four of the 11 fish species collected including swamp darter (*Etheostoma fusiforme* Girard), tessellated darter (*E. olmstedi* Storer), bluegill (*Lepomis macrochirus* Rafinesque), and American eel (Table 2). American eel (49–190 mm TL) was the most abundant and consistent of egg predators with 28% of 183 stomachs in 2016 and 18% of 63 stomachs in 2017 containing alosine eggs. On an individual basis, glass eels were less likely than elvers or yellow stage eels to feed on alewife eggs in the field. Eggs were found in 2.0% of glass eel stomachs in 2016 and in 20.0% in 2017. Eggs were found in 56.8% of elver stomachs in 2016 and 25% in 2017. The number of eggs in elver guts ranged from 0 to 99 ($\overline{x}$ = 10). On 14 April 2016, three elvers regurgitated eggs ($n = 21$, range = 2–14) after preservation and nine elvers, including the latter three, had eggs ($n = 248$, range = 10–48) in their stomachs. Yellow stage eel ($n = 16$) guts contained the most eggs (18.8%, $\overline{x}$ = 62 eggs), with counts ranging from 0 to one individual that had 952. In 2017, when there was visual evidence of spawning below the dam, eggs were present in the stomachs of glass eels and elvers, but not yellow eels. No glass eels or elvers had eggs in their stomachs in May of either year.

The essence of the field observations was confirmed by laboratory feeding observations. Glass eels in feeding observations ($n = 118$, 44–68 mm TL, $\overline{x}$=58 mm TL) consumed 95.8% of available larvae ($\overline{x}$ = 4.8) and only 34.0% of eggs ($\overline{x}$ = 5), showing a preference for larvae over eggs. This preference was not supported by gut content analysis of field-caught glass eels (Table 3). Elvers in feeding observations ($n = 106$, 61–100 mm TL, $\overline{x}$ = 78 mm TL) consumed 100% of available alewife larvae ($\overline{x}$ = 4.9) and 95.0% ($\overline{x}$ = 4.8) of eggs. Yellow eels ($n = 9$, 103–125 mm TL, $\overline{x}$ = 110 mm TL) consumed 100% ($\overline{x}$ = 5) of available alewife eggs. Only one yellow eel (109 mm TL) was presented with alewife larvae. All larvae ($n = 5$) were consumed.

Discussion

Alewife life history and status

Alewife, in all life history stages – eggs, larvae, juveniles, and adults – were the dominant alosine in the Mullica River – Great Bay estuary over the extensive sampling in this study, which supports the idea that these anadromous fishes are a keystone species (Wilson and Halupka 1995). This is evident because of their abundance and that they are important prey influencing the distribution of a major predator in the estuary, striped bass (Ng et al. 2007). This agrees with earlier studies and compilations in the study area (Zich 1978; NJDEP 2005). The patterns of alewife life history in the Mullica Valley mirror those of other alewife spawning and nursery areas in the northeastern U.S. (Thunberg 1971; Collette and Klein-MacPhee 2002). A possible exception is that these populations spawn in the upper limits of tidal freshwater streams as opposed to freshwater ponds, as occurs in many areas of southern New England (Richkus 1975; Kosa and Mather 2001; Iafrate and Oliveira 2008; Pierce et al. 2020).

For alewives, spawning in the spring, is common for these anadromous fishes, with a single upstream migration, frequently considered the norm (Collette and Klein-MacPhee 2002; McCartin et al. 2019). However, our observations suggest that spawning occurs in waves, as we observed in 2016 and 2017. The occurrences of these waves on the spawning grounds has been reported in Rhode Island, when the presence of spawning fish lasted one to several days in a freshwater pond (Cooper 1961). Similar short-term waves of spawning alewives have been reported elsewhere in Rhode Island and appear to be under the influence of freshwater temperatures and light intensity (Richkus 1974). Elsewhere, the temporal occurrence has been reported for longer time periods, but this was calculated as time spent in a lake or pond where spawning occurred (Kissil 1974) or over entire spawning seasons (Ogburn et al. 2017). More recently, a study of an alewife population in the Carmans River, Long Island, New York demonstrated more varied migratory patterns. These included oscillations between spawning in freshwater to downstream estuarine habitats where the adults spent a large amount of time (McCartin et al. 2019). Regardless of location, the frequency and location of spawning may be influenced by the low population sizes of alewife stocks (Limburg and Waldman 2009; Palkovacs et al. 2013) at the time of our observations.

Spawning in discrete but temporally isolated waves, as observed in our study area, may allow herring to retreat to deeper waters between reproductive events. This may be advantageous in that it could prevent predation by eagles, ospreys, and other predators in shallow water between spawning events. Perhaps spawning in waves is also consistent with asynchronous oocyte development in alewife (Ganias et al. 2015) and the closely related blueback herring (McBride et al. 2010). This interpretation, and associated "fallback" behavior after spawning, has been evaluated for river herring in Massachusetts streams (Frank et al. 2009; Eakin 2017; Rosset et al. 2017). The frequency and duration of visual verification in our study may be influenced by our ability to detect them. All of our observations were during the day. If they were spawning at night, as has been reported elsewhere (Graham 1956; Tyus 1974), our daytime observations may be underestimates of spawning occurrence. However, they do confirm the seasonal timeframe during which spawning took place.

The sizes of spawning adults at Batsto Dam are consistent with those of spawning adults in other studies (Cooper 1961; Mayo 1974). On each collection date, females had a larger average size, by about 25 mm, than males: yet another characteristic shared with other studies (Cooper 1961; Kissil 1974). Male-dominated spawning aggregations are characteristic of alewife spawning sites in other locations as well, especially early in the spawning season (Kissil 1974).

The occurrence of alewife larvae downstream to the freshwater-saltwater interface near Lower Bank is consistent with other studies (Campfield and Houde 2011). The occurrence of juveniles throughout the Mullica River from above Landing Creek to the entrance to Great Bay, and including Nacote Creek, suggests that this whole area is used as a nursery. However, the larger numbers of juveniles frequently collected at Landing Creek may be due to their concentrating there near the freshwater-saltwater interface that typically occurs in the region. While nurseries in freshwater are common, especially in the northeastern U.S., the frequency of estuarine nurseries is high in Massachusetts and Rhode Island and from Delaware and south (Tommasi et al. 2015; Turner and Limburg 2016). Use of estuarine waters as nurseries is found in other populations as well (Stokesbury and Dadswell 1989; Murdy et al. 1997), especially in more southern populations (Turner and Limburg 2016). The temperatures observed in our collections are consistent with those (20–33 °C) reported along the coast (Tommasi et al. 2015). As temperatures drop in the fall, juveniles are less abundant, as indicated by the reduced catches in this study, as they presumably move through the lower estuary and offshore for the winter (Milstein 1981; Able and Fahay 2010), as occurs in other populations (Kosa and Mather 2001; Yako et al. 2002; Turner and Limburg 2016). The return to the river to spawn does not occur until they reach sizes of 215–280 mm. While the emphasis in our studies has been the Mullica and Batsto rivers, the unobstructed Wading and Bass rivers may also have spawning runs (Zich 1978). Access to portions of other tributaries in the watershed, such as the Batsto, Oswego (near Rt. 539), Nacote Creek, and Hammonton Creek (near Rt. 30) have long been impeded by dams (Zich 1978; Pearce 2000). An earlier evaluation of alewife spawning sites in the Mullica Valley in 1974 and 1975 included a number of additional sites (Zich 1978) that were re-evaluated during this study. Sites previously reported as spawning sites include Nacote Creek at Mill Pond, Negro Creek, Upper Bass River and at a dam in State Forest, and Wading River at Rt. 542. Thus, the number of spawning sites in the watershed has declined markedly since that time. Two sites identified by Zich (1978) were confirmed in our study (Nescochogue Creek, Batsto Village dam). Another (Mullica River at Constable Bridge) was confirmed in spring 2019 (pers. obs.).

Earlier accounts from the 1800s imply that river herring were consistently abundant in the spring in the Mullica River – Great Bay estuary at Atsion Creek (a prior name for the Mullica River) (Beck 1963). The status of alewives in the study area may reflect the condition of populations in the northeastern US, which are declining (Limburg and Waldman 2009; Palkovacs et al. 2013), perhaps because of environmental effects (Lynch et al. 2015; Tommasi et al. 2015). Others have suggested offshore bycatch in pelagic fisheries (Hasselman et al. 2016) and overfishing (Hall et al. 2012; Turner et al. 2015) as causes for the decline. In addition, climate change, as it affects timing of spawning runs (Ellis and Vokoun 2009; Hall et al. 2011; Tommasi et al. 2015; Hare et al. 2016) may be a factor. Most would agree that habitat loss contributes significantly to alewife decline, especially through dam creation since European settlement because it eliminates the possibility of spawning upstream of a dam (Freeman et al. 2003; Walter and Merritts 2008; Hall et al. 2012; Januchowski-Hartley et al. 2013; Mattocks et al. 2017). This certainly occurs at the dam in Batsto Village (this study).

Interactions with American eels

For American eels in the Mullica River – Great Bay estuary, we know that the glass eels consistently enter from the ocean from winter through spring at sizes of 40–140 mm ($\overline{x}$ = 58 mm) (Able and Fahay 2010). As many move upstream into freshwater, some undergo metamorphosis into the elver stage, especially as water temperatures reach 10 °C (Sullivan et al. 2006, 2009). Their presence becomes much more obvious as their upstream passage is restricted or prevented at dams in this estuary, adjacent Barnegat Bay, and Great Egg Harbor estuary (Pohatcong Creek-NJDEP 2005). This restriction of upstream alewife passage by dams is critical. It also occurs for American eels at other locations in the northeastern United States (Kemp and O'Hanley 2010; Pess et al. 2014; Benchetrit and McCleave 2016; Castonguay and Durif 2016; Miller et al. 2016). In fact, this overlap below dams may create an ecological "hotspot" where predator-prey interactions between the early life history stages of these two species are magnified. This clearly occurs for the anadromous alewife and the catadromous American eel in overlapping temporal and spatial patterns at the dam at Batsto Village. Thus, they co-occur with the recently spawned alewife eggs in March through May, perhaps because adult alewife serve as an attractant for glass eels and elvers (Sorensen 1986).

The effect of the predation on alewife eggs is not known for certain but the likelihood of a significant impact by the thousands of glass eels and elvers concentrated below the dam at Batsto Village seems probable. Our estimates of ingestion from stomach content analysis may be underestimated because we did observe regurgitation of eggs when eels were preserved. Certainly, this realization of the role of other small predators on fishes in estuaries is becoming increasingly observed (Baker and Sheaves 2006; Able et al. 2007). The laboratory observations indicate that glass eels and elvers can feed on alewife larvae, but this was not verified in stomachs of eels found below the dam at Batsto Village. This general absence might be explained by the effects of fast water flow on these newly hatched larvae with poorly developed swimming abilities. Newly hatched larvae may have been swept downstream of our study area immediately below the dam before they could be fed upon. The impact of presumably nutrient-rich alewife eggs for glass eels and especially elvers and young yellow eels, where they are concentrated below the dam, may provide for accelerated growth and increased survival, but these ideas need to be tested relative to other areas that may not function as "hotspots."

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Compliance with ethical standards

All procedures performed in studies involving animals were in accordance with the ethical standards of the Rutgers University Institutional Animal Care and Use Committee, Protocol #88-042.

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