

Fish larval supply to and within a lagoonal estuary: multiple sources for Barnegat Bay, New Jersey

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Abstract We evaluated spatial variation in fish larval supply to a temperate, lagoon type estuary (Barnegat Bay, New Jersey) by determining species composition, size, and stage into inlets $(n = 2)$, thoroughfares between adjacent estuaries $(n = 3)$, and within the estuary $(n = 4)$ in seasonal, synoptic sampling on night time flood tides during 2010–2014. Larval supply, as sampled with identical plankton nets (1 m diameter, 1 mm mesh) was dominated by postflexion stage individuals (most 5–10 but reaching 70+ mm) from species spawned in the Atlantic Ocean from a variety of sources (e.g., Sargasso Sea, outer and inner continental shelf) and in the bay. While abundance for individual species varied among locations and years, in general, the larval composition was similar across inlets, thoroughfares, and within the bay within the same seasons. Homogenization across locations was likely the result of the tidal exchanges between the ocean, the estuary, and the adjacent locations. These exchanges provide numerous, redundant sources of larvae to this estuarine nursery. The similarity in larval supply among inlets, thoroughfares, and within the estuary indicates that the longer term study location behind Little Egg Inlet is representative for this, and probably other, estuaries along the New Jersey shore.

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Introduction

Fish larval supply to estuaries occurs worldwide (Haedrich [1983](#page-19-0); Norcross and Shaw [1984;](#page-20-0) Yanez-Arancibia [1985;](#page-20-0) Blaber [2000;](#page-19-0) Reis-Santos et al. [2013](#page-20-0)) in response to the presumed advantages of estuarine use including benign environmental conditions, enhanced growth, and survival (i.e. nurseries) (Boehlert and Mundy [1988;](#page-19-0) Beck et al. [2001](#page-19-0); Able [2005\)](#page-19-0). The same applies to estuaries along the east coast of the U.S. where larvae from diverse areas (in space and time) may contribute to larval supply (Hare et al. [2002;](#page-19-0) Able and Fahay [2010a;](#page-19-0) Ribeiro et al. [2015\)](#page-20-0). While there have been numerous studies of larval supply to individual estuaries these are typically from a single sampling location in each estuary. There have been fewer studies of systems that have multiple connections to the ocean and adjacent estuaries that may play a role in larval supply. Two studies in the Pamlico Sound estuary, North Carolina (Hettler and Chester [1990](#page-20-0); Hettler and Barker [1993](#page-20-0)) clearly demonstrated how supply differed between inlets, in large part because the larvae were distant (91 km between inlets) and located above and below a major faunal barrier at Cape Hatteras (see Grothues and Cowen [1999;](#page-19-0) Able and Fahay [2010a\)](#page-19-0). Other studies in Chincoteague Bay, Virginia, where two inlets, 59 km apart, were sampled during winter and spring found that there were few differences in larval fish assemblage between inlets during those seasons (Love et al. [2009](#page-20-0)). In the Guana-Tolomato-Matanzas estuary in Florida (Korsman et al. [2017](#page-20-0)) species composition did not vary between inlets 21 km apart. Further, larval supply in estuaries may vary between those arriving from the ocean and those spawned in the estuary from resident species. In addition, larvae may also be exported and resupplied via these types of connections (Brown et al. [2000;](#page-19-0) Chant et al. [2000](#page-19-0); Ooi and Chong [2011\)](#page-20-0).

Inlets are an especially important source of larval supply for barrier island lagoonal estuaries in which inlets open and close, either seasonally (e.g., many South African and Australian estuaries) (Lenanton and Hodgkin [1985](#page-20-0); Whitfield [1998](#page-20-0)) or over irregular and longer time scales. Many of the above characteristics are true of Barnegat Bay, a lagoonal estuary (Kennish and Paerl [2010](#page-20-0)) in which inlets have closed (Cranberry Inlet (Kennish [1984\)](#page-20-0)), become restricted (Barnegat Inlet [Chizmadia et al. [1984\]](#page-19-0)), or migrated over time (Beach Haven Inlet (Shepard and Wanless [1971;](#page-20-0) Chizmadia et al. [1984\)](#page-19-0)). Another source of variation in hydrographic connectivity into Barnegat Bay is flow between adjacent estuaries via man-made canals (Pt. Pleasant Canal (Kennish [1984;](#page-20-0) Able [2015\)](#page-19-0)) and natural thoroughfares.

Prior studies of larval supply to Barnegat Bay through Little Egg Inlet have been extensive. They have characterized the seasonal variation in species composition (Witting et al. [1999;](#page-20-0) Able et al. [2011b\)](#page-19-0) and climate change induced water temperature (Able and Fahay [2010b](#page-19-0)). Other efforts at this location have evaluated larval Paralichthys dentatus (Linnaeus) abundance relative to changes in stock status (Able et al. [2011c\)](#page-19-0). These sampling efforts have also determined that larval Brevoortia tyrannus (Latrobe) entering Little Egg and Beaufort, North Carolina inlets come from different spawning locations (Warlen et al. [2002](#page-20-0)) while glass eel-stage larvae of Anguilla rostrata (Lesueur) in the same inlets are arriving as a cohort from one source (Able et al. [2015\)](#page-19-0). Other studies compared Myrophis punctatus Lütken ingress across these two inlets as well as North Inlet, South Carolina and determined that they are likely from multiple sources (Able et al. [2011a](#page-19-0)).

The objective of this study is to evaluate spatial variation in fish larval supply and redistribution within the Barnegat Bay lagoonal estuary. More specifically, we determined synoptic patterns of larval ingress including species composition, length, and stage from 1) ocean inlets, 2) thoroughfares into Barnegat Bay from adjacent estuaries, and 3) within this estuary during all seasons over five years.

Materials and methods

Study site

The Barnegat Bay watershed is 1730 km². This complex is a shallow (average depth < 2 m, range 1–6 m), lagoonal estuary with a surface area of 279 km^2 that extends along the coast of New Jersey, USA, for approximately 70 km (Kennish [2001\)](#page-20-0) (Fig. [1\)](#page-2-0). This estuary is connected to the Atlantic Ocean at Little Egg Inlet and Barnegat Inlet. The Intracoastal Waterway channel, which runs the length of the bay, ranges from 1.5–3.7 m at mean low water. Exchanges between southern Barnegat Bay (Little Egg Harbor) and Great Bay occur at several thoroughfares through the Sheepshead Meadows which divides these two estuaries (Fig. [1\)](#page-2-0). On flood tides one source of exchange between these estuaries is the flow from southern Barnegat Bay into Great Bay through Little Sheepshead Creek (Charlesworth [1968;](#page-19-0) Chant et al. [2000](#page-19-0)). At other nearby thoroughfares, (Jimmie's Creek, Little Thorofare), flood tides flow from Great Bay into southern Barnegat Bay. Another source of exchange is through the Pt. Pleasant Canal between Barnegat Bay and the Manasquan River estuary.

Under normal conditions the water column in Barnegat Bay is well mixed although two layer flow may be evident in the deeper waters near the inlets and in the larger river tributaries (Carpenter [1963;](#page-19-0) Chizmadia et al. [1984](#page-19-0)). The flushing time for this bay varies seasonally and spatially and is reported to range from 27 to 71 days with the longest times during the summer (Guo et al. [1997](#page-19-0)). The tides are semidiurnal with highest velocities at Barnegat (>1 m/s) and Little Egg (> 2 m/s) inlets (Kennish [2001](#page-20-0)). Details of the circulation are available from Carriker ([1961](#page-19-0)), Chant [\(2001a\)](#page-19-0), and Defne and Ganju [\(2015\)](#page-19-0). Freshwater flow into Barnegat Bay comes from tributaries along the western shore of the bay with the largest tributaries north of Barnegat Inlet (Kennish [2001\)](#page-20-0). Total surface inflow of freshwater into the bay represents about 2–3% of the tidal prism with other substantial contributions from groundwater. Mean salinity in the bay is from 18 to 25 with the highest salinities near the two inlets (Kennish [2001](#page-20-0)). Salinity is lowest (<15) off Toms River and to the Fig. 1 Larval fish sampling locations at inlets (Little Egg [Little Sheepshead Creek], Barnegat), thoroughfares (Point Pleasant Canal, Jimmie's Creek, Little Thorofare), and within the bay (Oyster Creek Nuclear Generating Station [intake and discharge], and Rt. 37 and Rt. 72 bridges)

north until the vicinity of the Point Pleasant Canal where values are higher. Subtidal circulation in the bay is driven primarily by coastal pumping and to some extent by meteorological forcing (Chant [2001a,](#page-19-0) [b](#page-19-0)). Water temperature ranges from −1.4 to nearly 30 °C with the highest temperatures at the mouth of Oyster Creek due to thermal discharges from the Oyster Creek Nuclear Generating Station (Kennish [2001](#page-20-0)).

A combination of hydrodynamic and particle tracking models of circulation in Barnegat Bay postulate a pronounced northward subtidal flow from Little Egg Inlet in the lower bay to Point Pleasant canal in the upper bay (Defne and Ganju [2015](#page-19-0)). This pattern, based on springtime conditions, causes more flushing in the lower bay and particle retention in the upper bay.

Larval supply

To evaluate the fish larval supply to Barnegat Bay, we synoptically determined spatial variation in their occurrence and abundance at two inlets and three thoroughfares (Fig. 1, Table [1\)](#page-3-0). In addition, to assess the degree of larval redistribution within the bay, we sampled at four locations (one each near the Oyster Creek Nuclear Generating Station [OCNGS] cooling water intake and discharge canals, and bridges over waterways for Route 37 and for Route 72) away from the inlets (Fig. 1, Table [1](#page-3-0)). At all these locations larvae were collected with a 1 m-diameter (1 mm mesh) circular plankton net. The net was deployed at a fixed location with a flow meter to a depth of approximately 1.5 m. Collections

were during the night time flood tide for three consecutive 30 min sets (see Witting et al. ([1999](#page-20-0)) for more details of this approach). Collections were accompanied by measures of salinity, temperature, dissolved oxygen, and pH using a handheld logger (YSI, Yellow Springs Instruments, Ohio). All fish collected were brought back to the laboratory, preserved in ETOH, and measured for length by either ocular micrometer or caliper and staged as either pre-flexion, flexion, or post-flexion (Witting et al. [1999\)](#page-20-0).

Larvae were sampled in the vicinity of estuary inlets (Fig. [1](#page-2-0)) to determine exchanges of larvae between the ocean and Barnegat Bay. Collections of ingressing larvae at Little Egg Inlet were from a weekly, ongoing sampling program for early stage, estuarine-dependent fishes at the bridge over Little Sheepshead Creek (LSHCB) (3.8 km from inlet mouth) that has been in place since 1989 (Able and Fahay [1998;](#page-19-0) Witting et al. [1999](#page-20-0)). This location has been previously sampled to detect long-term trends in larval fishes timing and abundance up to 2006

(Able and Fahay [2010a,](#page-19-0) [b\)](#page-19-0). For the present study, an identical protocol of weekly sampling occurred over five years (2010–2014) during the major seasons of larval ingress as previously determined (Witting et al. [1999\)](#page-20-0). Sampling also occurred at Barnegat Inlet over a two-year period (2012–2013) (Table 1).

Larvae were also sampled at three locations as an indication of movement between estuaries through thoroughfares (Fig. [1,](#page-2-0) Table 1). These collections occurred at Jimmie's Creek, Little Thorofare, and Point Pleasant Canal. The first two locations, which connect southern Barnegat Bay (Little Egg Harbor) to Great Bay, were selected based on their flow rate. Little Sheepshead Creek receives ocean water from Little Egg Inlet and as a result, samples from this creek can be considered representative of both ingress of larvae into Little Egg Inlet from the Atlantic Ocean (as in this study) (e.g., Sullivan et al. [2009](#page-20-0); Able et al. [2011b,](#page-19-0) [c](#page-19-0)) and transport of the larvae of resident species through Little Sheepshead Creek from Little Egg Harbor to Great Bay (Witting et al. [1999](#page-20-0)). Little

Table 1 Sampling location and effort for larval fishes into and within Barnegat Bay during 2010–2014 with identical plankton nets. See Fig. [1](#page-2-0) for a map of sampling locations

Location	Sampling period	Sampling frequency	samples	Number of Temperature (Median and Range, °C)	Salinity (Median and Range, ppt)
Inlets					
Barnegat Inlet	$2012 - 2013$	2012: Feb, Apr, Jun, Aug 2013: Feb, Apr, Jun, Aug, Oct	9	$16.4, 5.6 - 25.7$	29.9, 27.7-36.8
Little Egg Inlet (Little Sheepshead Creek)	2010-2014	2010: May, Jun, Jul, Aug, Oct, Dec 2011: Feb, Apr 2012: Feb, Apr, Jun, Aug 2013: Feb, Apr, Jun, Aug, Oct 2014: Apr (early & late), Jun, Aug, Oct	22	$16.2, 3.0 - 25.8$	$29.6, 28.0 - 34.6$
Thoroughfares					
Point Pleasant Canal	2012-2013	2012: Feb, Apr, Jun, Aug 2013: Feb, Apr, Jun, Aug, Oct	9	$16.6, 6.1 - 25.5$	$23.0, 14.8 - 34.6$
Jimmie's Creek	2010-2011	2010: May, Jun, Jul, Aug, Oct, Dec 2011: Feb, Apr	8	$14.5, 2.1 - 26.0$	27.1, 23.4-31.9
Little Thorofare	2010-2011	2010: May, Jun, Jul, Aug, Oct, Dec 2011: Feb, Apr	8	$16.7, 1.7 - 26.6$	29.4, 25.12-30.3
Within the bay					
Oyster Creek Nuclear Generating Station: 2012–2014		2012: Feb, Apr, Jun, Aug 2013: Feb, Apr, Jun, Aug, Oct			
Intake		2014: Apr (early $&$ late), Jun, Aug, Oct 14		$18.8, 6.6 - 27.8$	$26.0, 22.0 - 30.9$
discharge			14	23.4, 11.3–32.9	$25.3, 22.5 - 29.8$
Route 37 bridge	2014	2014: Apr (early $&$ late), Jun, Aug, Oct 5		$16.1, 8.6 - 25.2$	18.1, 15.1-20.5
Route 72 bridge	2014	2014: Apr (early $\&$ late), Jun, Aug, Oct 5		$16.0, 8.5 - 25.3$	$26.5, 24.2 - 27.6$

Sheepshead Creek has the fastest flow rate and the greatest depth (3–4 m) of any thoroughfare sampled with flood tide waters moving from Little Egg Harbor into Great Bay. Jimmie's Creek has the slowest flow rate and shallowest depth $(\sim 1 \text{ m})$, and Little Thorofare has an intermediate flow rate and depth $(\sim 2.5 \text{ m})$. The latter two flood from Great Bay into Little Egg Harbor and Barnegat Bay. Another thoroughfare, the Pt. Pleasant Canal, connects northern Barnegat Bay to the Manasquan River and from there to the ocean (Fig. [1](#page-2-0)).

Fish larvae were also sampled at four locations within the bay, two on the eastern and two on the western sides of the bay on night flood tides (Table [1](#page-3-0), Fig. [1](#page-2-0)). Near Ship Bottom, samples were collected from a portion of the Rt. 72 bridge nearest to Long Beach Island at a location approximately equidistant between Little Egg and Barnegat Inlet (Fig. [1\)](#page-2-0). Samples were also collected from a portion of the Rt. 37 bridge nearest to the barrier island near Seaside Heights at a location approximately equidistant between Barnegat Inlet and the Point Pleasant Canal (Fig. [1\)](#page-2-0). At flooding tide, the flow at these two locations was from the south to the north. Two other sampling locations were located at the cooling water intake and discharge canals of OCNGS at approximately 3.6 and 2.6 km from the bay and nearly due west of Barnegat Inlet, respectively (Fig. [1](#page-2-0)). Both of these samples were collected from the bridges over Route 9. At these two locations, the flow was nearly continuously toward the OCNGS and away from the OCNGS in the respective canals due to the cooling water pumps at the plant. This unidirectional flow occurred irrespective of tide stage, although water depth changed with the tides (Kennish [1984\)](#page-20-0).

Data analysis

Species-specific counts of larval fish from each sampling event were standardized to density (catch-per- 1000 m^3 of water) using the average density of all three net sets per sample date and location. While all other analyses relied on the entire data set, only a subset of the data, balanced for spatial temporal consistency, was used in multivariate analyses to characterize larval supply among different inlets and thoroughfares and at those locations within the bay. To characterize larval supply to the bay, data from the two inlets and three thoroughfares (Fig. [1](#page-2-0), Table [1](#page-3-0)) sampled during 2010 (months used: June, August, October), 2011 (February, April), 2012 (February, April, June, August), and 2013 (February, April, June, August, October), were included in the analysis. To characterize larval distribution within Barnegat Bay, data from the four within-the-bay locations (Fig. [1](#page-2-0), Table [1\)](#page-3-0) sampled during 2014 (months used: April [early and late], June, August, October), were included in the analysis. Only larvae that could be identified to the species level were included in the multivariate analyses. Principal component analysis (PCA) characterized the latent trends of variation in larval fish distribution. Canonical correspondence analysis (CCA) examined those trends that could be significantly correlated with measured environmental variables known to be important as physiological constraints to larval fishes (temperature, salinity, pH, dissolved oxygen). In both cases, the categorical variables of sample location and month were excluded from the analysis but examined post-hoc by classifying samples graphically to see if latent or environmentally-correlated trends corresponded to these variables. Differences among locations or months were not tested for significance as this is exploratory (observational), but the total inertia and first eigenvalue were tested for significance using Monte Carlo tests to provide a warning against interpretation of what might be random trends.

Results

Environmental variation

Salinity and temperature were generally similar at inlets, thoroughfares, and within Barnegat Bay during the sampling periods with some notable exceptions (Table [1](#page-3-0)). Median salinity ranged from 23.0 to 29.9 with the exception of samples taken at the Route 37 bridge (Fig. [1\)](#page-2-0) with lower values (18.1). This was likely due to that location's proximity to Toms River, its distance from the nearest inlet, and its location in the upper bay where other larger rivers emptied into the northern portion of the bay. The median temperatures at most locations ranged from 14.5 to 16.7 °C. The high values at OCNGS (intake =18.8 \degree C, discharge =23.4 \degree C) were due to the inclusion of heated discharge waters from the power plant.

Larval fish supply

Supply into the bay The larvae collected at inlets and thoroughfares were represented by 37 families and 62 species (Table [2](#page-6-0)) that spawned in the ocean $(n = 29)$, the estuary ($n = 18$), or both ($n = 9$) (Table [3\)](#page-9-0). Another six species were of unknown spawning origin. Samples across inlets and thoroughfares were dominated by post-flexion stage larvae (Table [3](#page-9-0), Fig. [2\)](#page-11-0). Pre-flexion larvae constituted a small proportion at all of the above collecting locations; presumably as the result of the relatively large (1 mm) plankton net mesh size. The lengths of larvae were similar at inlets and thoroughfares (Fig. [3](#page-11-0)). The most abundant fish collected were 5– 10 mm with declining proportions at larger sizes.

The larvae entering Barnegat Bay varied by month (Fig. [4](#page-12-0)). Total larval fish density, across all locations and years, was highest at thoroughfares during the summer (July, August). The highest values at inlets also occurred during the summer (June, July, August). The species collected included residents, i.e. those that remain in the bay or come back into the bay to spawn (e.g. Anchoa mitchilli (Valenciennes), Gobiosoma bosc (Lacepède), Menidia menidia (Linnaeus), Pseudopleuronectes americanus (Walbaum), Syngnathus fuscus Storer) and transient species, i.e. those that spawned in the ocean and those which came into the bay from the ocean or adjacent estuaries (e.g., A. rostrata, Bairdiella chrysoura (Lacepède), Clupea harengus Linnaeus, P. dentatus), or both (Tables [2](#page-6-0) and [3\)](#page-9-0).

The larval supply to Barnegat Bay varied between years and locations for some representative species (Figs. [5](#page-12-0) and [6\)](#page-13-0). Among representative estuarine transient species spawned in the ocean, the annual pattern of abundance varied within species (Fig. [5](#page-12-0)). Some species were common at most locations (A. mitchilli). For A. rostrata, peaks occurred in 2011 at Jimmie's Creek and in 2012 at the Point Pleasant Canal, but this species was absent in 2013 at Barnegat Inlet and in 2010 at Little Thorofare (Table [2\)](#page-6-0). For B. tyrannus, the prominent peak for larvae entering the bay was at Little Egg Inlet (LSHCB) in 2013 but this species was not collected at Little Egg Inlet, Little Thorofare, or Jimmie's Creek in 2011, or Point Pleasant Canal in 2012. Other species (Scophthalmus aquosus (Mitchell), Tautogolabrus adspersus (Walbaum)) were infrequently collected at most locations, but abundant at a few locations during a single year. The density for several species varied between years as for A. mitchilli (greater in

2013 at Barnegat Inlet, but greater in 2012 at remaining locations) and P. americanus (greater in 2013 at all locations). For *B. tyrannus* and *A. rostrata*, the year of greater abundance varied with each location. For A. mitchilli, which may spawn in the ocean and the bay (Able and Fahay [2010a\)](#page-19-0), the largest peak was at Little Thorofare in 2010 and it was also very abundant in Little Egg Inlet in 2012 and Barnegat Inlet in 2013, but not abundant in Little Egg Inlet in 2013 or Little Thorofare in 2011.

The occurrence of some species that spawn in the bay varied between locations and, surprisingly, the collecting locations included ingressing larvae of these species from the ocean (Table [2](#page-6-0), Fig. [6](#page-13-0)). Many of these resident species were collected at both inlets and Pt. Pleasant (G. bosc, S. fuscus, P. americanus, M. menidia) (Fig. [6](#page-13-0)). P. americanus and sometimes S. fuscus, M. menidia, and G. bosc were more abundant coming into the bay. This might be explained by local spawning in Little Sheepshead Creek and collections there, but not at Barnegat Inlet.

Supply within the bay The larvae collected within the bay were represented by 29 families and 46 species (Table [4](#page-14-0)) that spawned in the ocean $(n = 20)$, the estuary $(n = 16)$, or both $(n = 4)$, with six other species of unknown origin (Table [3](#page-9-0)). The reduced number of families and species within the bay relative to inlet and thoroughfare collecting locations is likely due to the more limited sampling (i.e. only in 2014) at the Route 37 and Route 72 locations. Larval fish within the bay were also dominated by post-flexion larvae, as occurred at inlets and thoroughfares (Fig. [2\)](#page-11-0). Larval fish densities were fairly uniformly low during most sampling periods in 2014 (Table [4](#page-14-0)). Larval fish delivery to nursery areas (e.g. marsh creeks, shallow open waters) on the western shore of Barnegat Bay was monitored by sampling at the intake and discharge for the OCNGS (Fig. [1\)](#page-2-0). Those species which consistently occurred at the OCNGS included residents (e.g. G. bosc, S. fuscus, M. menidia), which is not surprising (Fig. [6](#page-13-0)). It is interesting that a number of species originating from spawning in the ocean also occurred consistently, and even abundantly, at OCNGS (e.g. A. rostrata, B. tyrannus) (Fig. [5](#page-12-0)). These could have come from the closest source (Barnegat Inlet) or the source with the greatest volume of exchange (Little Egg Inlet [LSHCB]) or through thoroughfares from Great Bay to Barnegat Bay or from a thoroughfare from the Manasquan River into Barnegat Bay.

Fundulus majalis $1 \t1$ 1 0.1 1 0.1 1 0.1 1 0.1 1 0.1 1 1 0.1 1 1 0.1 1 1 0.1 1 1 0.1 1 1 0.1 1 1 0.1 1 1 0.1 1 $1 \t1$ 1 0.1 1 $1 \t1$ 1 0.1 $1 \$

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Table 2 (continued)

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Table 3 Scientific and common names, origin $(O = ocean, E = es$ tuary, B = both, U = unknown) based on Able and Fahay [\(2010a](#page-19-0), [2010b](#page-19-0))), and stages for the larvae of each fish species collected at

inlets, thoroughfares, and locations within Barnegat Bay during 2010–2014. See Fig. [1](#page-2-0) for sampling locations

Table 3 (continued)

On the eastern side of the bay, at collecting locations at bridges on Rt. 37 and 72, there was similar variability across locations in 2014 (Table [4](#page-14-0), Figs. [5](#page-12-0) and [6](#page-13-0)). G. bosc and S. fuscus occurred at most locations while M. menidia was most abundant at the OCNGS intake and discharge and at Rt. 37 bridge (Fig. [6](#page-13-0)).

Multivariate analysis of temporal and spatial variability

Supply into the bay A total of 50 species were included in the into-the-bay principal component analysis, 23 of which were unique to inlet and thoroughfare collections. Of those 50 species, 13 were of estuarine origin, 24 were Fig. 2 Proportion of larval fish by flexion stage in Barnegat Bay. Locations are grouped into Inlets (Little Egg [Little Sheepshead Creek] and Barnegat), Thoroughfares (Jimmie's Creek, Little Thorofare, and Point Pleasant Canal), and locations within Barnegat Bay (Rt. 37 and Rt. 72 bridges, and the intake and discharge at the Oyster Creek Nuclear Generating Station). See Fig. [1](#page-2-0) for a map of each sampling location and Table [1](#page-3-0) for sampling effort at each location

of oceanic origin, eight originate from both estuaries and the ocean, and five are of unknown origin (Fig. [7](#page-16-0)a). Larval species composition at inlets and thoroughfares was similar (Fig. [7](#page-16-0)b), but the abundances of the species collected varied by location. The most striking difference was that larval supply to the bay varied by month, and this was apparent along the first (eigenvalue $=0.331$) and second (eigenvalue $=0.112$) eigenaxes. February had the lowest abundance of larvae collected over the sampling duration and the collections were characterized by Mugil curema Valenciennes, Gasterosteus aculeatus Linnaeus, and Lagodon rhomboides(Linnaeus). April collections were dominated by A. rostrata, C. harengus, and P. americanus. Species richness was greatest in June, and collections were characterized by S. fuscus, M. menidia, and Tautoga onitis (Linnaeus), among others. In August, larvae were most abundant and A. mitchilli dominated the catch. Larval abundance decreased in October relative to August, with collections characterized by Micropogonias undulatus (Linnaeus) and A. mitchilli. There was no discernable pattern on either principal component related to origin (oceanic, estuarine, both, unknown) of a species and the month or location of collection (Fig. [7](#page-16-0)b).

Supply within the bay A total of 35 species were included in the within-the-bay principal component analysis, eight of which were only found in collections from locations within the bay. Of the 35 species collected,

Fig. 3 Length frequency of larval fish in Barnegat Bay. Locations are grouped into Inlets (Little Egg [Little Sheepshead Creek] and Barnegat), Thoroughfares (Jimmie's Creek, Little Thorofare, and Point Pleasant Canal), and locations within Barnegat Bay (Rt. 37 and Rt. 72 bridges and the intake and discharge at the Oyster Creek Nuclear Generating Station). See Fig. [1](#page-2-0) for a map of each sampling location and Table [1](#page-3-0) for sampling effort at each location

15 were of estuarine origin, 12 were of oceanic origin, four originate from both estuaries and the ocean, and four are of unknown origin (Fig. [8](#page-17-0)a). Species composition was similar among sampling locations as expressed along both major principal components (eigenvalues 0.325 and 0.259 for the first and second

Fig. 5 Total larval fish density (numbers of fish per 1000 m^3) of some commonly collected transient fish. All of these species spawn in the ocean with the exception of A. *mitchilli* which may spawn in the estuary and the ocean (Able and Fahay [2010a\)](#page-19-0). Total number of fish and total volume were summed across all tows for a

given year and location. LSHCB = Little Sheepshead Creek (behind Little Egg Inlet), OCNGS = Oyster Creek Nuclear Generating Station. See Fig. [1](#page-2-0) for a map of each sampling location and Table [1](#page-3-0) for sampling effort at each location

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Fig. 6 Total larval fish density (numbers of fish per 1000 m^3) of some commonly collected resident fish. Total number of fish and total volume were summed across all tows for a given year and location. LSHCB = Little Sheepshead Creek (behind Little Egg

components respectively) (Fig. [8b](#page-17-0)); however, the abundances of the species collected differed between sampling locations. There was a strong seasonal trend in larval composition and abundance. The early April collections were dominated by P. americanus and A. rostrata and although both those species were present in the late April samples, they were not as abundant. In June, larval composition was dominated by M. menidia and S. fuscus with many other species also present (e.g. Sphoeroides maculatus (Bloch & Schneider), Fundulus heteroclitus (Linnaeus), B. tyrannus). The dominant species collected in August were A. mitchilli, G. bosc, B. chrysoura, and Microgobius thalassinus (Jordan and Gilbert). In October, A. mitchilli and B. tyrannus dominated the collections with Pomatomus saltatrix (Linnaeus), M. undulatus, S. fuscus, Hippocampus erectus Perry, and Gobiesox strumosus Cope among the many other species collected. There was no relationship between larval origin (oceanic, estuarine, both, unknown) and the month or location of collection (Fig. [8b](#page-17-0)).

Results of the CCAs for into-the-bay and within-thebay samples indicated both analyses were significant by

Inlet), OCNGS = Oyster Creek Nuclear Generating Station. See Fig. [1](#page-2-0) for a map of each sampling location and Table [1](#page-3-0) for sampling effort at each location

the Trace statistic (Table [5\)](#page-18-0). Temperature was highly correlated with the first axis of both into-the-bay (correlation = -0.9199) and within-the-bay (correlation = −0.9017) analyses. While temperature explained the majority of that variation, it was strongly negatively correlated with dissolved oxygen (correlations = −0.6179, −0.5619 for into- and within-the-bay analyses, respectively) as expected for nighttime samples, but that was always above 5.1 mg/L and 7.3 mg/L for inlets and thoroughfares and locations within the bay, respectively. The second axes of both analyses were explained by pH for into- (correlation = -0.7568) and within-the-bay $(correlation = -0.8691).$

Discussion

Limitations of study

There are several limitations that should be considered when interpreting the data from this study. First, the plankton net mesh is relatively large and this precludes Table 4 Larval fish supply within Barnegat Bay as estimated by larval fish density (D) and total number of fish collected (N). See Fig. [1](#page-2-0) for a map of each sampling location and Table [1](#page-3-0) for sampling effort at each location. For each year, total volume and

Table 4 (continued)

the collection of small, pre-flexion larvae for many species. Despite this, we did collect some larvae $<$ 5 mm and the vast majority were 5–10 mm. Mesh size is less of an issue, however, because a partial emphasis in this study was on species that spawned in the ocean and entered the estuary at larger flexion and post-flexion sizes and stages. Further, the plankton nets were capable of collecting the larger flexion and post-flexion stages of estuarine resident species. Second, the sampling, although synoptic (i.e. the same night flood tides) at all collections, was relatively infrequent with sampling typically only five times per year. A prior analysis at the Little Egg Inlet (LSHCB) location, based on six years of data, indicated that weekly samples were necessary to determine the pattern of seasonality for most species (Witting et al. [1999\)](#page-20-0). However, the same study identified five ecological seasons (winter, spring, early

summer, late summer, fall) and our sampling approximated those seasons over two to three years.

Larval composition and connectivity

The fish larval composition of the dominant species in Barnegat Bay, as discerned from the multiple sampling locations and times during 2010–2014, overlaps with that of a 1989–1994 study that analyzed data for the 20 most abundant species at Little Egg Inlet (Witting et al. [1999](#page-20-0)). In addition, the seasonal differences in species composition observed in this study were consistent with those previously identified based on six years of weekly sampling behind Little Egg Inlet (Witting et al. [1999\)](#page-20-0). A detailed analysis of the entire larval fish fauna collected behind Little Egg Inlet at Little Sheepshead Creek found fewer northern species $(n = 13)$, i.e. those spawned north

Fig. 7 a PCA for larval supply to the bay showing species distributed along the first two eigenaxes. Vectors point in the direction of increasing species abundance. Those species enclosed in boxes were present in the middle part of the plot, in the quadrant in which they are located, and were removed for clarity purposes. The letter in parentheses after the species name indicates its origin $(O = ocean, E = estuary, B = both, U = unknown)$. This plot is in

the same coenospace as the subsequent sample plot, but was separated for legibility. b PCA showing to-the-bay samples coded by sampling location (LSHCB = Little Sheepshead Creek [Little Egg Inlet], JIMMIES = Jimmie's Creek, LTHORO = Little Thorofare, BRNLIGHT = Barnegat Inlet, PTPLSNT = Point Pleasant Canal) and month. The number adjacent to the sample is indicative of the month in which it was sampled

Fig. 8 a PCA for larval supply within the bay showing species distributed along the first two eigenaxes. Vectors point in the direction of increasing species abundance. Those species enclosed in boxes were present in the middle part of the plot in the quadrant in which they are located and were removed for clarity purposes. The letter in parentheses after the species name indicates its origin $(O = ocean)$, $E =$ estuary, $B =$ both, $U =$ unknown). This plot is in the same coenospace as the subsequent sample plot, but was separated for legibility. b PCA showing within-the-bay samples coded by sampling location (OYSTERIN = Oyster Creek Nuclear Generating Station Intake, OYSTEROUT = Oyster Creek Nuclear Generating Station Discharge, RT 37 = Route 37 Bridge, RT 72 = Route 72 Bridge) and month. The number adjacent to the sample is indicative of the month in which it was sampled. The (E) and (L) designate early and late samples for the month of April, respectively

Table 5 Summary of results from Canonical Correspondence Analysis of into-the-bay and within-the-bay collections. Both into-the-bay and within-the-bay analyses were significant by the Trace statistic (Trace =1.057, F-ratio = 2.199, $P = 0.0020$ and Trace = 1.189, F-ratio = 2.057, $P = 0.0020$, respectively)

	Axes		Total inertia	
	1	\mathfrak{D}		
Into-the-Bay				
Eigenvalues	0.596	0.203	5.504	
Species-environment correlations	0.935	0.775		
Cumulative percentage variance of:				
species data	10.8	14.5		
species-environment relation	56.4	75.6		
Sum of all eigenvalues			5.504	
Sum of all canonical eigenvalues			1.057	
Within-the-Bay				
Eigenvalues	0.564	0.421	3.357	
Species-environment correlations	0.912	0.926		
Cumulative percentage variance of:				
species data:	16.8	29.3		
species-environment relation:	47.4	82.8		
Sum of all eigenvalues			3.357	
Sum of all canonical eigenvalues			1.189	

of Cape Cod, and more southern species $(n = 62)$, i.e. those spawned south of Cape Hatteras, over the period from 1989 to 2006 (Able and Fahay [2010b](#page-19-0)). Of these, there were three northern species and 25 southern species that were not collected in Barnegat Bay in the most recent sampling. This difference, especially for the southern species, is likely due to the reduced effort in Barnegat Bay during the late summer and early fall of 2012–2014 when many relatively rare southern species typically appear in the vicinity of Little Egg Inlet and Great Bay (Able and Fahay [2010a\)](#page-19-0).

The large proportion of larvae originating from spawning in Barnegat Bay (e.g. P. americanus, G. bosc, M. menidia, S. fuscus) that are collected at inlets on flood tides is likely due to outwelling and subsequent re-entry. This pattern has previously been identified for P. americanus larvae relative to larval transport in and out of Little Egg Inlet (Chant et al. [2000\)](#page-19-0). Similar findings have been reported for fish larvae in estuarine inlets elsewhere in the U.S. (Raynie and Shaw [1994](#page-20-0); Brown et al. [2000\)](#page-19-0). Larval supply to and within Barnegat Bay is broadly connected via multiple inlets,

thoroughfares, and internal bay circulation. This provides for multiple redundancies in larval supply and links ocean and estuarine habitats across space and time as occurs elsewhere including Chincoteague Bay, Virginia (Love et al. [2009\)](#page-20-0), in Louisiana (Raynie and Shaw [1994](#page-20-0)), and Australia (Sheaves and Johnston [2008](#page-20-0)). An exception to this local homogenization from multiple sources to estuaries occurred in North Carolina where distant (91 km) inlets into Pamlico Sound were located north and south of a major faunal barrier (Hettler and Chester [1990](#page-20-0); Hettler and Barker [1993](#page-20-0)).

The larvae collected within Barnegat Bay were composed of species that entered Barnegat Bay from distant seas (e.g. A. rostrata from the Sargasso Sea), adjacent continental shelf (e.g., P. dentatus), nearshore coastal ocean (e.g., B. tyrannus from inner shelf), and estuarine spawning (e.g., *M. menidia, P. americanus*). Those coming from outside Barnegat Bay may have come primarily from Little Egg Inlet, the largest inlet with the greatest flow, and been subsequently transported up the bay (Defne and Ganju [2015](#page-19-0)) to the eastern and western shore collecting locations.

Overall, the findings of the multivariate analyses support the observational analysis of the full data set. Larval supply to and within Barnegat Bay is highly seasonal and although the abundances of species may differ between sampling locations the species composition is fairly consistent between inlets and thoroughfares and between locations within the bay. Both of these spatial analyses together support the value of the longterm time-series behind Little Egg Inlet at Little Sheepshead Creek as an ideal sentinel location for fish larvae for both ingressing and resident species for Barnegat and Great bays as well as much of the coast of New Jersey.

Comparison to other estuaries

The composition of fish larvae in Barnegat Bay largely overlaps with other estuaries in the Middle Atlantic Bight. The most abundant species collected in a similar sampling program in Delaware Bay and Chesapeake Bay year-round (e.g., A. mitchilli, M. undulatus, B. tyrannus, P. dentatus, M. menidia) (Ribeiro et al. [2015](#page-20-0)) were also represented in Barnegat Bay. The same was true for winter-spring samples in Chincoteague Bay, Maryland, which were consistently dominated by A. rostrata, P. dentatus, and M. undulatus, while Leiostomus xanthurus Lacepède were occasionally

abundant (Love et al. [2009](#page-20-0)). Further south, in Chesapeake Bay, the larvae of more southern species were more abundant than in Delaware Bay including M. thalassinus, L. xanthurus, Symphurus plagiusa (Linnaeus), B. chrysoura, and Hypsoblennius hentz (Lesueur) (Ribeiro et al. [2015\)](#page-20-0). All of these species were shared in Barnegat Bay collections, but they were typically less abundant.

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