Distribution, movements, and habitat use of small striped bass (*Morone saxatilis*) across multiple spatial scales

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Abstract—Distribution, movements, and habitat use of small (<46 cm, juveniles and individuals of unknown maturity) striped bass (*Morone saxatilis*) were investigated with multiple techniques and at multiple spatial scales (surveys and tag-recapture in the estuary and ocean, and telemetry in the estuary) over multiple years to determine the frequency and duration of use of non-natal estuaries. These unique comparisons suggest, at least in New Jersey, that smaller individuals (<20 cm) may disperse from natal estuaries and arrive in non-natal estuaries early in life and take up residence for several years. During this period of estuarine residence, individuals spend all seasons primarily in the low salinity portions of the estuary. At larger sizes, they then leave these non-natal estuaries to begin coastal migrations with those individuals from nurseries in natal estuaries. These composite observations of frequency and duration of habitat use indicate that non-natal estuaries may provide important habitat for a portion of the striped bass population.

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A full understanding of the distribution, movements, and habitat use of juvenile and other subadult striped bass (*Morone saxatilis*) is central to deciphering the role, impacts, and management of this abundant and important species in estuarine and coastal ocean habitats. This is especially true for the populations between Chesapeake Bay and the Gulf of Maine where adults can be highly migratory and are seasonal participants in coastal migrations (Chapoton and Sykes, 1961; Boreman and Lewis, 1987; Waldman et al., 1990; Able and Grothues, 2007; Welsh et al., 2007; Grothues et al., 2009; Mather et al., 2010). More recently, it has become apparent that some components of these same populations may be resident in estuaries throughout their life cycle (Secor, 1999; Secor and Piccoli, 2007; Wingate and Secor, 2007). Despite the accumulating understanding of life cycle diversity for adults (see Secor and Kerr, 2009 for *M. saxatilis* and other species), we have an incomplete understanding for juveniles and other subadults (Pautzke et al., 2010). The conventional interpretation based on studies of natal estuaries, including Chesapeake Bay and other large estuaries (Merriman, 1941; Mansueti, 1961; Waldman et al., 1990), is that juveniles remain in estuaries for the first few years of life before leaving to join the coastal migration and may stay longer, if they are natal estuarine residents (Secor 1999; Ashley et al., 2000; Secor and Piccoli, 2007).

For those individuals that eventually become coastal migrants, the available data suggest that the duration of residency in estuaries appears to vary with location and between years, potentially relative to year class strength and associated density dependence (e.g., Kohlenstein, 1981), as well as size and maturity for males and females (e.g., Kohlenstein, 1981; Secor and Piccoli, 2007). For example, an early interpretation was that a mass emigration of small individuals takes place from Chesapeake Bay after ages 2 and 3 (Kohlenstein, 1981). More recently, analysis with otolith microchemistry suggests a gradual shift associated with sexual maturation at ages 5–8 for upper Chesapeake Bay individuals (Secor and Piccoli, 2007). In the Hudson River, it is estimated that emigration from the estuary can occur into adjacent Long Island Sound and the New York Bight at ages 1 and 2 (Secor and Piccoli, 1996) or earlier by age-0 individuals (Dovel 1992, Dunning et al., 2009).

Our understanding of the distribution, movements, and habitat use of small striped bass is largely based on studies that occurred before the recovery in the late 1980s (Nichols and Miller, 1967; Clark, 1968; Kohlenstein, 1981; Boreman and Lewis, 1987; Woolley et al., 1990; Richards and Rago, 1999). Further, most studies have focused on large natal estuaries such as the Hudson River (Secor and Piccoli, 1996), Chesapeake Bay (Mansueti, 1961; Kohlenstein, 1981; Secor, 2007), and to some extent the Delaware River (Waldman and Wirgin, 1994; Able et al., 2007). There has been little emphasis on non-natal estuaries even though small striped bass are common and even abundant components of the fauna (for reviews see Able and Fahay, 1998, 2010). Therefore, we lack a clear understanding of their pattern of habitat use within estuaries, duration of residency, and patterns of timing of emigration (Grothues et al., 2009). These patterns are especially confounded because the sources of small individuals in non-natal estuaries are largely unknown.

The purpose of this article is to evaluate the distribution, movements, and habitat use of small striped bass in and adjacent to non-natal estuaries in New Jersey and adjacent areas. We approach this evaluation using multiple sources including information from seasonal catches from trawl, seine, and gill net surveys, tag-recapture studies, and telemetry. Most of these data relate to a period during or after the recovery of the population along the east coast. Further, we evaluate these patterns of estuarine and coastal ocean use at three scales: throughout the Middle Atlantic Bight continental shelf (Cape Cod to Cape Hatteras); on the inner continental shelf off New Jersey; and in the Mullica River–Great Bay estuary in southern New Jersey. Although the focus is on small individuals, i.e., from young-of-the-year to sexual maturity, the duration of this stage is sometimes difficult to define because the age (and size) at maturity varies between sexes, populations, and even within the same estuary (see Fig. 1 in Specker et al., 1987). We define the upper size limit for our treatment as 46 cm total length (TL) (approx. age 3–5 years; Merriman, 1941). In addition, there appears to be a natural difference in the size modes of several extensive sampling programs around this size (see below). The rationale for using this cutoff is that it includes the size at first maturity for some populations and that it complements our earlier telemetry studies of larger striped bass in the Mullica River–Great Bay estuary (Able and Grothues, 2007; Ng et al., 2007; Grothues et al., 2009). Thus, those individuals <46 cm include those likely to be resident in estuaries, such as mature males (e.g., Wingate and Secor, 2007), but also include those that may begin leaving estuaries to participate in coastal migrations. For the purposes of this article, we make a distinction, where possible, between dispersal (from natal estuaries) by juveniles (<20 cm) and other individuals of unknown maturity (>20–46 cm) and dispersal by those that make (directed, annual) coastal migrations.

Materials and methods

Study areas

We used three geographical areas in this study (Fig. 1): 1) continental shelf waters (to depths greater than 450 m) along the east coast of the United States between Cape Hatteras and Cape Cod; 2) a portion of the inner continental shelf (depths of 5.5–27.4 m) off the coast of New Jersey; and 3) the Mullica River–Great Bay estuary (average depth 2 m, some portions to 26 m) which is part of the Jacques Cousteau National Estuarine Research Reserve (JCNERR). Aspects of the geomorphology and hydrology of each of these areas is characterized in further detail elsewhere (Able and Fahay, 1998; 2010).

Occurrence and distribution based on surveys

Seasonal, coast-wide distributions for small (<46 cm) striped bass on the continental shelf were determined with data from National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center bottom trawl surveys (Azarovitz, 1981; Grosslein and Azarovitz, 1982) (Fig. 1, Table 1). Samples were collected on the continental shelf at stratified random stations between Cape Hatteras, North Carolina, and the Gulf of Maine during fall (September–October), winter (January–February) and spring (March–April) (Grosslein and Azarovitz, 1982; Able and Fahay, 2010). The geographical limits of the sampling program, however, varied with season and between years. Similar sampling effort and distribution of samples occurred in the fall (n=7379 tows) and spring (n=7418 tows) over the period from 1982 through 2003. The winter sampling effort was reduced in terms of number of tows (n=1552 tows) and geographical extent during the years in which it occurred (1992–2003). It was limited to the southern portion of Georges Bank and south of Cape Cod to just north of Cape Hatteras. In addition, the number of samples in the shallow waters (less than 25 m) off Massachusetts and from New Jersey to North Carolina was reduced in the winter but not in the fall and spring. The distribution of samples over all seasons varied with depth as well, with some less than 20 m (17%), a large portion less than 100 m (81%), fewer between 100 and 250 m (16%) and fewer still in depths >251 m (2%). See Able and Fahay (2010) for additional details. An estimate of the length distribution by age of striped bass was based on data from Mansueti (1941) and Able and Fahay (1998) and back-calculated length at age was based on otoliths of striped bass collected in Delaware Bay by the New Jersey Department of Environmental Protection (Baum[1]).

Distribution data for small (<46 cm) striped bass off New Jersey were collected seasonally by otter trawl from 1996 to 2003 by randomly selecting sites in each of 15 sampling strata by the New Jersey Department

[1] Baum, T. 2006. Personal commun. New Jersey Dep. Environmental Protection, Nacote Creek Research Center, Port Republic, NJ 08241.

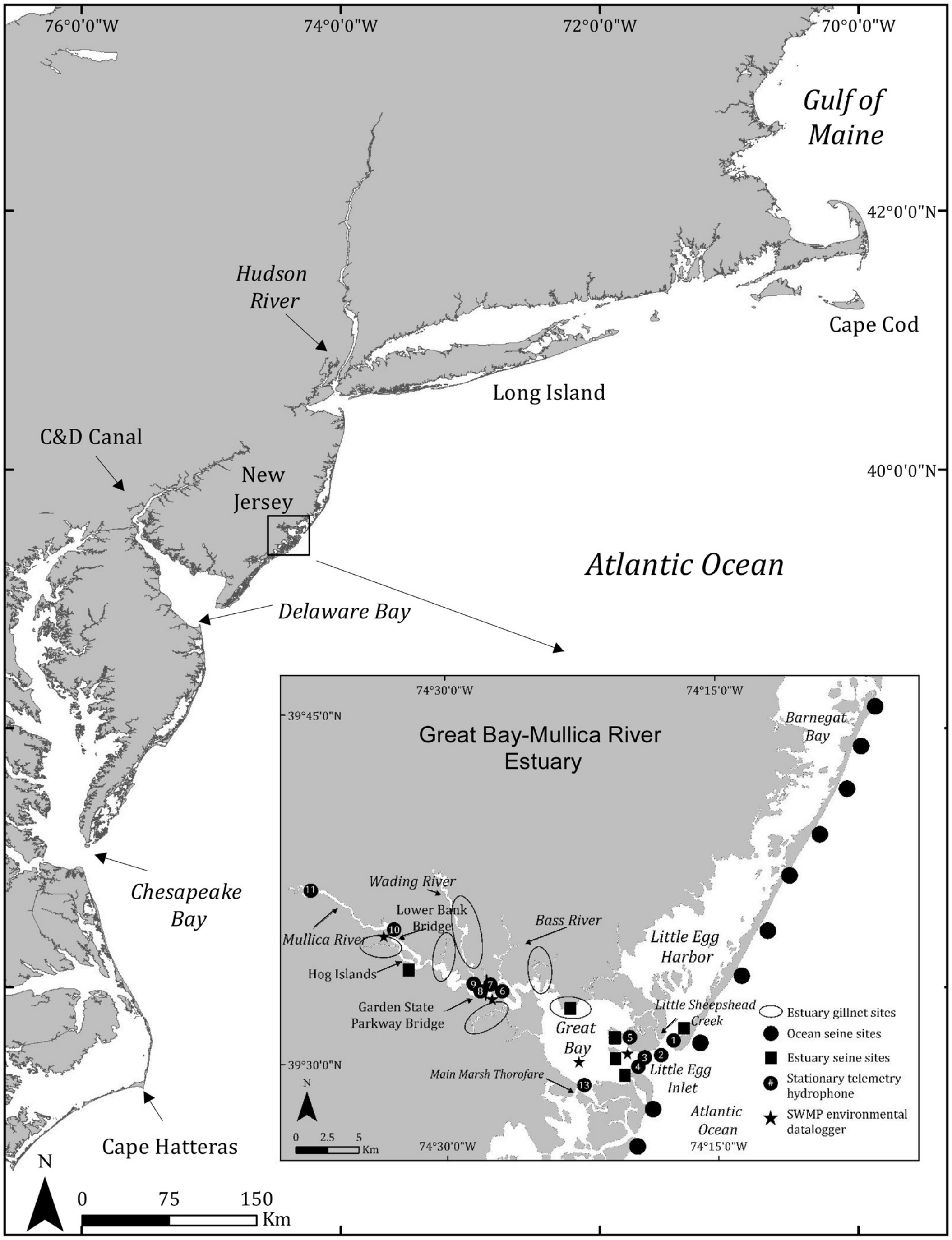

Figure 1

Collection sites for striped bass (*Morone saxatilis*) within the Mid-Atlantic Bight. Striped bass were collected by the National Marine Fisheries Service's otter trawl survey (between Cape Cod and Cape Hatteras), New Jersey Department of Environmental Protection's otter trawl survey (coast of New Jersey), and Rutgers University Marine Field Station's estuarine-ocean beach-seine and estuarine gillnet surveys. Stationary telemetry hydrophone and water quality data logger locations (in the vicinity of Little Egg Inlet and the Mullica River–Great Bay estuary [inset]) are also shown. See Table 1 for timing of sampling.

of Environmental Protection (NJDEP) (Fig. 1, Table 1). See Byrne[2] and Sackett et al. (2007) for additional details. These sites were divided into three depth strata and categorized as inshore (5.5–9.1 m), mid-shore

[2] Byrne, D. M. 1989. New Jersey trawl surveys. *In* Special Report No. 17 of the Atlantic States Marine Fisheries Commission (Azarovitz, T. R., J. McGurrin, and R. Seagraves, eds.), p. 46–48. Atl. States, Marine Fish. Comm.,Woods Hole, MA.

(9.1–18.3 m), and offshore (18.3–27.4 m). Trawl locations were mapped with GIS (ArcGIS[3], vers. 9.2, ESRI, Redlands, CA). The entire otter trawl data matrix consisted of 2872 records of catch per unit of effort (CPUE; number of individuals per tow), average depth, date, season (spring, April; summer, June–August; fall, September–October; winter, January–February), and depth category (inshore, midshore, and offshore). Additional collections from the surf zone adjacent to and within the Mullica River–Great Bay estuary were collected by seine during 1998–99 and 2004–06 (Table 1, Fig. 1). See Taylor et al. (2007) for additional details.

In order to determine the estuarine distribution of other small (<46 cm) striped bass in space and time, we sampled with anchored multimesh gill nets (15 m×2.4 m nets with five panels of five box-mesh sizes 2.5, 3.8, 5.1, 6.4, and 7.6 cm) in the Mullica River–Great Bay estuary at several locations (Table 1, Fig. 1). Gill nets were set (for approximately 60 min during the day) at biweekly intervals during the spring, summer, and fall in upper creek, creek mouth, and nearshore bay habitats. Within each area, the position in which each net was set varied such that no two locations were sampled twice. See Able and Fahay (2010) for additional details.

Another sampling program was conducted with small otter trawls between 1988–90 and 1996–2009 at a variety of stations and habitats located throughout the Mullica River–Great Bay–Inner Continental Shelf corridor (Table 1). These stations were distributed along the salinity gradient from the ocean to tidal freshwater. Other individuals were collected in composite surveys in Delaware Bay with a variety of gear types and from habitats during 1998–2006 (Table 1; Able et al., 2007; Able and Fahay, 2010). Still others came from an extensive seine survey in the Hudson River estuary (Table 1).

Tag-recapture

The tagging procedure outlined in Boreman and Lewis (1987) for their study with American Littoral Society (ALS) data is consistent with the protocol followed in our study. After initial capture, code-specific loop tags were inserted into the dorsal region of each fish and the fish was released. Length, general capture and release location, and date were recorded for each animal on a supplied tagging card and mailed to ALS. The ALS sends raw data to the National Marine Fisheries Service in Woods Hole, Massachusetts, for processing and entry into a long-term database (Shepherd[4]). We limited the query of records to two subsets of data: 1) striped bass initially captured in New Jersey waters and recaptured at less than 46 cm TL along the eastern United States coast; and 2) striped bass initially captured in nearby natal estuaries (Hudson and Delaware rivers) and recaptured in New Jersey waters at less than 46 cm TL (Table 1). The latitude and longitude coordinates associated with each general capture and recapture location were assigned by ALS and NMFS by calculating the spatial average of each location submitted by volunteer taggers.

Telemetry

We determined dynamic habitat use and movements of small (32.4–42.5 cm fork length [FL]) striped bass in the Mullica River–Great Bay estuary using acoustic telemetry. Wireless hydrophones were moored as a series of gates in order to determine occurrence and residency of tagged individuals along the estuarine gradient (Fig. 1). Fishes surgically implanted with individually coded acoustic transmitters (76.8 kHz) were detected when they came within range (approximately 500 m) of moored wireless hydrophones (WHS-1100, Lotek Wireless, Inc., St. Johns, Newfoundland, Canada) suspended at a depth of approximately 3.2 m (see Grothues et al. [2005] for additional details). Permanent environmental-monitoring instruments in the Jacques Cousteau National Estuarine Research Reserve included data loggers recording salinity, temperature, pH, and water depth (Kennish and O'Donnell, 2002) along the estuarine gradient (Fig. 1).

In addition, mobile tracking methods were used to determine fine-scale patterns of habitat use. In order to spatially and temporally standardize tracking, 113–120 fixed locations were georeferenced with a global positioning system (GPS) unit in universal transverse mercator (UTM) coordinates by using a GIS software package (ArcGIS, vers. 9.2, ESRI) and visited with a directional mobile hydrophone on a weekly basis (LHP_1; Lotek Wireless). Listening range with the mobile hydrophone was typically about 500 m, determined by signal range tests. At each of the above locations, the hydrophone was lowered 1.0 m into the water and pointed at the four principal ordinates for 5 seconds in each direction. When a fish was detected, its position was triangulated by moving until a reading of 115 dB or above was detected at a gain of 15 or less (approximately 2 m from the hydrophone). Measurements of water temperature and salinity were collected (YSI Model 85; Yellow Springs Instruments, Inc., Yellow Springs, Ohio), along with date, time, tag number, and depth at each confirmed fish detection. Tracking was not conducted when the listening range was less than 500 m (which corresponded to wind velocities greater than 30 km/h) or on days when there was heavy rainfall or thunderstorms. See Ng et al. (2007) and Sackett et al. (2008) for further details on mobile tracking protocol. To determine patterns of seasonal habitat use in relation to physical habitat variables, the distances of individually tagged striped bass from emergent (marsh) and submerged (channel) embankment edges were calculated by using a GIS software package. The locations of submerged edges were derived from estuarine bathymetry data by calculating high slope areas (i.e., channel edges; >2.5°) and submerged or emergent edge

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4] Sheperd, G. 2009. Personal commun. NMFS Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026.

Table 1

Summary of data sources for juvenile striped bass (*Morone saxatilis*) examined in the current study. See Fig. 1 for sampling locations.

General habitat	Geographic location	Sampling gear	Sampling frequency/duration
Ocean	Atlantic coast	Otter trawl	Fall, winter, spring/1982–2003
	Atlantic coast	Tag-recapture	Fall, winter, spring, summer/1962, 1967, 1973, 1977–2009
	New Jersey coast	Otter trawl	Fall, winter, spring, summer/1988–2003
	Central New Jersey coast	Seine	Biweekly/June – November 1998, May–October 1999–2000, July 2004, May–October 2005, August–October 2006
Estuary	Mullica River-Great Bay	Otter trawl	Monthly/July and September 1988–1990, 1996–2009
	Mullica River-Great Bay	Multi-mesh gill net	Monthly/August–October 2001; Semi-monthly/May–October 2002
	Mullica River- Great Bay	Seine	Biweekly/June – November 1998, May–October 1999–2000, July 2004, May–October 2005, August–October 2006
	Mullica River-Great Bay	Acoustic telemetry	Mobile (Weekly/2006–2008) Passive (Continuous/2006–2008)
	Delaware Bay	Otter trawl/weirs	Monthly/April – November 1996–2000; May–November 2001–2005
	Hudson River	Seine	July–November 1990–2009

distances were calculated as the straight-line distance (m) to the nearest edge.

Results

Occurrence and distribution based on surveys

Small (<46 cm TL) striped bass were represented in multiple sampling gears from multiple locations throughout the study area (Table 1, Fig. 2). However, individuals <20 cm (presumed age 0–1 years) were seldom collected in the coastal ocean, including the NMFS trawl survey between Cape Hatteras and Cape Cod (n=2 individuals), the NJDEP trawl survey (n=61 individuals), and the Rutgers University Marine Field Station (RUMFS) beach seine survey along the inner continental shelf off New Jersey (n=21 individuals) despite the large number of samples. These smaller individuals were also not abundant in estuarine seine, gill net, or otter trawl collections within the Mullica River–Great Bay estuary based on over 3100 samples (Table 1, Fig. 2). Of these, individuals <20 cm were collected only within the estuary during otter trawl (n=21, 3.4–19.5 cm) and gillnet (n=1, 16.4 cm) sampling. Alternatively, large numbers of small individuals <20 cm have been collected from the Delaware River and Hudson River estuaries, both known spawning areas (Fig. 2, G and H). Larger juveniles (21–46 cm, presumed age 2–5 years) were better represented in surveys in most locations including the Mullica River–Great Bay estuary (n=55; Fig. 2).

The seasonal patterns of distribution were similar regardless of the spatial scale examined. Individuals 20 to 46 cm, according to the NMFS surveys on the continental shelf, were seldom collected in the fall and winter (a period of restricted sampling in shallow waters) surveys. During the spring (February–March) they were more abundant and largely restricted to the inner portion of the shelf according to composite collections during 1982–2003 (Fig. 3). Most were restricted to an area from north of the Chesapeake Bay mouth to Long Island including the coast of New Jersey.

A similar shallow-water distribution, in space and time, of individuals <46 cm is evident from depth stratified sampling off the coast of New Jersey during all seasons from 1988 through 2003 (Figs. 4 and 5). Both smaller (<20 cm), although less common, and larger (21–46 cm) individuals were most abundant in the spring but also occurred during the winter months and were either rare or absent in the summer and relatively rare during the fall. Over all these seasons, both of these size groups were most abundant in the nearshore depth strata (5.5–9.1 m) with a trend to decreasing abundance with depth with the least number of collections in the offshore strata (18.3–27.4 m). During the winter and spring the larger individuals (21–46 cm) were found all along the coast from the mouth of Delaware Bay to the tip of Sandy Hook (Fig. 5).

Sampling events or tows (*n*)	Water depths sampled (m)	No. of individuals (<46 cm)	Data source
>16,000	5–481	438	National Marine Fisheries Service; Grosslein and Azarovitz (1982); Able and Brown (2005)
>300,000 (captures); >19,000 (recaptures)	No data	1529 (recaptures)	American Littoral Society; current study
2872	3–80	2930	New Jersey Department of Environmental Protection; Byrne (1989); current study
526	<2	9	Able et al. (2003); current study
2328	0.35–26.0	27	Able and Fahay (2010)
599	0–8	28	Able and Fahay (2010)
243	<2	9	Able et al. (2003); current study
Mobile (80) Passive (>50,000)	1–25	14	Current study
>15,000	1–24	5343	Nemerson and Able (2003); Able et al. (2007)
—	<2	108,445 (1–39 cm)	New York Department of Environmental Conservation

Movements determined with tag-recapture methods

Tagged and recaptured individuals revealed that they could move from natal estuaries to the vicinity of nonnatal sources along the New Jersey coast and that those individuals that were found along the New Jersey coast could move to other areas. Few individuals tagged in the nearest natal estuaries (Hudson River and vicinity, n=25, and Delaware River, n=1) were recaptured along the New Jersey coast (n=26 total, Fig. 6A). Small striped bass captured in neighboring natal estuaries ranged in size from 30–46 cm before being recaptured in New Jersey (33–46 cm). Days at liberty for fish captured in nearby natal estuaries ranged from 13–892 (mean 276 days). Individuals tagged in or along the New Jersey coast (n=152 total) were recaptured throughout the northeastern United States from northern Chesapeake Bay (n=4; 3%), Delaware Bay (n=19; 13%), and Long Island and Connecticut (n=27; 18%), with some found as far north as Cape Cod and Maine (n=21; 14%). The majority of recaptures, however, occurred along the New Jersey coast (n=81; 53%; Fig. 6B). The time between capture and recapture was similar for this subset of fish (1–868 days; mean 244 days). For those fish originally captured in New Jersey and recaptured elsewhere along the coast, sizes were generally smaller than in the other subset of fish analyzed and lengths ranged from 25 to 46 cm during capture and from 28 to 46 cm during recapture. A relatively small number of fish were recaptured at sizes less than 40 cm TL (n=18; 11.8%), with all but one of these individuals recaptured less than 100 km from their original release location in New Jersey waters (Fig. 6B).

Estuarine habitat use determined with acoustic telemetry

From 2006 through 2008, 14 small striped bass (32.4–42.5 cm FL) were tagged with acoustic transmitters within the Mullica River–Great Bay estuary in southern New Jersey (Tables 1 and 2, Fig. 7). Most were consistently detected (11 of 14 individuals, n=114 detections) based on mobile telemetry. An examination of the seasonal distribution revealed consistent use of the mesohaline portions of the river all the way up to, and occasionally above, the freshwater-saltwater interface, whereas fewer were found in polyhaline waters near Little Egg Inlet (see Fig. 1). In the summer, fall, and spring some individuals were detected downstream near Little Egg Inlet, or in Great Bay, but during the winter all juveniles were detected upstream in the river (Fig. 7). During December 2006, four fish (42–48 cm FL) were tagged in the ocean off Long Beach Island (Fig. 7C). Of these, one (code 104) moved into the estuary by way of Main Marsh Thorofare (see Fig. 1) on December 24 and remained there for approximately 125 days.

The use of upriver habitats (such as Lower Bank) was evident by the temperature (Fig. 8A) and salinities (Fig. 8B) at which tagged juvenile striped bass were frequently detected. Juveniles inhabited the warmer water temperatures found upstream in the summer

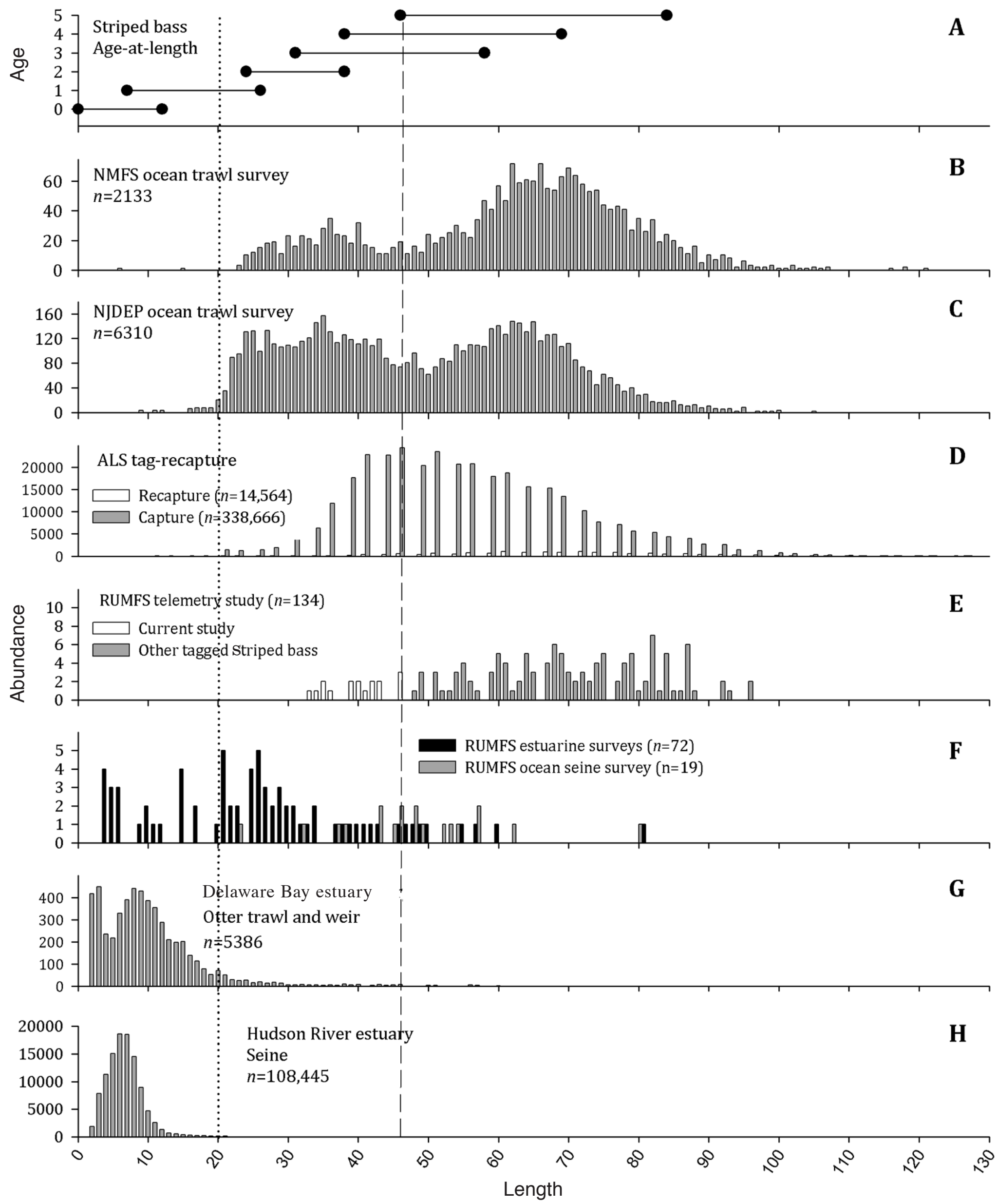

Figure 2

Age (**A**) and length frequency for several continental shelf (**B, C**), estuarine (**E, G, H**), or both (**D, F**) sampling programs. Samples (n) reflects total number of striped bass (*Morone saxatilis*) caught. Juvenile striped bass captured during Rutgers University Marine Field Station estuarine surveys shown in (F) include otter trawl (n=28), gillnet (n=31), and seine (n=13) collections. All lengths are expressed as total length (TL), except for (E) which uses fork length (FL). NMFS=National Marine Fisheries Service, NJDEP=New Jersey Department of Environmental Protection, ALS=American Littoral Society, RUMFS=Rutgers University Marine Field Station. See Table 1 for further sampling details.

when the largest temperature gradient occurred relative to downstream areas. In contrast, winter water temperatures were similar at both the inlet and upriver, although fish were detected only upriver. Fish were detected within a wide range of salinities throughout the year. However, most fish were detected within intermediate salinities between the two salinity extremes of the upriver and inlet habitats. The upriver wintertime distribution of tagged individuals revealed a consistent use of lower salinity habitats. These same individuals

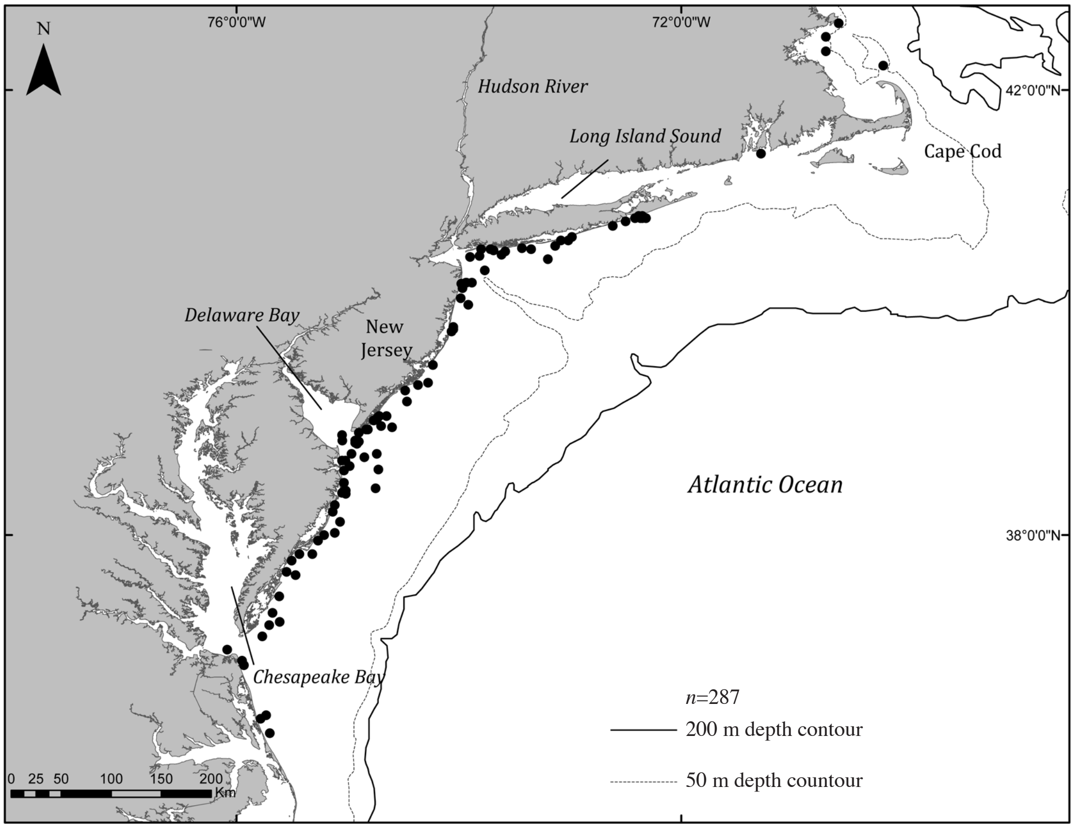

Figure 3

Composite springtime distribution (1982–2003) of small (21–46 cm total length) striped bass (*Morone saxatilis*) north of Cape Hatteras based on National Marine Fisheries Service trawl surveys.

Table 2

Characteristics and detection history of individual acoustically tagged striped bass (*Morone saxatilis*) (<46 cm total length [TL]), in the Mullica River–Great Bay estuary, 2006–08. See Figure 7 for tagging locations: BB=Rutgers University Marine Field Station Boat Basin; LBI=Long Beach Island (Atlantic Ocean); DpPt=Deep Point (Mullica River); DrPt=Doctor's Point (Mullica River); Pkwy=Garden State Parkway Bridge (Mullica River). Seasonal detections are indicated by F=Fall (September–November), W=Winter (December–February), Sp=Spring (March–May), Su=Summer (June–August).

Tag code	Size (cm TL)	Battery life (d)	Tagging location	Tagging date	Mobile tracking detections (*n*)	Passive array detections (*n*)	Seasons detected (mobile tracking)
15	39.4	229	BB	11/12/2007	3	1158	Su
104	41.9	139	LBI	12/11/2006	2	12,926	W Sp
107	41.9	139	LBI	12/11/2006	0	0	—
111	42.5	139	BB	11/16/2006	1	170	Su
113	42.5	139	LBI	12/11/2006	0	0	—
128	34.3	139	DpPt	6/13/2006	0	0	—
132	33.7	139	DpPt	6/13/2006	11	6181	Su
134	35.6	139	DpPt	6/13/2006	6	26,545	F Su
135	40.6	229	DrPt	10/15/2007	15	31,320	F W Sp Su
141	34.3	139	DpPt	6/13/2006	14	344,662	F Su
143	32.4	139	DpPt	6/13/2006	7	95,394	F Su
201	38.7	229	Pkwy	11/14/2007	20	72,096	F W Sp Su
202	38.1	229	Pkwy	11/14/2007	18	24,921	F W Sp Su
209	39.4	229	DrPt	10/15/2007	18	98,040	F W Sp Su

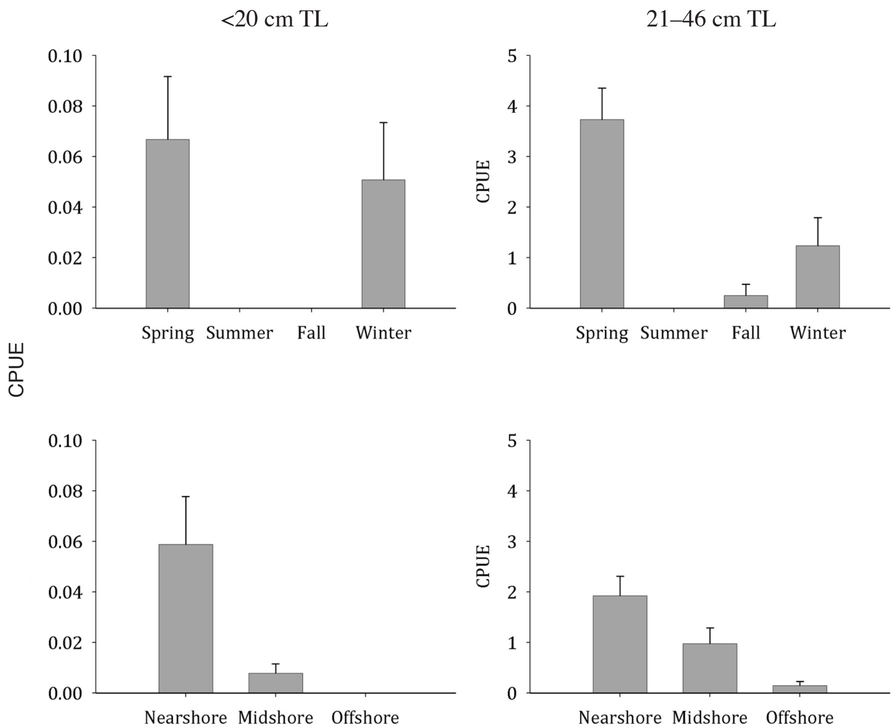

Figure 4

Catch per unit of effort (CPUE) of smaller (<20 cm total length [TL]) and larger (21–46 cm TL) striped bass (*Morone saxatilis*) by season and depth strata (inshore [5.5–9.1 m] mid-shore [9.1–18.3 m], and offshore [18.3–27.4 m]) on the inner continental shelf based on New Jersey Department of Environmental Protection trawl surveys. Error bars represent standard error of the mean. See Figure 5 for description and location of depth strata.

were detected at depths of 0.9–8.3 m (mean 3.6 m). They also showed a differential use of emergent (marsh bank) and submerged (channel edge) embankments across the seasons. Fish were found relatively close to emergent marsh banks across all seasons but were most consistently found there in the spring and fall (85 and 87 m average distances, respectively) and farther away in the summer and winter (190 and 151 m average distances, respectively). Association with channel edges was greatest in the summer (average distance 414 m), and greater average distances were observed during the remaining seasons (1170–1831 m).

Additional tracking based on the passive listening array in this system also detected most (11 of 14, n=713,413 detections) tagged individuals across several seasons (Tables 1 and 2). These were most consistently detected in the Mullica River portion of the estuary (hydrophone nos. 7, 9, 10) but they made movements into the bay (hydrophone nos. 4, 5) as well (see Fig. 1 for locations). One individual (code 141) was resident near hydrophone no. 7 from early summer through fall. Another (code 134) was resident in the bay near hydrophone no. 5 over a similar time period but made occasional movements up to the vicinity of hydrophone 7 in the river. Two other individuals (codes 135 and 201) were resident at hydrophone no. 7 from fall through the following summer but made an initial excursion down into the bay (hydrophone no. 5) and more frequent movements up to the freshwater-saltwater interface near hydrophone no. 10 during the winter. Another individual (code 202) was less frequently detected as it moved from the tagging location in the lower river (hydrophone no. 7) up into the upper river at the freshwater-saltwater interface (hydrophone no. 10) on five occasions during the winter and then back down to the lower river (hydrophone no. 7) later in the spring.

The physical habitat surrounding these extensively used habitats at hydrophones 7 (Chestnut Neck; Fig. 1) and 10 (Lower Bank; Fig. 1) can be similarly characterized by their location within the main stem of the Mullica River (i.e., approximately 250 and 200 m wide, respectively, and adjacency to a channel approximately 4 and 9 m deep, respectively), but these locations vary in aspects of their water quality. Lower Bank is located at the freshwater-saltwater interface of the Mullica River–Great Bay estuary (daily average 3.3 ppt, range: 0.0–17.7 during 2006–08) and Chest-

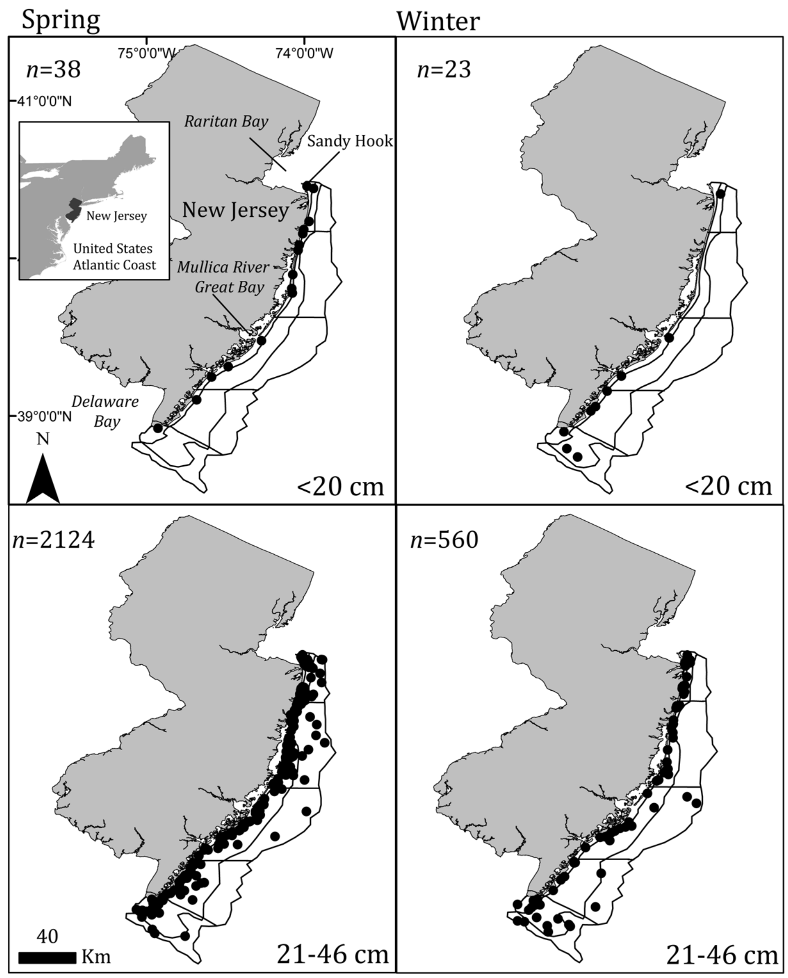

Figure 5

Composite spring and winter distributions for two size classes of small striped bass (*Morone saxatilis*) (<20 cm total length [TL] and 21–46 cm TL) at multiple depth strata (inshore [5.5–9.1 m], midshore [9.1–18.3 m] and offshore [18.3–27.4 m]) on the New Jersey inner continental shelf based on New Jersey Department of Environmental Protection trawl surveys.

nut Neck is characterized by intermediate salinities (daily average 15.2 ppt, range: 0.2–29.7 during 2006–08). Lower pH values (daily average: 6.1, range: 3.4–8.5 during 2006–08) are also present at Lower Bank due to the natural influx of tannins from the surrounding watershed, whereas Chestnut Neck experiences more neutral pH levels (daily average: 7.4, range: 5.2– 8.5 during 2006–08) moderated by the effect of incoming ocean and bay waters. Dissolved oxygen (DO) levels never reached anoxia during the study period at either hydrophone site. However, in the summer of 2006, DO dropped to hypoxic levels during short periods of the day at hydrophone nos. 7 and 10 (0.2 and 0.8 mg/L, respectively). Otherwise, daily mean DO levels remained relatively high and were similar throughout the study period at both sites (Lower Bank daily average: 9.0 mg/L; Chestnut Neck daily average: 8.8 mg/L).

Discussion

Sources of striped bass for non-natal estuaries

The assumption has long been that the sources of small striped bass that occur along the New Jersey coast and in non-natal estuaries have been major river estuaries to the north (Hudson River: Dovel, 1992; Secor and Piccoli, 1996; Dunning et al., 2009) and south (Chesapeake Bay: Mansueti, 1961; Kohlenstein, 1981; Dorazio et al., 1994) including the Delaware River (Waldman and Wirgin, 1994; Weisberg et al., 1996). This interpretation has become accepted because there are no accounts of reproduction in other systems between Cape Cod and Cape Hatteras (Collette and Klein-MacPhee, 2002; but see Little, 1995). This interpretation is further supported by the large number of small juveniles (<20 cm) encountered in Delaware Bay in the last decade (Able et

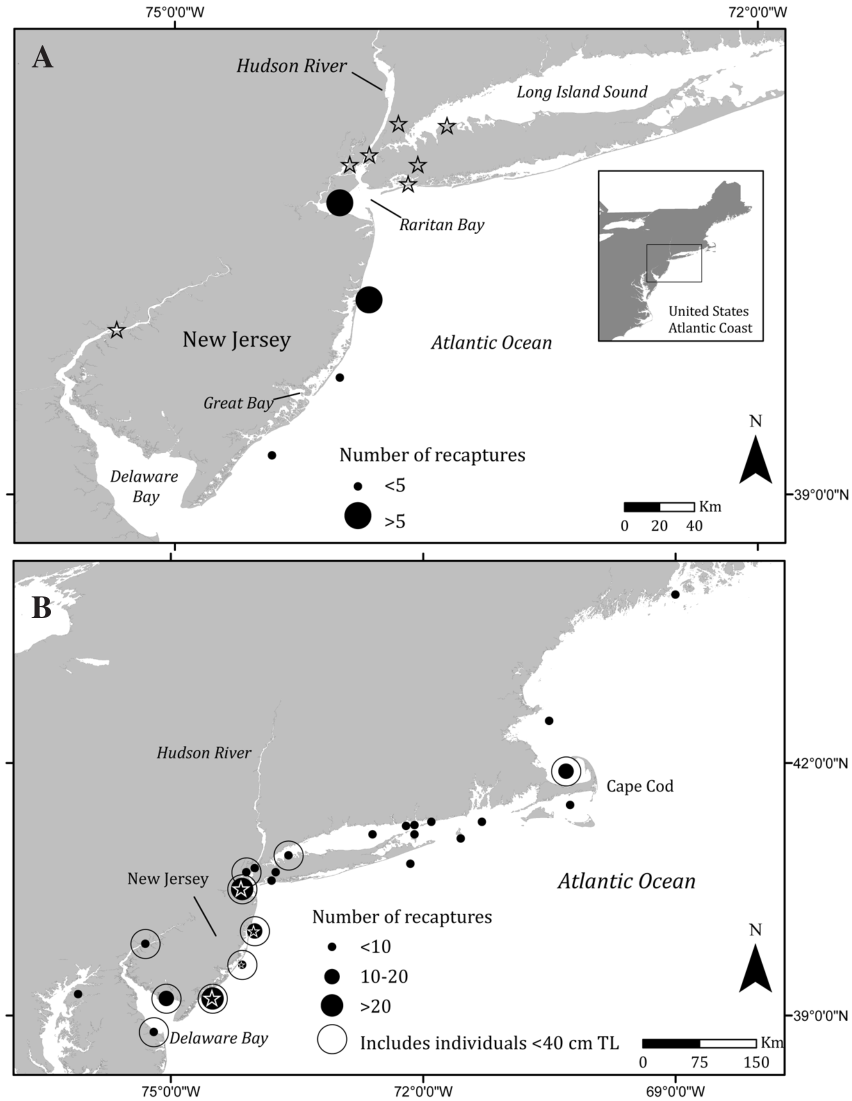

Figure 6

Spatial distribution and abundance of recaptures of small (<46 cm total length [TL]) striped bass (*Morone saxatilis*) tagged during the American Littoral Society tagging program (**A**) near potential source (natal) populations in the Hudson River estuary (including New York Harbor, Jamaica Bay, and western Long Island Sound) and the Delaware Bay and recaptured along the ocean coast of New Jersey, and (B) near potential non-natal sources along the ocean coast of New Jersey and recaptured along the Atlantic coastline. Circled recaptures shown in (**B**) represent fish recaptured at less than 40 cm TL.

al., 2007), as well as by data (Fig. 2) and many studies in the Hudson River (Hurst and Conover, 1998; Hurst et al., 2000; Dunning et al., 2009; Fig. 2) and Chesapeake Bay (Mansueti, 1961). Further, the tag-recapture data for small striped bass reported along the coast of New Jersey support the interpretation of movement from the Hudson River and Delaware Bay. Although there are movements of some ultrasonically tagged adults up to the freshwater-saltwater interface, as if for spawning, in the Mullica River–Great Bay estuary (Able and Grothues, 2007; Grothues et al. 2009), very few small individuals less than 20 cm (n=27) have been collected there despite intensive sampling over two decades (Table 1).

It is difficult to evaluate whether the sources of small striped bass have changed since the recovery in the 1980s (Wooley et al., 1990; Richards and Rago, 1999). Clearly the major estuaries that support natal populations appear to be the same, i.e., Chesapeake Bay and its tributaries and the Hudson River. It is

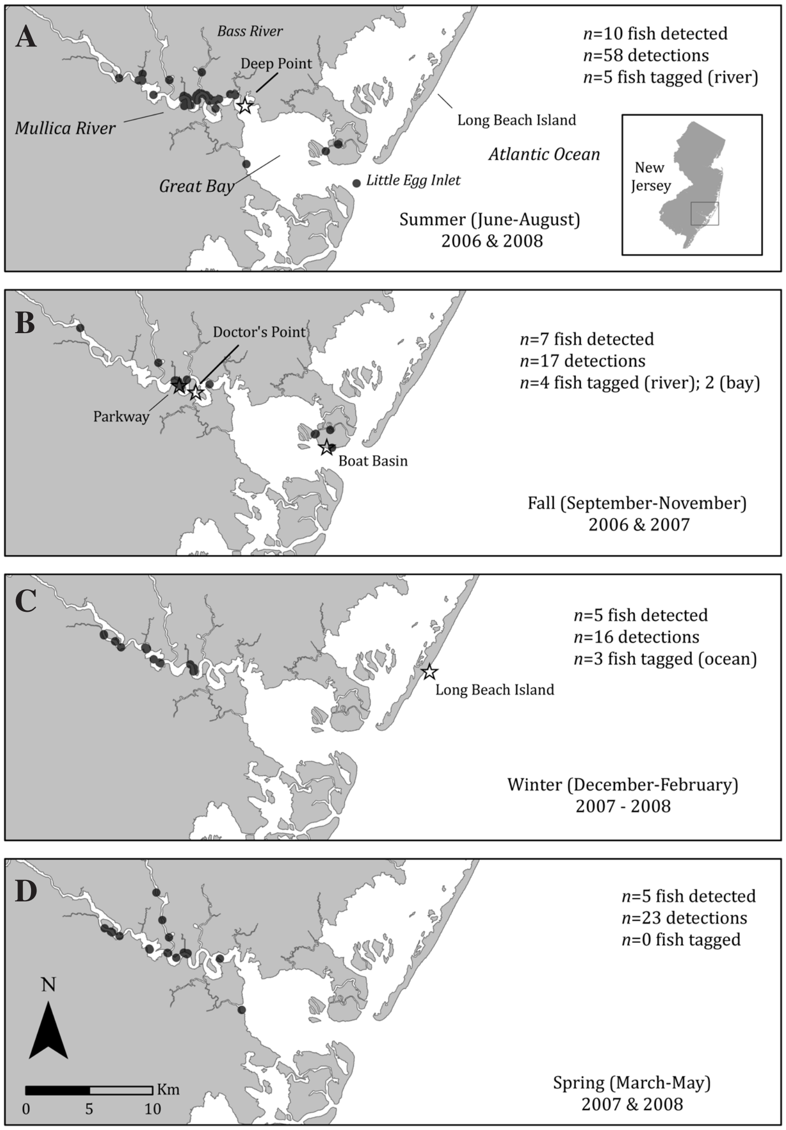

Figure 7

Seasonal tagging locations and distributions of ultrasonically tagged small (<46 cm total length) striped bass (*Morone saxatilis*) in the Mullica River-Great Bay estuary based on mobile telemetry during the (**A**) summer, (**B**) fall, (**C**) winter, and (**D**) spring. See Figure 1 for locations mentioned in the text.

also clear that the Delaware River population is distinct (Waldman and Wirgin, 1994) and has recovered (Weisberg et al., 1996) on the basis of the large number of juveniles in the system (Nemerson and Able, 2003; Able et al., 2007). Also, movement of juveniles from the coast of New Jersey determined with the ALS tag-recapture data, is consistent with earlier patterns (Boreman and Lewis, 1987) in that most recaptures are found to the northeast of the New Jersey tagging sites.

A second assumption has been that young-of-the-year and small juveniles remain in the natal estuary for several years until they begin moving into the ocean and making coastal migrations (Merriman, 1941; Zlokovitz et al., 2003). However, in the Hudson River, movement out of the estuary by postyolksac larvae (Dunning et al., 2009) and age 0, 1, and 2 juveniles (McKown[5]; Dovel, 1992) could account for the occurrence of small striped bass in non-natal estuaries. This dispersal of small juveniles (<20 cm) is not detected in NMFS surveys (n=2), despite the intensive sampling

[5] McKown, K. A. 1991. An investigation of the movements and growth of the 1989 Hudson River year class. *In* A study of the striped bass in the marine district of New York, 2010, p. 5. NY State. Dep. Environ. Conserv., Albany, NY.

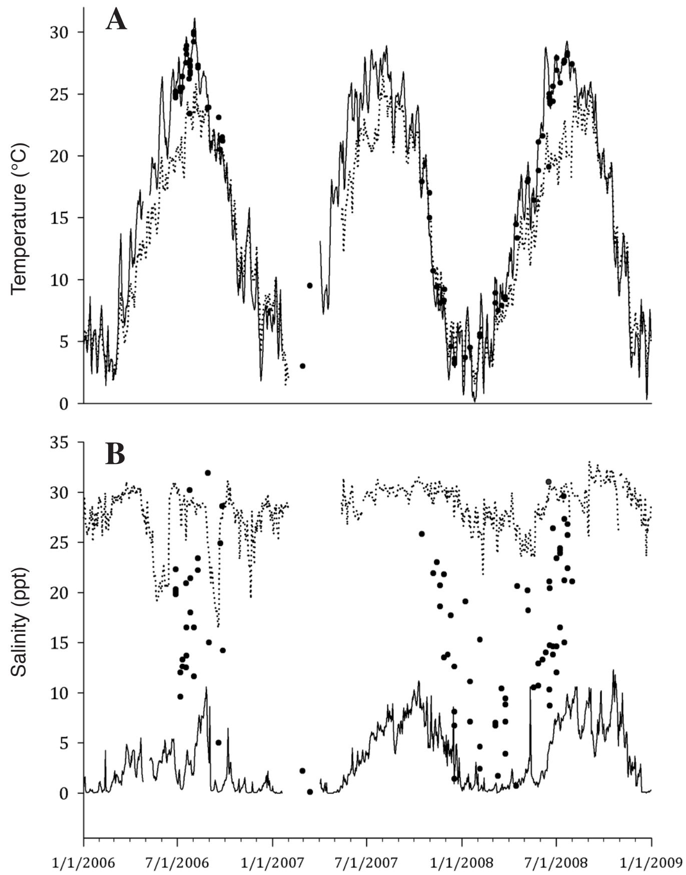

Figure 8

Daily mean (**A**) temperature (°C) and (**B**) 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 (dashed line) and Lower Bank (dark continuous line) water quality data loggers from 2006 through 2008 (see Fig. 1 for locations). Filled black circles represent the temperature and salinity values at locations where ultrasonically tagged small (32.4–42.5 cm total length) striped bass (*Morone saxatilis*) were detected during mobile telemetry tracking efforts during the same time period.

(Table 1), in part, because these small individuals remain in shallow coastal waters where they are not available to these surveys (Figs. 2 and 3). However, a few of this size have been detected along the shallowest depth strata along the coast of New Jersey in NJDEP otter trawl and RUMFS ocean beach surveys (Figs. 2, 4, and 5). At these sizes they can be detected in the winter and spring as they move out of the estuaries. Further support for these movements occurs in the tag-recapture observations of small striped bass that are captured in potential natal estuaries and disperse to other areas along the New Jersey coast (Fig. 6). Thus, dispersal of young-of-the-year and other small juveniles from natal estuaries such as the Hudson River estuary, Delaware Bay, and even the Chesapeake Bay (possibly through the C and D Canal; Fig. 1) could account for the smaller individuals (<20 cm) that occur in the non-natal Mullica River–Great Bay estuary (Fig. 2) because of the absence of successful spawning there (Able and Grothues, 2007; Grothues et al., 2009).

The motivation for leaving the natal estuary and the primary nursery, regardless of whether they are partial migrants or entrained (Secor and Kerr, 2009), has been attributed to age (Kohlenstein, 1981), exploration due to density dependence (Secor and Kerr, 2009), and sex specific variation (i.e., females tend to leave and males tend to stay) (Kohlenstein, 1981). What is not clear is what motivates small striped bass to enter and become resident in non-natal estuaries, although optimal resources (e.g., food, benign environmental conditions) are likely causes (e.g., Mather et al., 2009). Further, the long duration of their stay in a non-natal estuary enhances the possibility of learning behavior at a young age that may lead to contingent formation (Secor, 1999).

Distribution and habitat use in a non-natal estuary

Once small striped bass dispersed into the estuary at Mullica River–Great Bay, regardless of the source of these individuals, a large proportion of them took up residence there for months. Their residency is evident by their presence in the system during all seasons (Table 2, Fig. 7). During this time they were most frequently observed in the Mullica River but less frequently in Great Bay. This is a very different pattern from that of the larger juveniles and adults who are typically present only seasonally in this estuary, particularly during the spring and fall (Able and Grothues, 2007; Grothues et al., 2009). It is consistent with the interpretations of coastal migrations by the larger and older individuals through non-natal estuaries, as also occurs in Massachusetts (Mather et al., 2009; Pautzke et al., 2010).

As a result of our analysis, based on multiple spatial scales and multiple techniques, it seems clear that the Mullica River–Great Bay estuary, and probably other non-natal estuaries in the Middle Atlantic Bight, are commonly used by small striped bass that disperse from natal estuaries and take up residence in this and other non-natal estuaries (Able and Fahay, 2010). Thus, should these non-natal estuaries be considered nurseries? A reevaluation of the nursery concept (Beck et al., 2001) and subsequent dialogue (Dahlgren et al., 2006; Sheaves et al., 2006; Fodrie et al., 2009) clarify several points regarding this question. First, we do not know whether the pattern of dispersal to and colonization of the non-natal Mullica River–Great Bay estuary is common to other non-natal estuaries and whether this colonization is accomplished by immature or maturing individuals. Second, if colonization does occur commonly, we do not know the degree of the contribution of these individuals to adult reproduction or population growth, in part, because there are so few studies of the dispersal of young striped bass (<20 cm), or any species, out of estuaries (Deegan, 1993; Beck et al., 2001; Gillanders et al., 2003). Third, it should not be surprising that a mosaic of habitats (e.g., Sheaves, 2005; Sheaves et al., 2006), including non-natal estuaries, is used by striped bass, and other species (Gillanders et al., 2003; Dahlgren et al., 2006) and the complexity of the mosaic may influence population growth (e.g., Fodrie et al., 2009) and add to a population's buffering capacity against unfavorable habitat dynamics (e.g., Secor, 2007). One possible solution is to consider natal estuaries, and their subsequent use by young-of-the-year and small juveniles, as primary nurseries and non-natal estuaries as secondary nurseries for slightly older individuals. This approach has been useful in identifying shark nurseries (Bass, 1978; Merson and Pratt, 2007).

Egress from a non-natal estuary

It appears that small striped bass leave non-natal estuaries, such as the Mullica River–Great Bay system, to begin coastal migrations at the same sizes as those in natal estuaries. This departure of juveniles to become coastal migrants may vary after months, to perhaps years, of residency. Others have suggested that movement from natal estuaries to join the coastal migration may be size or age related such that juveniles may begin to leave estuaries after two years (Merriman, 1941; Kohlenstein, 1981; Setzler-Hamilton and Hall, 1991; Secor and Piccoli, 1996; Zlokovitz et al., 2003). It is known that egress from Chesapeake Bay by immature females occurs in early spring at age 2 and 3 (Merriman, 1941). These patterns are consistent with the occurrence of striped bass of similar sizes along the coast determined by tag-recapture of striped bass in the ALS tagging program. For instance, a majority of fish recaptured along the coast of New Jersey after release in natal estuaries were larger individuals (>40 cm TL) that may be joining the annual coastal migration. These larger individuals were also frequently recaptured in presumably non-natal habitats in the Gulf of Maine and along the coasts of Connecticut and Rhode Island after initial release in New Jersey waters. This same pattern has been reported for age 2 and 3 fish moving into non-natal estuaries, such as the Connecticut River (Kynard and Warner, 1987) and in Massachusetts where 40–50 cm TL individuals (most age 2–5) apparently feed during the summer, make coastal migrations during the fall through spring, but return in subsequent years (Mather et al., 2009, 2010; Pautzke et al., 2010). Certainly, other estuarine-dependent fish species leave estuaries when they reach a size threshold (Rountree and Able, 1992; Potter et al., 1997). This pattern for striped bass may vary with sex, i.e., females are likely to leave at earlier ages or smaller sizes, whereas males tend to remain, at least in natal estuaries, for longer periods of time (Secor and Piccoli, 1996).

In general, overall patterns of use of a non-natal estuary and scheduling of departure appear similar between natal and non-natal estuaries and we also suspect that there are no major changes in these patterns before and after the recovery of the striped bass population in recent years (Boreman and Lewis, 1987). However, we hasten to point out that there was little emphasis on non-natal estuaries as secondary nursery habitat before the recovery.

Conclusion

As we have demonstrated, non-natal estuaries are potentially important habitat for small (20–46 cm) striped bass. This finding may further complicate our understanding of life cycle diversity (see Secor and Kerr, 2009) for this species because the prior focus has been on natal estuaries. Further, as these individuals from non-natal estuaries join the annual coastal migration, grow, and mature, one wonders where they are likely to spawn. One possibility is that they will attempt to spawn in the non-natal estuaries where they have previously spent several months to years. This could account for the seeming unsuccessful attempts in the Mullica River–Great Bay estuary (Able and Grothues, 2007; Grothues et al., 2009). One could also argue that these individuals may be responsible for colonizing new spawning sites, as has previously been suggested (Grothues et al., 2009). Alternatively, they may join other maturing individuals as they migrate back to their natal rivers and streams that provided primary nurseries. Otolith microchemistry might be the appropriate means to distinguish the ultimate source of individuals that use non-natal estuaries and the site of their subsequent spawning.

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