

Abstract—For most migratory fish, little is known about the location and size of foraging areas or how long individuals remain in foraging areas, even though these attributes may affect their growth, survival, and impact on local prey. We tested whether striped bass (*Morone saxatilis* Walbaum), found in Massachusetts in summer, were migratory, how long they stayed in non-natal estuaries, whether observed spatial patterns differed from random model predictions, whether fish returned to the same area across multiple years, and whether fishing effort could explain recapture patterns. Anchor tags were attached to striped bass that were caught and released in Massachusetts in 1999 and 2000, and recaptured between 1999 and 2007. In fall, tagged striped bass were caught south of where they were released in summer, confirming that fish were coastal migrants. In the first summer, 77% and 100% of the recaptured fish in the Great Marsh and along the Massachusetts coast, respectively, were caught in the same place where they were released. About two thirds of all fish recaptured near where they were released were caught 2–7 years after tagging. Our study shows that smaller (400–500 mm total length) striped bass migrate hundreds of kilometers along the Atlantic Ocean coast, cease their mobile lifestyle in summer when they use a relatively localized area for foraging (<20 km²), and return to these same foraging areas in subsequent years.

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Use of non-natal estuaries by migratory striped bass (*Morone saxatilis*) in summer

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For most migratory fish species, little is known about the size of their feeding areas, the duration of time that individuals spend there, and whether fish return to the same feeding area year after year. Migration is an essential part of the life history and ecological niche of many taxa and has been observed in marine, freshwater, and diadromous fish (Thorrold et al., 2001; Dingle and Drake, 2007). Many fish migrate between some combination of spawning area, feeding area, and overwintering area (Harden Jones, 1968; Robichaud and Rose, 2001). Many anadromous fish return to natal systems for spawning (Klemetsen et al., 2003; Quinn and Myers, 2004), but a return to feeding areas has been shown for only a few fish species (Buzby and Deegan, 2000; Solmundson et al., 2005). Consequently, an important but unresolved issue is the extent to which individuals migrate to the same specific, non-natal, feeding area.

Populations of striped bass (*Morone saxatilis* Walbaum) exhibit a variety of movement patterns. Coastal popu-

lations at the northern and southern end of their range may move offshore from their natal estuaries in summer but do not migrate north and south along the coast (Collette and Klein-MacPhee, 2002). The U.S. Atlantic coast striped bass stocks spawn in the Chesapeake Bay, Delaware River, and the Hudson River. In the spring, some members of these stocks migrate northward along the coast to New England (Maine; New Hampshire; Massachusetts; Rhode Island; and Connecticut) and then return south in the fall (Berggren and Lieberman, 1978; Dorazio et al., 1994). Coastal migrants are caught seasonally in fisheries off all U.S. states between Chesapeake Bay and Canada (Boreman and Lewis 1987, Rulifson et al. 2008). Many of these fish are caught by hook and line, a method that targets feeding fish. These captures indicate that a wide range of possible foraging areas exist for coastal migrants. Although the spawning locations of migratory striped bass, the basic directions of coastal movements, and some size and sex-specific char-

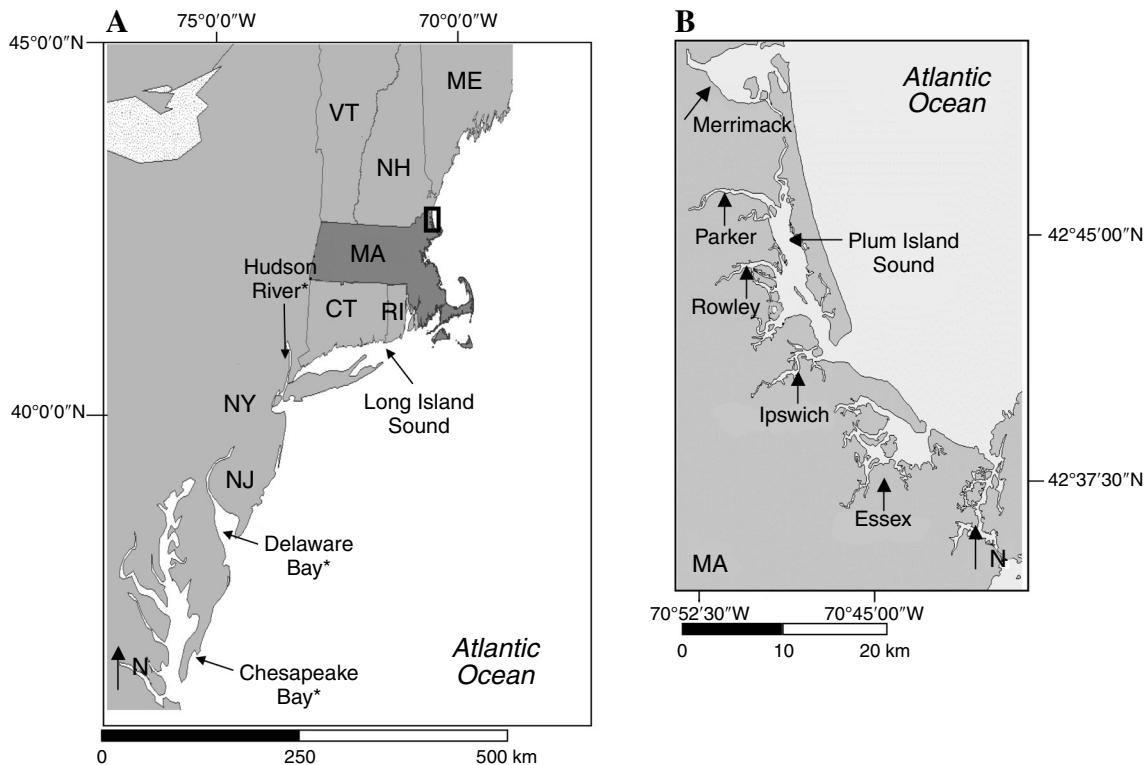


Figure 1

(A) Spawning areas and northern range of U.S. Atlantic coast striped bass (*Morone saxatilis*), the latter of which represents the largest scale by which recaptures were grouped (Massachusetts, MA). The box delineates the Great Marsh (GM). Asterisks show major spawning areas. (B) The Great Marsh in northern Massachusetts consists of the Merrimack, Parker, Rowley, Ipswich, and Essex river estuaries and represents the smaller scale by which recaptures were grouped. The arrangement of estuaries in the Great Marsh served as the basis for random model 2 (RM-2).

acteristics of migrants are known, regional patterns of coastal migration related to the use of specific summer areas by individual fish have not been identified.

Migratory fish that are present in non-natal estuaries during the nonbreeding (summer, fall) and nonoverwintering seasons are most likely feeding. Although the migratory stock of striped bass is widely distributed throughout New England in summer, the specific feeding areas for individual fish are not known. Migratory striped bass can stay and forage in a specific estuary that they encounter during migration or they may continue to move along, feeding in multiple estuaries for short periods. They also may either return to the site where they spent the previous summer or choose a different site each year from the many estuaries they encounter. We tested whether striped bass found in Massachusetts estuaries in summer migrated, how long they stayed in the non-natal estuaries where they were tagged, whether observed spatial patterns differed from the predictions of random models, whether fish returned to the same area over multiple years, and whether fishing effort alone could explain the recapture pattern.

Materials and methods

From June 1999 through November 2000, 1939 striped bass (3–5 yr old, predominately the 1996 year class) were tagged with internal anchor tags. All fish (mean total length [TL]=442 mm, standard error [SE]=7.0 mm; mean wet weight=0.91 kg, SE=0.05 kg) were caught, tagged, and immediately released along the Massachusetts coast, excluding Cape Cod (Fig. 1A). The specific estuary in which fish were tagged and released, date of tagging, total length, wet weight, and tag number of fish were recorded. Several tagging (Parker, Rowley, and Essex river estuaries) and recapture sites (Merrimack and Ipswich river estuaries; Fig. 1B) are part of the Great Marsh barrier beach dune and salt marsh estuary that includes 10,117 ha of contiguous salt marsh on the North Shore of Massachusetts.

In 1999–2007, anglers voluntarily returned tags with recapture data to the U.S. Fish and Wildlife Service (USFWS) Cooperative Striped Bass Tagging Program. These recapture data included tag number, recapture date, recapture location (state, town), and approximate size of fish. Because the anchor tag was removed as

part of the reporting procedure, for most individuals, only a single recapture record existed. An approximate location (latitude, longitude, ± 4 km) was created by assigning the recapture to the center of the nearest water body. When more information was included (e.g., mouth of the Merrimack River estuary), that datum was assigned a more specific recapture location. Most recapture records referenced specific locations and therefore there was relatively little error in estimating recapture location this way. Because most fish were recaptured by recreational anglers, tag reporting rate was likely similar across recapture locations.

By comparing release and recapture locations, we examined whether striped bass tagged in Massachusetts were part of the coastal migratory stock, whether they stayed in a localized area for a prolonged period in summer, and whether they returned to the same location after several years. To confirm the migratory status of striped bass tagged in Massachusetts, the location where tagged fish were recaptured in late fall, winter, or early spring was compared to the release location. To determine if striped bass remained in the same area throughout the summer, recapture locations in summer were compared to the location where fish were released. For this, two nonexclusive, spatial recapture scales were used: the larger Massachusetts coast area (MA; Fig. 1A) and the smaller Great Marsh area (GM; Fig. 1B). Two time periods were considered: the first season in which they were tagged (≤ 104 days and before 21 September, i.e., summer), and all times combined. Without extensive movement records on individual fish, the possibility that tagged fish moved out of the release estuary in the summer and then returned there in the fall cannot be discounted. However, to minimize this possibility, recapture records from the early (May 1 through 10 June) and late migration (22 September through 31 November) periods were excluded because these were times when migratory striped bass were hypothesized to be in transit. To determine if migratory striped bass returned to the same area in subsequent years, the number of fish that were recaptured in the area in which they were released was quantified for recaptures that occurred >12 months after release.

To examine whether the number of striped bass recaptured in their release location was different than expected by random movement models, simple, discrete time, stochastic Markov chain models were used (Agresti, 2002). These were parameterized by a series of model states (locations in the estuary or ocean where migratory striped bass could occur) connected by transition probabilities (rates at which striped bass may move between these geographic locations). Although other models have been used for animal movement, especially when large amounts of telemetry data are available (Jonsen et al., 2003; 2006), Markov chains are simple, require the least amount of data, and have been used to model biological processes (Shull, 2001; Steel et al. 2001) including movement (Hestbeck et al., 1991; Johnson et al., 2004). Furthermore, Markov chains require

few assumptions; for example, all that is needed to predict the next location of an animal with this approach is knowledge of the animal's present location.

Small-scale models were used to address how many recaptures would be expected at two scales of release (MA, GM) if striped bass movements were random. Although many movement models were plausible, the examples below provide insights into how to interpret observational recapture data for migratory striped bass. In random model 1 (RM-1), model states represented three localized, geographic locations in which a feeding, migratory striped bass could be found: 1) the target or release area (A_t at two scales, GM, MA); 2) the ocean; or 3) another adjacent area (A_o) (Fig. 2A). The probability of staying in the release or target area was p_e , the probability of leaving that area was $1-p_e$. In the first random model (RM-1), a fish must move through the ocean to get to another location. In RM-1, the probability of staying in the ocean (p_o) was 0.50, and the probabilities of staying in the two non-ocean estuaries were the same, although not necessarily 0.50 (RM-1; Fig. 2A). An assumption of RM-1 was that the fish did not prefer the release area over the adjacent area and that fish were equally likely to stay in the ocean or go to an estuary. A weekly time step was used. Transition probabilities for a striped bass in a model state always summed to 1.0.

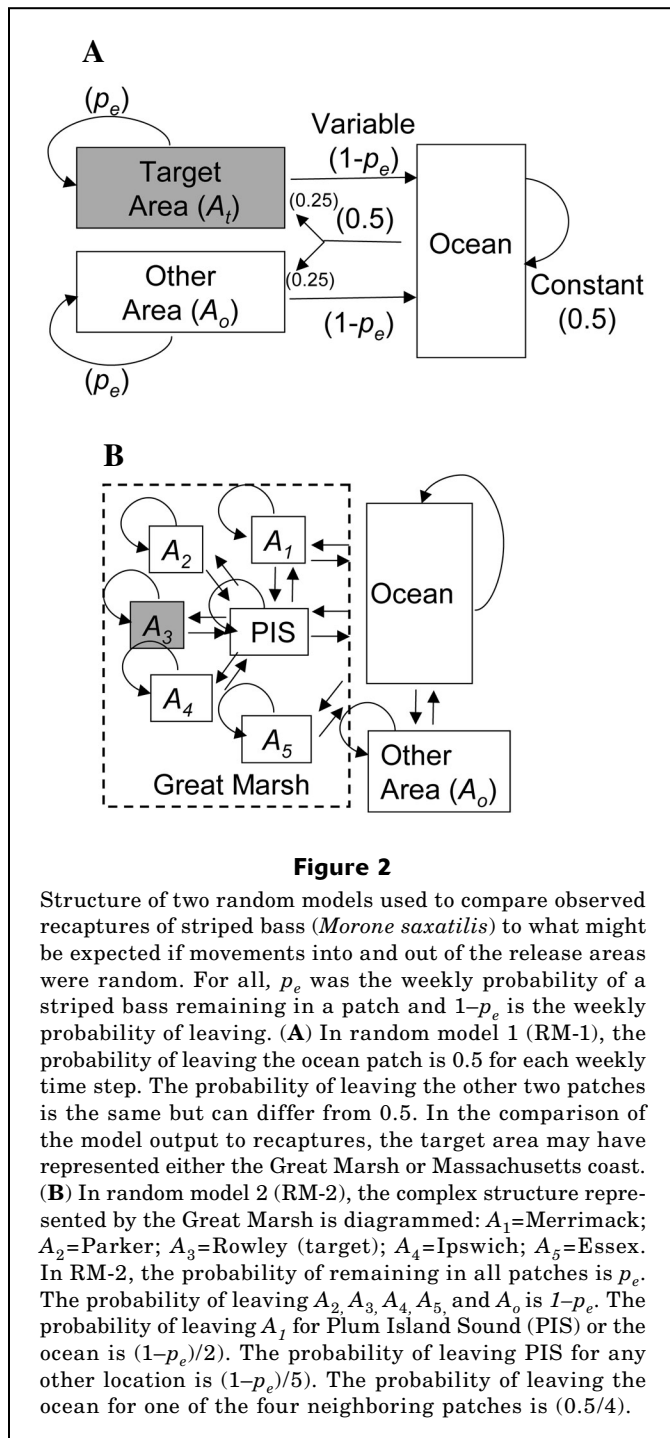
In random model 2 (RM-2), eight states were used to simulate the complexity of the Great Marsh (Figs. 1B and 2B). Four estuarine areas (A_1 – A_4) had direct connections to Plum Island Sound and represented the Merrimack (A_1), Parker (A_2), Rowley (A_3), and Ipswich (A_4) estuaries. Three of these (A_2 – A_4) were connected to the ocean through Plum Island Sound whereas the Merrimack River estuary (A_1) was also connected directly to the ocean. The Essex River (A_5) was adjacent to Plum Island Sound, connected to the ocean, but not directly connected to Plum Island Sound. Neighboring estuaries that were not part of the Great Marsh were represented by (A_o)

Both models began with the release of 100 striped bass (individuals or schools) from the target area (A_t for RM-1, or A_3 for RM-2) and continued until the numbers of migratory striped bass in each model state stabilized (10 weeks). The outcome predicted what proportion of model fish would be recaptured in the release estuary if movements in all directions were equally likely, i.e., random. P_e , the proportion of fish still in the release area after 10 weeks, was adjusted to fit observed recapture proportion data for the first summer (≤ 104 days and before 21 September). This weekly probability of fish remaining in the tagging estuary was matched against the observed recapture proportion. The observed recaptures for the Great Marsh were fitted to both models; the observed recaptures for Massachusetts were fitted only to the first, general model. Fitting to recaptures was possible because the model had only one parameter, p_e . Density dependence and intraspecific interactions were not included in these simple models. Observed and expected were compared by using χ^2 .

Equal catchability and effort were assumed because anglers made most recaptures and angler effort per mile of coastline was similar. This assumption allowed us to use a simpler model than the complex model of Hilborn (1990), which assumed unequal capture probabilities.

To test whether the recapture rate in the first summer after tagging was explained by patterns of fishing effort, data from the Marine Recreational Fisheries

Statistics Survey were used.¹ Effort data were obtained for five bimonthly periods (March–April, May–June, July–August, September–October, November–December) in 1999 and 2000, the two years that fish were tagged. For the Coastal Household Telephone Survey (CHTS), fishing effort data were obtained from shore and private-boat anglers who live in coastal counties. Correction factors, derived from an intercept survey, were used to account for trips taken by noncoastal residents, out-of-state anglers, and anglers who live in households without telephones. Data collection occurred during a two-week period at the end of each two-month sample period. For the CHTS, a computer-assisted, random digit dialing (RDD) approach was used to contact full-time residential households who were screened to determine if any household members participated in marine recreational fishing during the previous two months. Each active angler was asked to recall the number of saltwater fishing trips that were taken during the bimonthly period, as well as asked to provide details about each trip. Institutional housing, businesses, wireless phones, and pay phones were excluded from the survey. Within each state, samples were allocated among coastal counties in proportion to household populations. For each coastal county, data from the CHTS were used to estimate the average number of trips per household and then expanded by the county household population to estimate total trips. County estimates were summed and then expanded by intercept survey adjustment factors to produce state-level effort estimates. Private-boat and shore-angler modes for trips directed towards striped bass were combined for each New England state (Maine, New Hampshire, Massachusetts, Rhode Island, and Connecticut). To compare effort expended for striped bass across states, these effort estimates were divided by km of shoreline.² To assess whether recaptures in Massachusetts mirrored general trends in fishing effort, the calendar dates when striped bass were recaptured in the Great Marsh and Massachusetts were compared to the timing of fishing effort. To test whether striped bass were recaptured in Massachusetts in summer, because fishing effort did not exist elsewhere in New England, bimonthly patterns of recaptures were related to summer effort scaled by coastline for all five New England states by using a Spearman correlation.

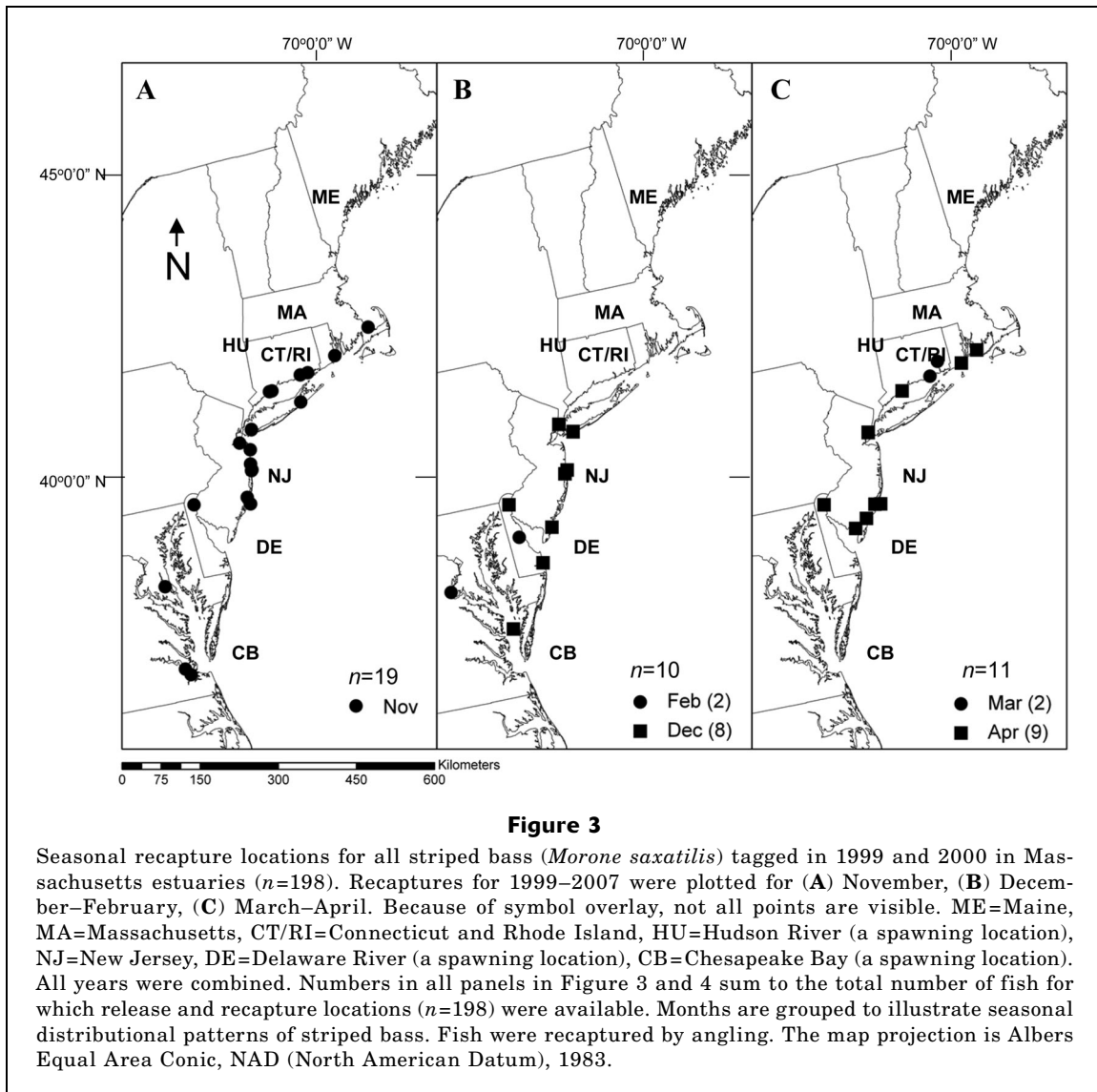


Results

Striped bass recaptures were distributed along the Atlantic Ocean coast from Maine to the Chesapeake

¹ Van Voorhees, David. Personal commun. 2000. National Marine Fisheries Service, Fisheries Statistics Division, Silver Spring, MD.

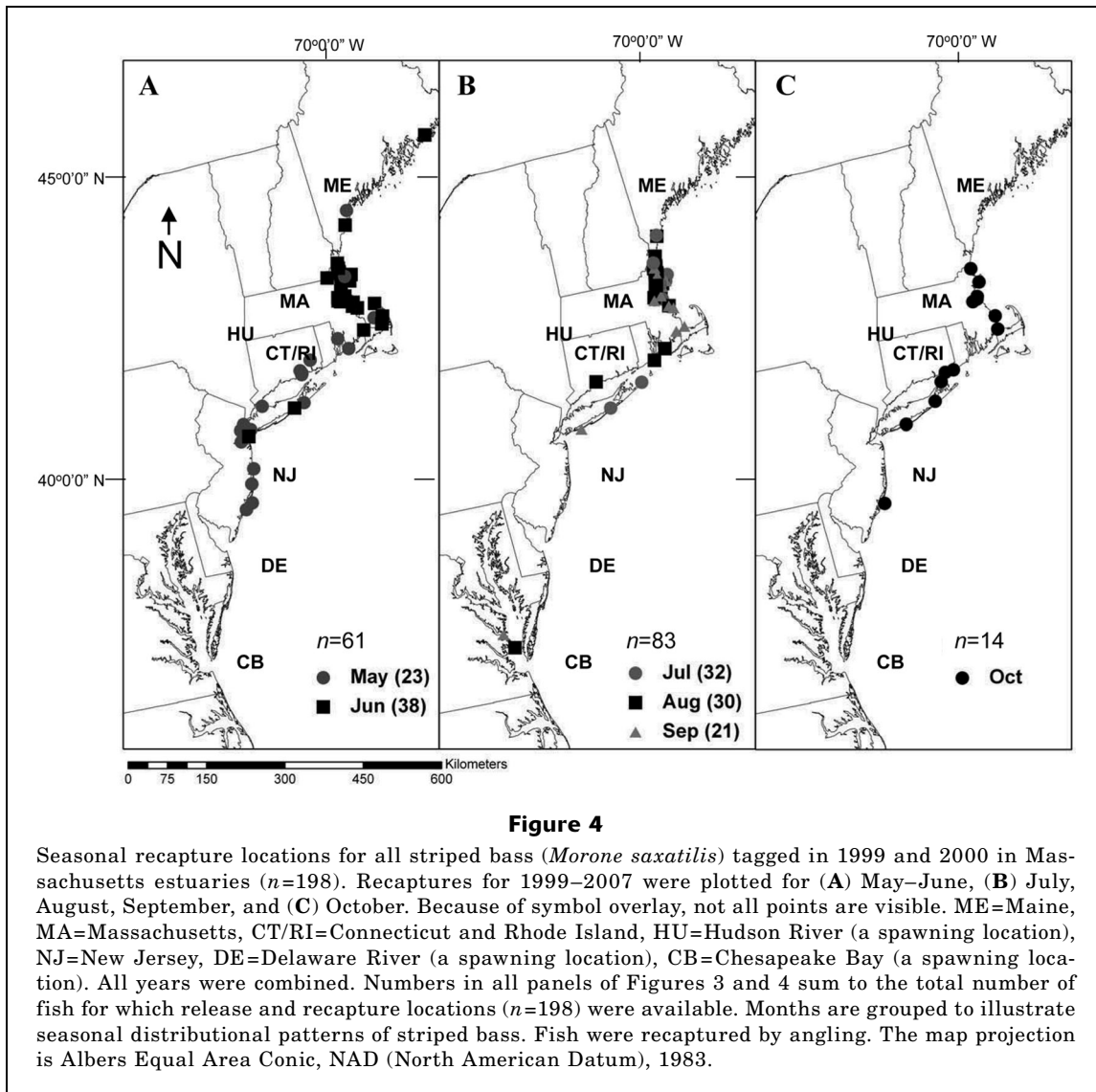
² Millhouser, W. C., J. McDonough, J. P. Tolson. 1998. Personal Commun. Report to National Oceanic and Atmospheric Administration, Managing Coastal Resources. 1315 East West Highway, Silver Spring, Maryland 20910.



Bay (Figs. 3 and 4; $n=198$), indicating that striped bass tagged in Massachusetts were migratory fish. Without exception, striped bass recaptured in the late fall, winter, and early spring (November–April) were recaptured south of where they were initially tagged and released (Fig. 3, A–C). In November (end of migration), December–February (winter), and March–April (beginning of migration), with two exceptions, all recaptures occurred south of Massachusetts. For the two exceptions still in Massachusetts waters, the fish were recaptured south of where they were released. Most recaptures were made in the spring and summer when the sport fishery was most active (Fig. 4, A and B). In May and June, recaptures for all years were distributed throughout the migratory range of striped bass from New Jersey to Maine (Fig. 4A). During July, August, and September, most tagged fish, across all years, were recaptured in Massachusetts (Fig. 4B). In October, during the fall

migration, striped bass were captured both within and south of Massachusetts (Fig. 4C). Fish recaptured in Massachusetts in October were caught south of the location where they were released.

Of the fish that were recaptured in the summer of the year that they were tagged ($n=41$, tag to recapture ≤ 104 days), most stayed where they were tagged. For example, 77% (17 of 22) of the striped bass recaptured in the Great Marsh in the first summer were released there (Table 1). The Merrimack River, the northernmost river in the Great Marsh, appeared to attract striped bass with 9% of the recaptures made there even though this estuary was not a release site. All first summer recaptures were taken along the Massachusetts coast (Table 1). No striped bass tagged in Massachusetts were recaptured in any other New England state (ME, NH, RI, CT) in the first summer after tagging (Table 1).



The summer locations of striped bass along the Massachusetts coast and in the Great Marsh were not the result of random movement. If fish were choosing either the ocean or the estuary randomly, the first model predicted that only 0.25 of the tagged striped bass would be present in the release location during the first summer. This is significantly less than the proportion observed in both the Great Marsh and along the Massachusetts coast (GM, 0.77, $\chi^2=74.6$, $df=2$, $P=0.005$; MA, 1.0, $\chi^2=151$, $df=2$, $P=0.005$). The model can be used to back calculate the required probability that striped bass remained in the estuary by adjusting p_e until the model output matches the observed proportion of observed recaptures. Based on RM-1, this approach indicated that to obtain the observed proportion of recaptures (0.77) for striped bass released and recaptured in the Great Marsh, the weekly probability that a striped bass remained in the Great Marsh was high ($p_e=0.95$; Table 2). Similarly, in order for all the observed recaptures (1.0)

to have occurred in Massachusetts during the first summer, the weekly probability of remaining in waters off the Massachusetts coast was very high, ($p_e=1.0$; Table 2). Using the more spatially complex and realistic model (RM-2), to obtain the observed proportion of recaptures (0.77) in the Great Marsh, we found that the weekly probability of striped bass remaining in the Great Marsh was again high ($p_e=0.75$; RM-2, Table 2).

Many fish were caught where they had been released in subsequent years, and this finding would indicate that these fish return to non-natal estuaries. Across all years and times of year, 38% (41 of 108) of the recaptured fish released in the Great Marsh and 61% (120 of 198) of the tagged fish released along the Massachusetts coast were recaptured where they were released (Table 1). Across all times, of the fish recaptured where they were released (41 in GM; 120 in MA), 59% (24 of 41) were recaptured in the Great Marsh and 66% (79 of 120) were recaptured in Massachusetts 2–7 years after

Table 1

Recaptures of adult striped bass (*Morone saxatilis*) tagged and released in the Great Marsh region (GM), and for all Massachusetts estuaries combined (MA). Data are shown for striped bass recaptured within the first summer of release (≤ 104 days and before 21 September), after the first summer (2–7 years after tagging), and at all times. Detailed recapture locations are divided into two spatial scales; Great Marsh (GM) and Massachusetts (MA). For example, row 1 shows that 22 fish were recaptured in the Great Marsh in the first summer and of those 17 were released there. Recapture data are shown as numbers (n) and percentages (%). Numbers for recapture across scales are not exclusive and therefore columns do not sum to total recaptures. Also shown are fish tagged and released in MA in summer and recaptured in other New England states in the first summer. ME=Maine, NH=New Hampshire, RI = Rhode Island, CT= Connecticut.

Release location	Total (n)	Recaptures							
		GM		MA		ME (n)	NH (n)	RI (n)	CT (n)
		(n)	(%)	(n)	(%)				
First year									
GM	22	17	77	22	100	0	0	0	0
MA	41			41	100	0	0	0	0
2–7 years after tagging									
GM		24							
MA				79					
Total recaptures									
GM	108	41	38						
MA	198			120	61				

Table 2

Observed proportion of first summer recaptures of striped bass (*Morone saxatilis*) in release location from field data and weekly probabilities of model fish remaining where tagged if striped bass movements were random. Observed proportions correspond to data in Table 1. For weekly probabilities of remaining, shown are two different model scenarios (RM-1 and RM-2). Data are shown for two regions of release and recapture: the Great Marsh (GM) and all Massachusetts estuaries combined (MA). P_e is the proportion that would need to remain in the recapture location each week to obtain the observed proportion of recaptures over 10 weeks.

Release location	Observed recaptures (Proportion)	GM-weekly probability of remaining where tagged		Observed recaptures (Proportion)	MA-weekly probability of remaining where tagged	
		RM-1	RM-2		RM-2	
		P_e	P_e		P_e	
GM	0.77	0.95	0.75	1.00	1.00	
MA				1.00	1.00	

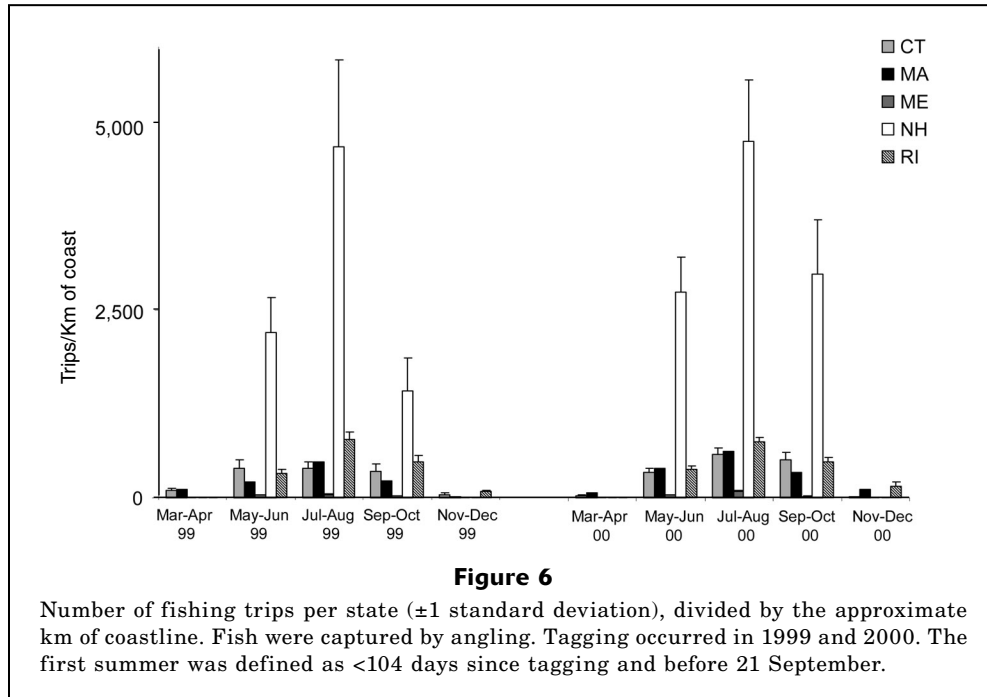
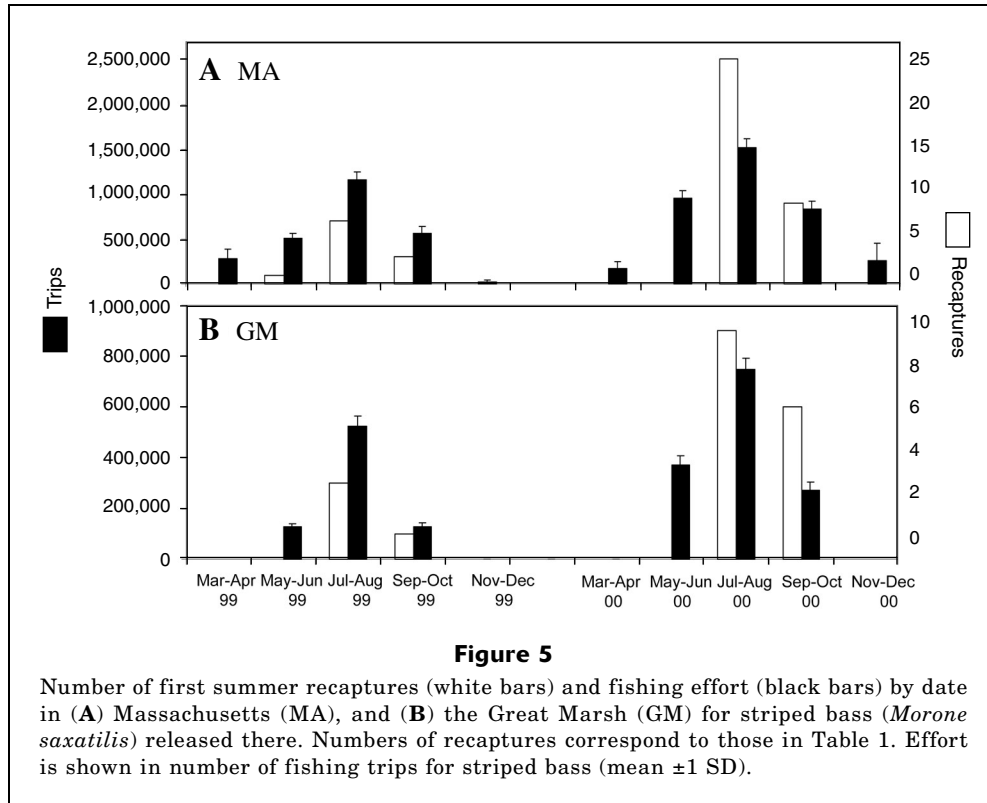
tagging (Table 1). Thus, in subsequent migration cycles, many fish were recaptured in the location where they had been tagged.

Recapture patterns were not caused by effort alone. Striped bass recaptures in both Massachusetts and the Great Marsh in the first summer after tagging were highest in July and August in 1999 and 2000 (Fig. 5, white bars), the same months when recreational fishing effort was concentrated (Fig. 5, black bars). However, when scaled by kilometer of coastline, the fishing effort for striped bass in summer was as high in Connecticut and Rhode Island as in Massachusetts and higher in New Hampshire (Fig. 6). Nevertheless, in spite of heavy effort across the entire New England coast, no striped

bass tagged in Massachusetts during the summer was recaptured in any of the other four New England states in the first summer (Spearman correlation $P=0.55$).

Discussion

Our study provides the first evidence that smaller striped bass make repeated, seasonal, long distance movements between natal and non-natal estuaries. The striped bass we tagged in Massachusetts in the summer were caught in late fall, winter, or early spring, south of the location where they had been released. If striped bass that were tagged in Massachusetts in summer were spawning or



overwintering there, they would have no reason to go south towards the traditional overwintering or spawning grounds in the late fall. In addition, 33 of 46 striped bass implanted with acoustic tags in the Great Marsh, MA, in 2006 were detected by acoustic receivers in Delaware

Bay or Long Island Sound (474–939 km one-way migration) in the winter, 2006–07 (Mather, unpubl. data). The U.S. Atlantic coast striped bass stocks that spawn in Chesapeake Bay, Delaware River, and the Hudson River have been observed previously off New England (Berg-

gren and Lieberman, 1978), but these coastal migrants were larger (>450 mm; Dorazio et al., 1994). We provide evidence that small adult striped bass, captured in Massachusetts during the summer, were also part of the coastal migratory stocks.

These recaptures of migratory fish at the location where they were tagged were much higher than our model predicted if movements were random. In this study, during the first summer after tagging, many striped bass were recaptured in a relatively small, local area (<20 km²). Striped bass recaptured in the Great Marsh (77%) used only 0.73% of the New England coastline available for feeding by migratory striped bass. Striped bass recaptured along the Massachusetts coast (100%) used only 25.1% of the New England coastline. Furthermore, no fish tagged and released in Massachusetts in summer was recaptured in other New England states in summer, in spite of high fishing effort.

These results indicate that some highly mobile striped bass that have traveled hundreds of kilometers to feed, cease their mobile lifestyle, and remain in relatively local areas (i.e., the Great Marsh or the Massachusetts coast) for a prolonged period in summer. Summer is an important period for food acquisition, and understanding why striped bass may choose one feeding area over another is critical to managing a fish that uses multiple habitats separated by hundreds of kilometers. Migration patterns of striped bass may be linked to different conditions across habitats. High temperatures, low oxygen, and inadequate prey may deter striped bass from remaining in specific habitats (Coutant and Benson, 1990; Hartman and Brandt, 1995). In addition, growth can be higher in some locations than in others (Welsh et al., 2003). As such, migration may have evolved to move striped bass away from poor conditions (e.g., high temperature, low oxygen, or poor prey conditions) or towards better foraging conditions (e.g., seasonally abundant prey, moderate water temperatures). Prey resources may be available during a longer period of physiologically suitable conditions in northern estuaries than in southern estuaries. This feature could facilitate prolonged use of feeding habitats in northern estuaries in summer.

The degree of site fidelity observed was surprisingly high given that this highly mobile fish migrates hundreds of kilometers annually, encounters tens of estuaries, and has the potential for multidirectional movement. Site fidelity has been documented in freshwater (Buzby and Deegan, 2000; McCairns and Fox, 2004), marine (Thorrold et al., 2001; Szedlmayer and Schropfer, 2005), and anadromous fish (Stewart et al., 2004; Minakawa and Kraft, 2005). However, many of these examples of site fidelity are within physically constrained riverine systems. Some site fidelity has been observed for striped bass in freshwater (Jackson and Hightower, 2001), but it has only recently been examined for coastal migrants (Wingate and Secor, 2007; this study).

Home range, or the habitats used over a period of time (day, season, year), can be a useful way of thinking about a species distribution and its relationship to

environmental conditions. The size of a home range can vary with sex, season, availability of resources, body size, feeding strategy, and group size (Baker, 1978). Although home range can be measured for any animal, the concept of home range may make little sense for animals that roam widely. For migratory fish that feed throughout their entire range or that use a large ocean feeding area, the concept of a feeding home range may have limited utility. However, a feeding home range provides a useful conceptual framework for understanding movements of fish like striped bass that may migrate between discrete spawning and feeding areas. This discrete feeding home range of individual fish can also have implications for fisheries management. Migratory fish that stay in a specific area for a prolonged time may adopt different feeding strategies based on previous experience in the estuary, and these feeding strategies may result in spatially explicit patterns of growth. In addition, local fishing pressure may influence feeding groups such that migratory fish that stay in a local area for a prolonged period may be caught and released more frequently, resulting in higher mortality. Consequently, knowing the movements of individual migratory fish in foraging areas is crucial for appropriate management.

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