Abstract—We analyzed tag returns from a long-term tagging program to evaluate the movement patterns of the Albemarle Sound–Roanoke River (AR) stock of Striped Bass (*Morone saxatilis*) during a period of stock recovery in 1991–2008. The AR stock was found to increase its movement outside the Albemarle Sound estuary (from <4% to 15–31%) as it recovered from 1991 to 2008. Analysis with multinomial logistic regression where recapture area was modeled as a function of fish size and stock abundance indicated that Striped Bass from the AR stock exhibit a strong size-dependent emigration pattern. Larger (older) adults >600 mm in total length (TL) were much more likely to emigrate to ocean habitats (after spawning) than were smaller adults (350–600 mm TL), which mostly remained in inshore estuarine habitats. Smaller adults showed evidence of density-dependent movement and were recaptured only in adjacent estuarine systems, the Pamlico Sound and lower Chesapeake Bay, during periods of increased stock abundance. Assessment and management strategies for the AR stock of Striped Bass could be improved by accounting for movement (and hence harvest) outside the currently assumed stock boundary. More broadly, this study illustrates that changes in the demographics, such as size structure and total abundance, within fish populations can result in major shifts in their distribution and that long-term tagging data are useful in detection of such population-level changes in movement patterns.

Effect of demography on spatial distribution: movement patterns of the Albemarle Sound–Roanoke River stock of Striped Bass (*Morone saxatilis*) in relation to their recovery

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The demographics of fish populations can be important in shaping their movement patterns. Numerous species have been shown to increase their distributional range or movement distances as population abundance increases (Swain and Wade, 1993; Brodie et al., 1998; Overholtz, 2002; Abesamis and Russ, 2005; Dunning et al., 2006), a response presumably due to density-dependent mechanisms (e.g., intraspecific competition for food or the saturation of optimal habitats) (MacCall, 1990). In addition, changes in movement patterns with ontogenetic changes in fish are common because habitat requirements change as species age (Werner and Gilliam, 1984; Dahlgren and Eggleston, 2000).

The demographics of fish populations are continually shifting for reasons that include changes in fishing pressure and the natural environment (e.g., recruitment variation) that can alter age structure and abundance (Longhurst, 2002; Berkeley et al., 2004; Hutchings and Baum, 2005) and in turn cause population-level changes in movement patterns. Understanding if and how population-level movements (and distribution) change over time is of particular importance for exploited fishery species because such changes can pose challenges for assessment and management techniques, for which stock boundaries are often assumed to be static and not dynamic (Winters and Wheeler, 1985; Hammer and Zimmermann, 2005; Link et al., 2011).

Striped Bass (*Morone saxatilis*) occur throughout the East Coast of the United States and have supported important fisheries there for centuries (Merriman, 1941). Tagging studies clearly have shown that spawning populations (or stocks) of Striped Bass in the mid-Atlantic region, which includes the Hudson River, Delaware River, and Chesapeake Bay, generally exhibit an anadromous life-history strategy and undergo extensive seasonal migrations. After spawning in the freshwater portion of their respective estuaries, many adults emigrate to Atlantic

Ocean waters from New Jersey to Maine in early summer, move south in the fall to overwintering habitats in coastal waters from New Jersey to Cape Lookout in North Carolina, then return to their natal estuary in subsequent springs to spawn (Boreman and Lewis, 1987; Waldman et al., 1990; Dorazio et al., 1994; Welsh et al., 2007). In contrast, the Albemarle Sound–Roanoke River (AR) stock of Striped Bass, hereafter referred to as the "AR stock," has historically been viewed as a nonmigratory stock, and most fish are believed to remain in their natal estuarine system, the Albemarle Sound estuary, throughout their lives (Merriman, 1941; Hassler et al.[1]). Indeed, in the most extensive tagging study to date on the AR stock by Hassler et al.[1], virtually all (99%) of the 2428 returns of the 9220 adults tagged in the Roanoke River during the springs of 1959–77, occurred within the Albemarle Sound estuary. The few returns that occurred outside Albemarle Sound (<1% of the total) were from an adjacent estuary (Pamlico Sound); remarkably, no returns were from ocean waters (Hassler et al.[1]).

These differences in migration patterns may have been due to differences in life-history strategies (nonanadromous vs. anadromous) between the AR stock and more northerly stocks, or it could have been a result of a historic lack of larger, older fish (>600 mm in total length [TL]) in the AR stock because of high harvest levels. Differences in life-history strategy would be perplexing given that these stocks occur in the same zoogeographic province (mid-Atlantic coast of the United States) and given that some of them are in close latitudinal proximity (e.g., the AR and Chesapeake Bay stocks). In 1988, the North Carolina Division of Marine Fisheries (NCDMF) began a cooperative tagging program with the North Carolina Wildlife Resources Commission (NCWRC) to address this question and to further investigate the migration dynamics of the AR stock of Striped Bass.

Much of the past work of tagging individuals from the AR stock was done when Striped Bass were at low levels of abundance and overfished (NCDMF and NCWRC[2]). In more recent years (1991–2008), the AR stock, as well as the Chesapeake Bay stock (Richards and Rago, 1999), made a dramatic recovery from their depleted state in the late 1970s and 1980s. The estimated total abundance of the AR stock nearly doubled during the 1990s, increasing from 1.0 to 1.9 million fish, and remained at high levels (>1.8 million fish) throughout the 2000s (NCDMF and NCWRC[2]). In addition, the age and size structure of the stock expanded as larger (>600 mm TL) and older (age 9+) fish became more prevalent as the stock recovered (NCDMF and NCWRC[2]). The recovery of the AR stock was a result of a combination of factors, namely more stringent fishing regulations that increased development to older age classes and improvements in environmental conditions that enhanced spawning habitat and recruitment of young Striped Bass (e.g., regulated river flows that were more conducive for the transport and survival of eggs and larvae) (Rulifson and Manooch, 1990; NCDMF and NCWRC[2]).

For this study, we first addressed the following question: Have Striped Bass of the AR stock increased their movement outside of the Albemarle Sound estuary since population rebuilding in the 1990s? After showing that the movement of the AR stock out of the estuary has indeed increased, we then related recapture locations of tagged individuals to both fish size and total annual stock abundance (density) in an effort to explain this increase in emigration over the past 2 decades (1991–2008). Lastly, we discuss the management implications of this increased movement given the stock is currently considered to be resident.
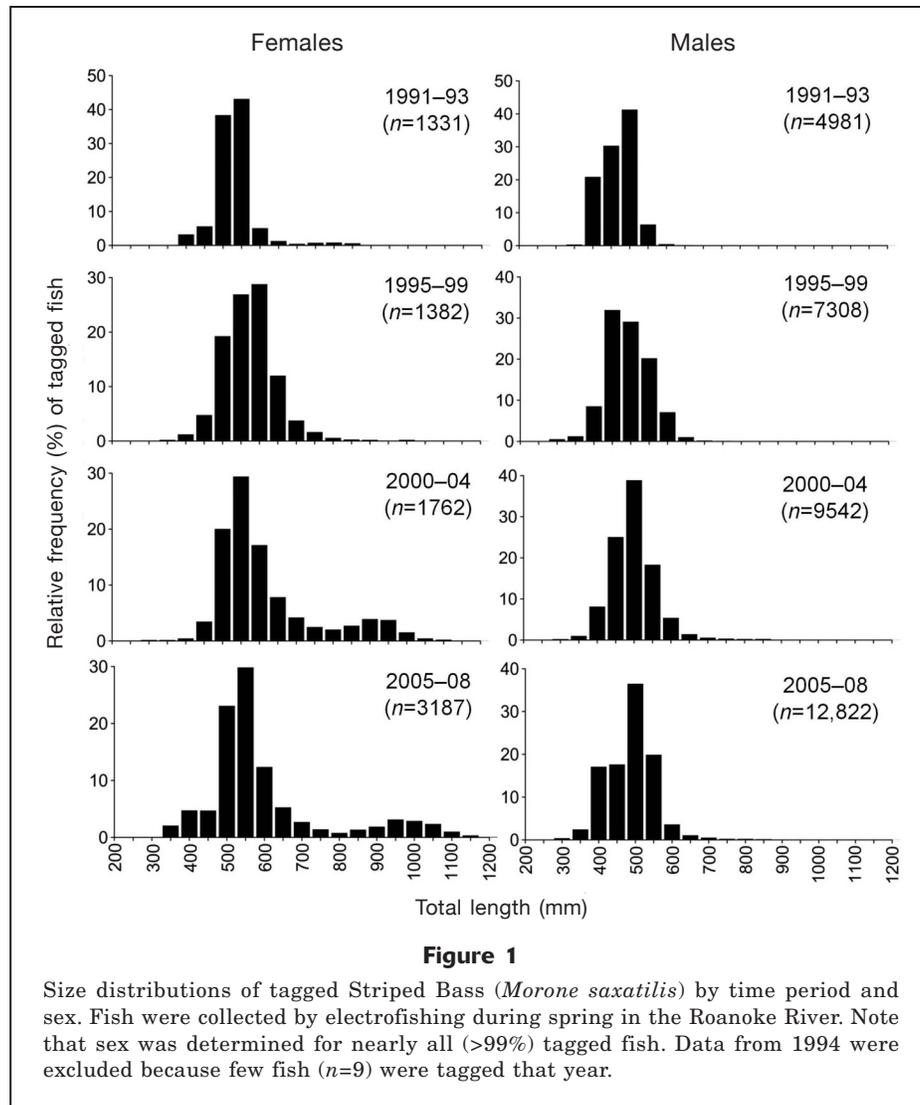
Materials and methods

Fish tagging

During the springs of 1991–2008, 42,534 adult Striped Bass from the AR stock (mostly >350 mm TL; Fig. 1) were tagged and released on their well-described spawning grounds (Hassler et al.[1]) ~200 km upstream of the mouth of the Roanoke River in North Carolina (Fig. 2A). During weekly sampling events throughout April and May, Striped Bass were collected with an electrofishing boat and transported to a tagging vessel, where they were held in a "live well" until processing. Fish in good condition were measured (TL to the nearest millimeter), weighed (to the nearest gram), and sex was determined by expression of gonadal products. The fish were then tagged just above the posterior tip of the pelvic fin with a Floy (model FM-84[3]) internal anchor tag (Floy Tag, Inc., Seattle, WA). Fish were immediately released after tagging. The streamer of the tags indicated a "reward" (US $5 or a baseball cap) would be offered for reporting information on recaptured Striped Bass (e.g., recovery date and location, and tag number)

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[1] Hassler, W. W., N. L. Hill, and J. T. Brown. 1981. The status and abundance of striped bass, Morone saxatilis, in the Roanoke River and Albemarle Sound, North Carolina, 1956–1980. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Special Scientific Report 38, 156 p. [Available from the Division of Marine Fisheries, 3441 Arendell St., Morehead City, NC 28557.

[2] NCDMF (North Carolina Division of Marine Fisheries) and NCWRC (North Carolina Wildlife Resources Commission). 2013. Amendment I to the North Carolina Estuarine Striped Bass Fishery Management Plan, 420 p + appendices. North Carolina Division of Marine Fisheries, North Carolina Department of Environment and Natural Resources, Morehead City, NC. [Available from http://portal.ncdenr.org/c/document_library/get_file?uuid=d3fdf967-82d5-4653-8b79-20247c5ed5ad&groupId=38337, accessed January 2014.]

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

Figure 1

Size distributions of tagged Striped Bass (*Morone saxatilis*) by time period and sex. Fish were collected by electrofishing during spring in the Roanoke River. Note that sex was determined for nearly all (>99%) tagged fish. Data from 1994 were excluded because few fish (*n*=9) were tagged that year.

to the NCDMF, whose contact information was printed on the tag.

Data analysis

We used multinomial logistic regression to evaluate the effects of fish size and stock abundance on the recapture location (i.e., to evaluate the movements) of Striped Bass of the AR stock. For this analysis, recapture locations of tagged fish were assigned to 1 of 4 broad geographic areas: 1) the Albemarle Sound estuary, 2) the Pamlico Sound estuary, 3) ocean waters of North Carolina, or 4) northern coastal waters from Virginia to Massachusetts (Fig. 2B). Therefore, recapture area constituted a multicategory response variable. Explanatory variables were fish size (TL at tagging) and total annual abundance of the AR stock (1991–2008). Annual abundance estimates (of age 1+ fish) were obtained from a statistical catch-at-age

model from the most recent AR stock assessment (NCDMF and NCWRC[2]) and served as a proxy for the annual densities of conspecifics (AR stock only) with which tagged Striped Bass were expected to interact each year. Sex was not included as an explanatory variable because it was confounded with fish size beyond 800 mm TL because all but 4 tag returns from this size range were from females. However, across smaller sizes (400–800 mm TL), over which sexes were more equally represented, similar-size males and females were generally recaptured in the same areas, indicating that movements differed little between sexes.

For the purpose of our analyses, we included only tag returns that occurred after the first 2 weeks but within the first calendar year at liberty. By restricting returns to those returns that occurred within the first calendar year at liberty (on or before 31 December), movement between tagging and recapture loca-
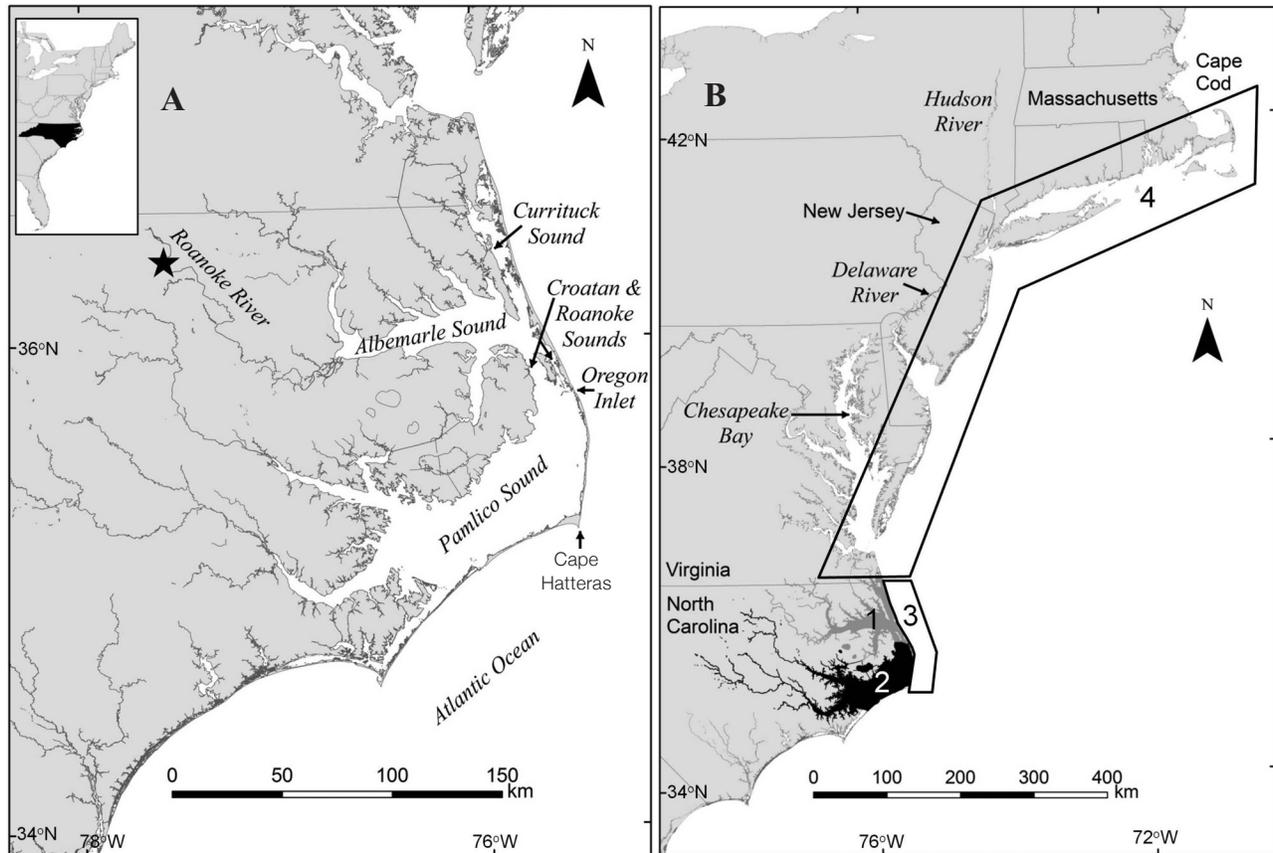
Figure 2

(A) Capture and release location (represented by the star in the upper Roanoke River) of tagged Striped Bass (*Morone saxatilis*) during the period of 1991–2008 and reference map for waterbodies in coastal North Carolina. **(B)** Geographic areas of recapture used in data analyses: 1) Albemarle Sound estuary (area shaded in gray), 2) Pamlico Sound estuary (area shaded in black), 3) North Carolina ocean waters (box 3), and 4) northern coastal waters (box 4).

tions could be known to occur during a given year. This restriction allowed movements (recapture area) to be directly related to stock abundance, which was estimated on an annual basis (i.e., each calendar year) from 1991 to 2008, the terminal year in the assessment. In addition, restriction of returns to a relatively short time period at liberty (<9 months) minimized the opportunity for growth between tagging and recapture, thereby ensuring that fish lengths at tagging (the size variable used in our analyses) were representative of the size of fish when movement occurred.

To reach another recapture area (outside the Albemarle Sound estuary), tagged fish would have had to travel a considerable distance (>300 km) from their release site in the upper Roanoke River. Therefore, to reduce the likelihood of underestimation of fish movement, we excluded tag returns from the first 14 days at liberty, affording tagged fish a more realistic period of time to complete movement or migration to another system. Indeed, the earliest tag return from outside the Albemarle Sound estuary (in North Carolina ocean waters) occurred at 16 days after tagging, providing justification for our 14-day exclusion window. Finally, data from 1994 were excluded from analyses because of reduced tagging efforts in that year (only 9 fish were tagged and 1 returned).

To determine which explanatory variables affected movements of Striped Bass and to assess their relative importance, we used an information-theoretic approach. A multinomial logistic regression model was run for each of the 5 possible combinations of explanatory variables: 1) length, abundance, length×abundance (interaction model), 2) length and abundance, 3) length only, 4) abundance only, and 5) intercept only (no effects model). Akaike's information criterion (AIC) values were obtained for each candidate model. We considered the model with the lowest AIC value as the most parsimonious or "best," but we also computed additional diagnostics, Akaike differences (Δ_i) and Akaike weights (w_i), to assess how other models performed in comparison to this single best model (Burnham and Anderson, 2002). The first of these other diagnostics was calculated as

$$\Delta_i = AIC_i - AIC_{\min},$$

where AIC_i = the AIC value of a given model (i); and
      AIC_{min} = the AIC value of the best model (mini-mum AIC).

As a general guideline, models with Δ_i close to zero have considerable empirical support, models with Δ_i of 4–7 have much less support, and models with Δ_i of 9–14 have little support (Anderson, 2008). The following equation was used to calculate w_i values:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)}.$$

Note that R refers to the set of models being evaluated. Values of w_i can be interpreted as the probability that a particular model (i) is the best model for the data set given that one of the models must be selected as the best (Anderson, 2008).

We based our inferences on parameter estimates from the model (i.e., on the combination of explanatory variables) deemed most parsimonious from AIC diagnostics. For example, if the third model (length effect only) was determined to be the best model, values of the parameters (i.e., regression coefficients) that represented the effect of fish length were used to calculate the predicted relative probability of Striped Bass being recovered in each recapture area as a function of their

size at tagging. We assessed the fit of the best model through the use of both Pearson and deviance good-ness-of-fit tests. Because explanatory variables were continuous, it was necessary to group data for these tests (Agresti, 1996). For this purpose, we used 100-mm bins and abundance bins of 0.1 million fish. All statistical analyses were performed in SAS, vers. 9.1.3 (SAS Institute, Inc., Cary, NC) with α =0.05.

Results

Tag return summary

From 1991 to 2008, 1197 tagged Striped Bass were reported as having been recaptured within their first 9 months at liberty (late April–December); analyses conducted for this study were based on data from these individuals. Hook-and-line (recreational) anglers accounted for a majority (84%) of tag returns. Although most returns (80%) were from fish 400–600 mm TL (at tagging), fish lengths ranged from 287 to 1105 mm TL. Moreover, nearly all tag returns (154 of 156) of larger Striped Bass (>600 mm TL) were from years in which stock abundance exceeded 1.5 million fish (Table 1).
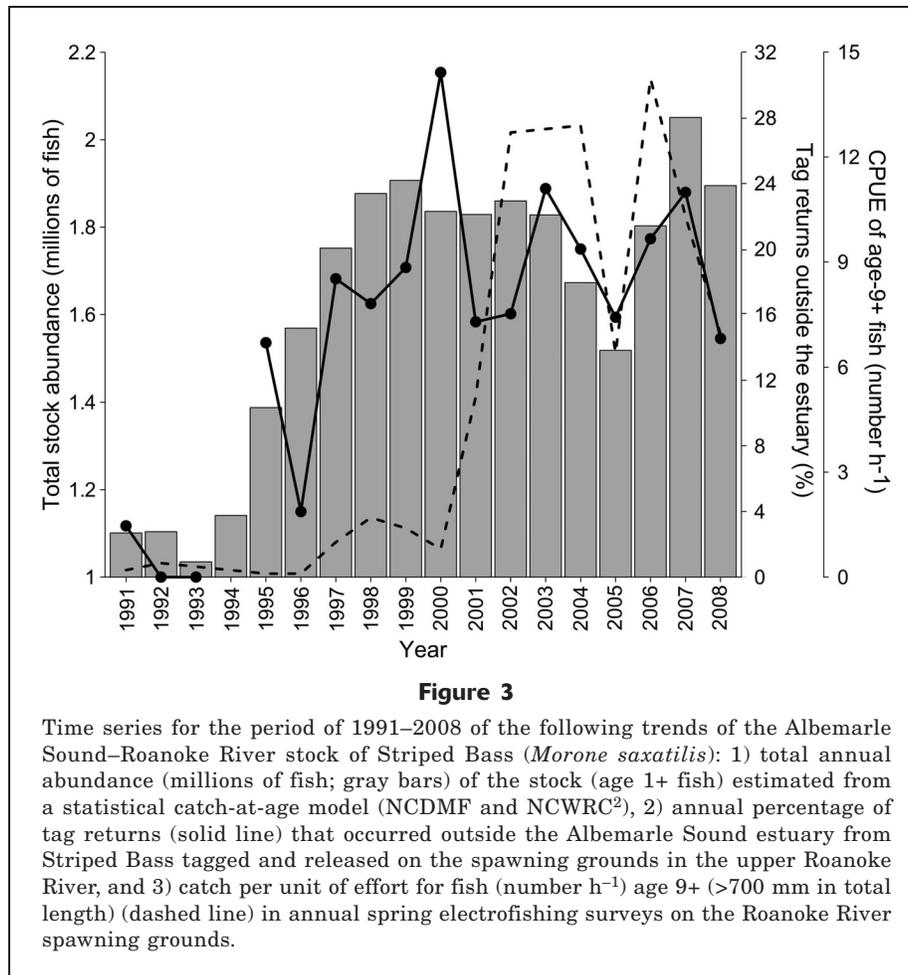
Temporal recapture trends

The AR stock of Striped Bass increased their movement outside of the Albemarle Sound estuary as the

Table 1

Number of tag returns of Striped Bass (*Morone saxatilis*) per combination of total annual stock abundance (millions of fish) and interval of total length (TL) at tagging. Annual abundance estimates (1991–2008) of Albemarle Sound–Roanoke River Striped Bass were obtained from a statistical catch-at-age model (NCDMF and NCWRC[2]). Only those tag returns occurring after the first 2 weeks but within the first calendar year at liberty were included in data analyses and are enumerated here. "–"=no tag returns for that year.

Abundance (millions)	Year	Number of returns per size (mm TL) interval							
		<400	400–499	500–599	600–699	700–799	800–899	900–999	>1000
1.035	1993	–	37	15	–	–	–	–	–
1.101	1991	10	17	5	–	–	–	–	–
1.104	1992	2	48	7	1	1	–	–	–
1.388	1995	–	4	17	–	–	–	–	–
1.518	2005	1	68	36	7	2	–	6	–
1.569	1996	4	7	13	1	–	–	–	–
1.673	2004	–	17	8	–	1	3	1	–
1.752	1997	6	38	28	4	1	–	–	–
1.803	2006	–	54	80	6	5	3	9	3
1.828	2003	7	20	36	7	2	1	3	–
1.829	2001	1	35	38	12	2	2	–	–
1.836	2000	1	29	16	4	2	–	–	–
1.860	2002	2	27	39	4	7	1	–	1
1.877	1998	4	41	23	7	3	–	–	–
1.895	2008	38	42	13	3	–	3	5	6
1.907	1999	1	29	17	5	1	–	–	–
2.051	2007	–	19	40	11	3	1	5	2

Figure 3

Time series for the period of 1991–2008 of the following trends of the Albemarle Sound–Roanoke River stock of Striped Bass (*Morone saxatilis*): 1) total annual abundance (millions of fish; gray bars) of the stock (age 1+ fish) estimated from a statistical catch-at-age model (NCDMF and NCWRC[2]), 2) annual percentage of tag returns (solid line) that occurred outside the Albemarle Sound estuary from Striped Bass tagged and released on the spawning grounds in the upper Roanoke River, and 3) catch per unit of effort for fish (number h^{-1}) age 9+ (>700 mm in total length) (dashed line) in annual spring electrofishing surveys on the Roanoke River spawning grounds.

population rebuilt over the past 2 decades (1991–2008). In the early 1990s, few tag returns occurred outside the Albemarle Sound estuary: <4% annually across the years of 1991–96, with the exception of 1995 (Fig. 3). However, as the stock increased in abundance and its age structure expanded, returns from regions outside the Albemarle Sound estuary increased considerably and ranged from 15% to 31% annually during the years of 1997–2008 (Fig. 3).

Effects of fish size and stock abundance on recapture area

Fish size and stock abundance affected recapture area. The best multinomial logistic regression model included the main effects of both fish length and stock abundance but not their interaction (Table 2). Goodness-of-fit tests indicated this model fitted the sample data well (Pearson goodness of fit, χ^2=117, degrees of freedom=126, P=0.70; deviance goodness of fit, χ^2=104, degrees of freedom=126, P=0.93). Although the best model showed that recapture area depended on both fish size and stock abundance, AIC diagnostics across the suite of models indicated that fish length exerted a much stronger effect than abundance. Specifically,

the model that included only fish length had moderate empirical support (Δ_i=3.8, w_i=0.12), but the model that included stock abundance alone had very little support (Δ_i=462.2, w_i=0) (Table 2).

Striped Bass of the AR stock exhibit a strong size-dependent migration pattern, whereby both the incidence of emigration and the distance emigrants move increase with fish size. The best model predicted that the probability of emigration from (i.e., recapture outside) the Albemarle Sound estuary increased dramatically with fish size. Specifically, the probability of recapture within Albemarle Sound declined sharply (from values >90%) beyond 600 mm TL, the size at which recapture probabilities began to increase in other areas, such as Pamlico Sound and ocean waters (Fig. 4). The model predicted that Striped Bass 700–800 mm TL in length were most likely to be recaptured in ocean waters of North Carolina (Fig. 4C) and that the largest fish (>850 mm TL) were most likely to be recaptured in the northern coastal region (Fig. 4D).

Empirical tag return data supported the movement pattern indicated by the best model. Nearly all (92%) of the tag returns of smaller fish (<600 mm TL;

Table 2

Diagnostics with Akaike's information criterion (AIC) for candidate multinomial logistic regression models that relate the recapture area (Albemarle Sound estuary, Pamlico Sound estuary, North Carolina ocean waters, or northern coastal waters from Virginia to Massachusetts) of tagged Striped Bass (*Morone saxatilis*) to fish length and total annual stock abundance for the years 1991–2008. Each model represents a different combination of these explanatory variables. Note that Δ_i=Akaike's differences and w_i=Akaike's weights, where lower values of Δ_i and higher values of w_i indicate greater relative empirical support for a model.

Model	AIC	Δ_i	w_i
Length + abundance	1003.2	0.0	0.80
Length only	1007.0	3.8	0.12
Length + abundance + length x abundance	1007.8	4.6	0.08
Abundance only	1465.4	462.2	0.0
Intercept only	1496.1	492.9	0.0

n=1040) occurred within the Albemarle Sound estuary (Fig. 5A). Yet, only 47% of returns of fish 600–799 mm TL (n=102) and 2% of returns of fish >800 mm TL (n=55) occurred in Albemarle Sound; most tag returns of these larger fish occurred in ocean waters (Fig. 5, B and C). Interestingly, the majority (78%) of tag returns of the largest fish in this study (800–1105 mm TL) occurred in distant coastal waters from New Jersey to Cape Cod, 780 to 1250 km from the release site (Fig. 5C).

Stock abundance also affected the areas in which Striped Bass were recaptured. The best model predicted a slight increase (~5%) in recapture of small Striped Bass (<600 mm TL) in the Pamlico Sound region as stock abundance increased from 1 to 2 million fish (Fig. 4B). This trend also was evident in empirical tag return data. Returns from the Pamlico Sound estuary, ~6% of all returns, occurred only during years in which stock abundance exceeded 1.4 million fish. There were no returns from the Pamlico Sound estuary during years of lower abundance (1.0–1.1 million fish) (Fig. 6).
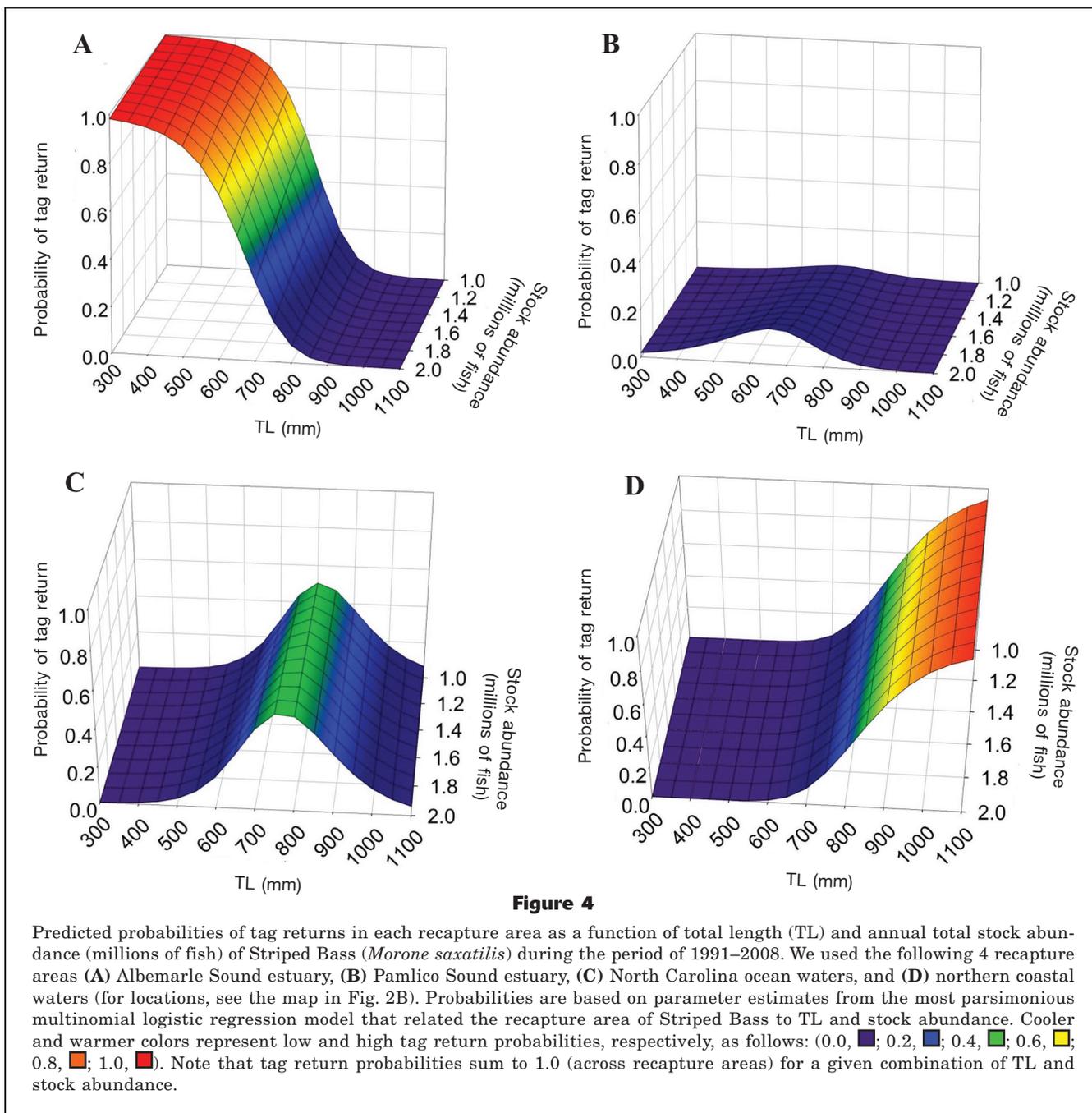
Discussion

Continuous tagging over a 20-year period, a length of effort that is rare in most fisheries, allowed us to determine the strong effect of fish size and relatively smaller effect of stock abundance on a fish stock's spatial distribution. Multiple stocks of Striped Bass co-occur along the East Coast of the United States during nonspawning periods. Therefore, by tagging fish on their natal spawning grounds (when stocks are separated), we were able to investigate stock-specific movements and spatial distribution—information that could otherwise not have been resolved with approaches such as fisheries-independent surveys (e.g., trawl surveys). In this section, we provide further details on the effects of fish size and stock abundance on the spatial distribution of the AR stock of Striped Bass and on the implications for management of Striped Bass.

Effects of fish size on recapture area

The increase in tag returns of the AR stock from regions outside its natal estuary over the past 2 decades was largely due to expansion of the age and size structure of the stock as it recovered. The majority of returns (67%) that occurred outside the Albemarle Sound estuary during the stock recovery period were from ocean waters. Model results and empirical data both showed the probability of Striped Bass being recaptured in ocean waters increased dramatically with fish size beyond 600 mm TL, to the point where the largest individuals (>800 mm TL) were almost exclusively captured in ocean waters. Therefore, it is not surprising that returns from ocean waters increased over the past 2 decades as more fish from this largest size class (which was the class most likely to emigrate to ocean habitats) became available for tagging and recapture as the age and size structure of the AR stock expanded.

The strong size-dependent emigration pattern of Striped Bass revealed by this study helps explain the lack of recaptures in ocean waters by Hassler et al.[1], who also focused on the AR stock. To collect fish for tagging, Hassler et al.[1] primarily used small-mesh (<150 mm stretched) gill nets that likely selected for smaller fish. Indeed, of the 2428 returns in their study, most (86%) were from fish 400–550 mm TL at tagging, and only 2 returns (<0.1%) were from fish >800 mm TL at tagging. Moreover, the vast majority (88%) of tag returns in their study occurred within the first year at liberty. Therefore, given the small sizes of tagged fish and short-term nature of returns (i.e., small tagged fish did not have time to grow into larger size categories because of high har-

Figure 4

Predicted probabilities of tag returns in each recapture area as a function of total length (TL) and annual total stock abundance (millions of fish) of Striped Bass (*Morone saxatilis*) during the period of 1991–2008. We used the following 4 recapture areas **(A)** Albemarle Sound estuary, **(B)** Pamlico Sound estuary, **(C)** North Carolina ocean waters, and **(D)** northern coastal waters (for locations, see the map in Fig. 2B). Probabilities are based on parameter estimates from the most parsimonious multinomial logistic regression model that related the recapture area of Striped Bass to TL and stock abundance. Cooler and warmer colors represent low and high tag return probabilities, respectively, as follows: (0.0, ■; 0.2, ■; 0.4, ■; 0.6, ■; 0.8, ■; 1.0, ■). Note that tag return probabilities sum to 1.0 (across recapture areas) for a given combination of TL and stock abundance.

vest), the lack of ocean recaptures by Hassler et al.[1] is not surprising. Nearly all fish recaptured in their study (>99%) were smaller than the size at which appreciable ocean emigration occurs (>800 mm TL), as indicated in our study.

Although other factors, such as prey availability and susceptibility to predation, may be involved, water temperature appears to be a salient factor in explanation of the size-dependent migration and distribution patterns of the AR stock. A change in tempera-

ture preferences with fish size has been hypothesized to be the main driver of the size-dependent emigration pattern observed previously for other stocks of Striped Bass (Coutant, 1985), especially the Chesapeake stock (Dorazio et al., 1994; Secor and Piccoli, 2007).

Decreases in temperature optima with fish size can be explained by bioenergetic principles. Specifically, the temperature threshold beyond which the increase in total metabolic load starts to become stressful (i.e., the point at which the scope for activity and growth begins
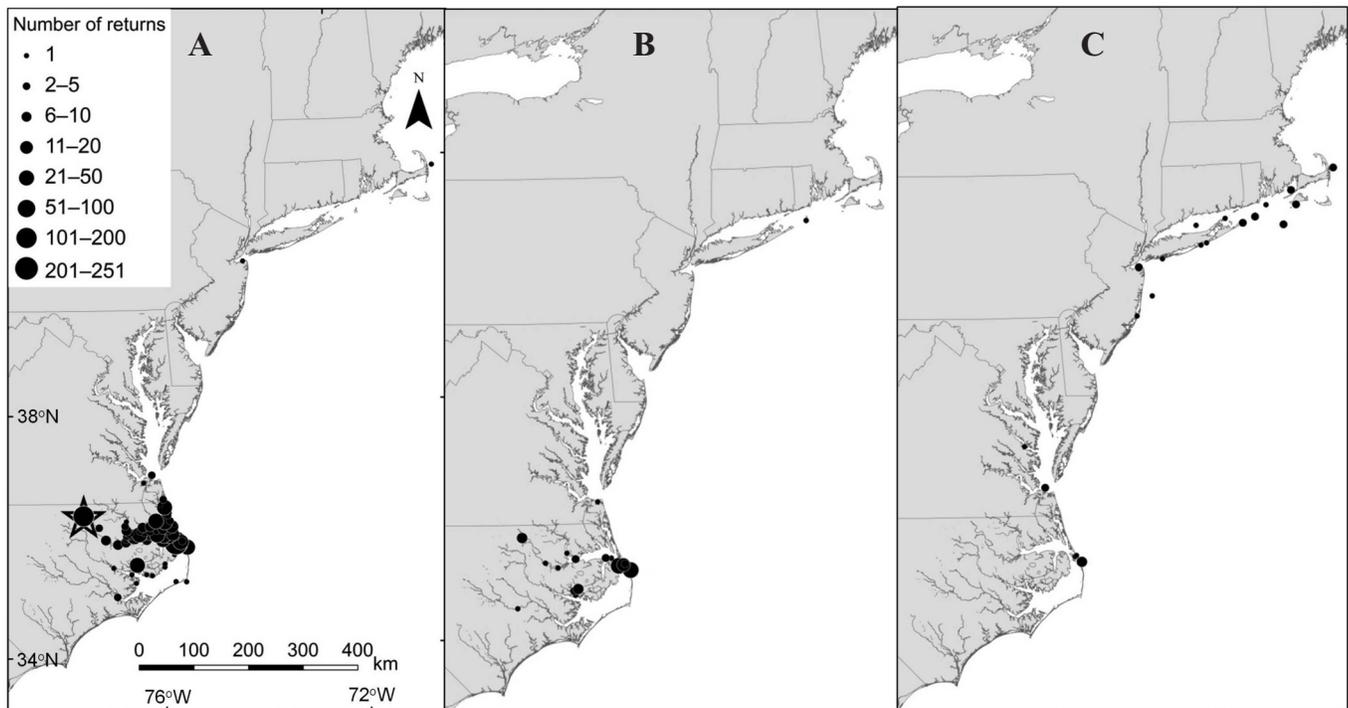
Figure 5

Tag return locations of Striped Bass (*Morone saxatilis*) along the eastern seaboard of the United States by length group (data pooled across years): **(A)** fish 287–599 mm in total length (TL) (*n*=1020 returns), **(B)** fish 600–799 mm TL (*n*=101 returns), and **(C)** fish 800–1105 mm TL (*n*=55 returns). Bubble sizes represent the number of tag returns from each location (within each length group). The star in panel A denotes the location where Striped Bass were tagged and released during annual spring electrofishing surveys conducted in the Roanoke River in 1991–2008. Only those tag returns that occurred after the first 2 weeks but within the first calendar year at liberty were included in analyses and are shown. The location of 21 tag returns (of the 1197 total) could be assigned only to 1 of the 4 broad geographic recapture areas (shown in Fig. 2B) and are, therefore, not shown.

to decline) occurs at progressively lower temperatures as fish size increases because larger individuals have a greater total metabolic demand than smaller individuals on the basis of body size alone (Hartman and Brandt, 1995). Therefore, after spawning, most large Striped Bass may emigrate, as we found, to cooler northern ocean habitats, which would provide a metabolic reprieve, rather than spend their summers in warm estuarine waters.

Interestingly, Striped Bass of the AR stock in the intermediate size range of 700–850 mm TL, were mainly recaptured in ocean waters off North Carolina, from the Oregon Inlet north to the border of North Carolina and Virginia. No Striped Bass were recaptured in ocean waters south of Cape Hatteras, where summer temperatures (>26°C; http://www.ndbc.noaa.gov, Station#41036) are similar to summer temperatures in Albemarle Sound. Therefore, nearby ocean waters may provide an adequate thermal refuge (23–26°C; http://www.ndbc.noaa.gov, Station#44100) during summer for Striped Bass in the size range of 700–850 mm TL. One intriguing question is whether the size at which the onset of ocean emigration occurs will shift to a smaller size as inshore estuarine waters, which already approach 30°C in sum-

mer (http://waterdata.usgs.gov, Gage#0208114150), are expected to continue warming under current projections for climate change (IPCC, 2007). Continuation of the long-term tagging program on the AR stock of Striped Bass could help address this question.

Previous research on northern stocks of Striped Bass has provided evidence for diverse lifetime migration patterns: some members of a given population reside in freshwater or estuarine environments throughout their life (resident contingent) and others are more exploratory and engage in large-scale coastal migrations (migratory contingent) (Clark, 1968; Secor, 1999). There is particularly strong evidence for this "contingent" behavior in Striped Bass in the Hudson River (Secor and Piccoli, 1996; Secor et al., 2001; Zlokovitz et al., 2003). Our study, however, provides little indication of this phenomenon in the AR stock of Striped Bass. If contingent behavior had been prevalent, one would have expected that some large fish would have remained and been recaptured in the Albemarle Sound after spawning. Yet, of the 50 fish exceeding 855 mm TL that were recovered in our study, none were recaptured within Albemarle Sound and, instead, all were taken in the ocean. It is possible that contingent behavior is not
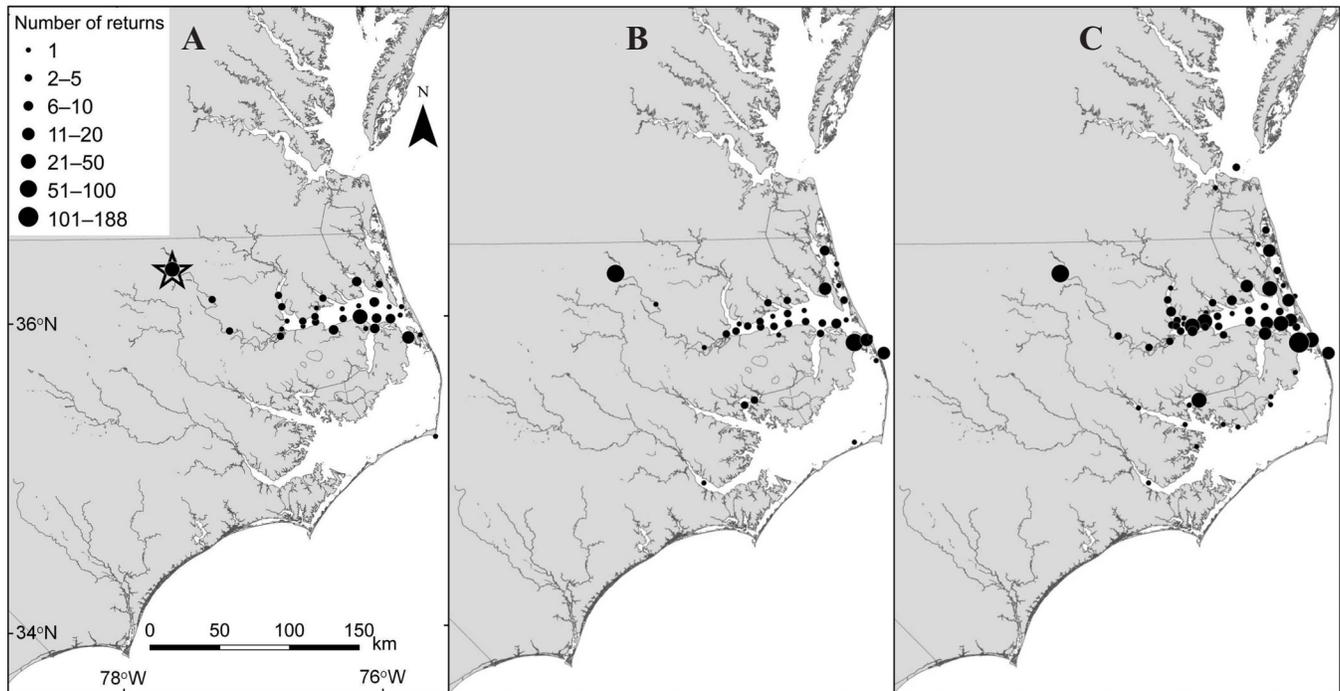
Figure 6

Tag return locations of Striped Bass (*Morone saxatilis*) <600 mm in total length in North Carolina and Virginia coastal waters by stock abundance in the year of release: **(A)** annual abundance values of 1.0–1.1 million fish (*n*=138 returns), **(B)** annual abundance values of 1.4–1.7 million fish (*n*=169 returns), and **(C)** annual abundance values of 1.8–2.0 million fish (*n*=713 returns). Bubble sizes represent the number of tag returns from each location (within each abundance group) as indicated in the legend. The star in panel A denotes the location where Striped Bass were tagged and released during annual spring electrofishing surveys in the Roanoke River in 1991–2008. Only those tag returns that occurred after the first 2 weeks but within the end of the first calendar year at liberty were included in analyses and are shown. The location of 20 tag returns (of the 1040 total) could be assigned to only 1 of the 4 broad geographic recapture areas (shown in Fig. 2B) and are, therefore, not shown.

beneficial, and, therefore, it does not manifest in the AR stock because of high inshore water temperatures during summer that would be unsuitable for "resident" fish once they attain a large size. The possibility for latitudinal differences in the frequency of contingent behavior in Striped Bass and other fishes warrants future investigation.

Effects of stock abundance on recapture area

Stock abundance in the year of release was included in the best model explaining where Striped Bass were recaptured. This effect was primarily a result of smaller Striped Bass being recaptured in the adjacent estuarine systems of Pamlico Sound and lower Chesapeake Bay only in the years of highest abundance (Fig. 6C). Also, evidence of recapture patterns within the Albemarle Sound estuary were indicative of a density effect. Namely, tag returns were much more common in the eastern portions of Albemarle Sound, particularly in Currituck Sound (6% vs. 1% of returns) and Croatan and Roanoke sounds (32% vs. 6%), during years in which stock abundance exceeded 1.4 million fish in contrast to years when it was

below this level (Fig. 6). Therefore, although adults generally may remain inshore until they reach larger sizes (>600 mm TL), the distances they disperse *within* estuarine habitats, after spawning, tend to increase with the abundance of conspecifics, presumably because of density-dependent mechanisms. These movements likely are important ecologically to prey of Striped Bass because the smallest size groups (<600 mm TL) are the most numerous in this population (i.e., predation effects may change with stock abundance). Future research should investigate these possibilities and better isolate the effects of density by controlling for environmental covariates, such as the abundance of competitor species and changing habitat suitability, as suggested by Shepherd and Litvak (2004).

Management implications

Results from this study have important implications for the management of Striped Bass along the East Coast of the United States. With current assessment strategies, Striped Bass from the AR stock are assumed not to contribute to the Atlantic Ocean mixed stock

fishery (ASMFC[4]). However, this study revealed that some members of the AR stock, those fish surviving to sizes >800 mm TL, are indeed migratory and, therefore, unequivocally contribute to (i.e., are harvested by) the mixed stock fishery of the Atlantic coast. Because management benchmarks for the mixed stock fishery, such as the threshold fishing mortality (F_{MSY}=0.41; ASMFC[4]), currently are based on data from Chesapeake, Hudson, and Delaware stocks that are potentially more productive than the AR stock, it is possible that the mixed stock fishery could affect the AR stock disproportionately. Accordingly, future research should establish the productivity of the AR stock of Striped Bass in relation to other stocks. If the AR stock is found to be less productive, then future work also should determine the implementation costs of more stringent fishing regulations in the mixed stock fishery, namely the amount and value of harvest that would be lost from more productive stocks (Chaput, 2004; Crozier et al., 2004; Hilborn et al., 2004).

Results from this study also have implications for the assessment and management of Striped Bass within North Carolina. Currently, landings of Striped Bass outside the Albemarle Sound estuary (region 1; Fig. 2B) are not included in the AR stock assessment (NCDMF and NCWRC[2]). Stock status is based on the estimate of fishing mortality ($F_{threshold}$=0.27) for fully recruited Striped Bass of age 4–6 and 400–600 mm TL, a size group for which fish were found in this study to increase their movement to adjacent estuarine systems outside the stock boundary as they increased in abundance. Therefore, by not including fish that move to and are harvested in adjacent systems, the AR stock assessment underestimates fishing mortality. Accordingly, future research should examine the sensitivity of fishing mortality estimates from the AR stock assessment to additional landings of age-4–6 Striped Bass of AR origin outside the Albemarle Sound estuary.

Caveats

It is important to note that the analyses in this study indicate the probability of recapture location; movements are inferred from these data. Fishermen behavior (e.g., spatiotemporal differences in fishing effort or size targeting because of regulations and economic value) can affect and potentially bias tag returns and inferences about movement patterns (Hilborn, 1990; Gillanders et al., 2001). The size-dependent migration pattern that we observed could be due to differences in selectivity between ocean and estuarine fisheries; that is, small tagged fish could have migrated to the ocean but not been caught in the fishery. However, fisheries-

independent data indicate that it is predominantly the large Striped Bass of the AR stock that migrate to ocean waters. In a mobile telemetry study, Haeseker et al. (1996) searched the Albemarle Sound during summer (May–August) for the presence of 26 telemetered Striped Bass (all but 1 fish <600 mm TL) that participated in the April Roanoke River spawning run. They relocated 25 (96%) of these fish in the Albemarle Sound at least 1 month after spawning, providing evidence that smaller Striped Bass mostly remain in the estuary after spawning. Furthermore, in an ongoing telemetry study, 163 Striped Bass ranging in length from 445 to 1146 mm TL (mean=580 mm TL) were telemetered in the Roanoke River during spring, beginning in 2011, by Harris and Hightower.[5] Most large fish in their study (15 of the18 individuals >900 mm TL at tagging) have been detected by coastal receiver arrays in Massachusetts, New York, New Jersey, Delaware, and Virginia, but no smaller individuals have been detected in these northern ocean waters (Harris and Hightower[5]). Hence, results from these fisheries-independent telemetry studies corroborate the strong size-dependent emigration pattern of the AR stock of Striped Bass that we inferred from tag recaptures in our study.

A limitation of our study was that nearly all tag returns (99%) from larger fish (>600 mm TL) occurred during years of higher stock abundance (>1.5 million fish). Therefore, it is possible that the observed ocean emigration of larger fish was due in part to the higher abundance of similar size conspecifics (i.e., density-dependent mechanisms). However, ocean emigration of the AR stock of Striped Bass appears to be a size-dependent phenomenon related to bioenergetics as described and is probably largely independent of ambient population density or abundance. Two lines of evidence support this notion. First, data on large Striped Bass (>600 mm TL) across the more restricted range of annual values of stock abundance (1.5–2.0 million fish) indicate that density had little effect (an increase <3%) on the probability of large fish being recaptured in ocean waters. Second, just as we found in our study, Dorazio et al. (1994) found a strong size-dependent emigration pattern for the Chesapeake Bay stock: most fish >800 mm TL were recovered in northern ocean waters from New Jersey to Maine. Their study occurred in 1988–91, years when the Chesapeake Bay stock was at relatively low abundance levels and still rebuilding, demonstrating that substantial ocean emigration of large fish, albeit from a different stock, still occurs at low densities.

[4] ASMFC (Atlantic States Marine Fisheries Commission). 2003. Amendment 6 to the Interstate Fishery Management Plan for Atlantic Striped Bass. Fishery Management Report No. 41 of the Atlantic States Marine Fisheries Commission, 63 p. [Available from http://www.asmfc.org/uploads/file/sbAmendment6.pdf.]

[5] Harris, J. E., and J. E. Hightower. 2013. Unpubl. data. North Carolina Cooperative Fish and Wildlife Research Unit, U. S. Geological Survey, and Department of Applied Ecology, North Carolina State Univ., Raleigh, NC 27695.

Conclusions

Our study revealed major changes in the movements and associated distribution of a fish stock as it recovered from a depleted state. During the early phases of rebuilding, the stock was largely confined to its natal estuary but dramatically expanded its distribution, and degree of anadromy, as recovery continued. This major shift in distribution was due to changes in the demographics—namely size structure and total abundance—of the stock as it recovered. Size structure has received little attention in the fisheries literature in regard to its effects on stock distribution but appears to be important.

Although the recovery of Striped Bass often is regarded as one of the few success stories in fisheries management (Richards and Rago, 1999), many global fish stocks are either currently experiencing rebuilding or have recently recovered, for example, nearly one-third of the 166 stocks examined worldwide by Worm et al. (2009). It is possible that the spatial dynamics of these and other rebuilding stocks will differ from their depleted state. For instance, as stocks recover and more individuals are allowed to reach larger sizes (e.g., through a reduction in fishing mortality; Berkeley et al., 2004), the spatial distribution of stocks may shift or expand because larger, older fish often have different migratory behaviors and habitat preferences than smaller, younger individuals (Heifetz and Fujioka, 1991; Macpherson and Duarte, 1991; Shepherd et al., 2006; Grüss et al., 2011). Such changes in the movement and distribution of fish populations can have important consequences for stock assessments, as argued previously, and also affect ecosystem dynamics (e.g., as predators move into new areas, they can exert top-down changes in community structure; Casini et al., 2012). Therefore, resource managers should be aware of potential changes in the movement and distribution of recovering fish stocks and account for them accordingly if they manifest. As indicated in our study, long-term tagging and monitoring data are useful for detection of population-level changes in the movement and distribution of fishes.

Acknowledgments

Literature cited

Abesamis, R. A., and G. R Russ.
    2005.   Density-dependent spillover from a marine reserve: long-term evidence.   Ecol. Appl. 15:1798–1812.
Agresti, A.
    1996.   An introduction to categorical data analysis, 1st ed., 290 p.   John Wiley & Sons, New York.
Anderson, D. R.
    2008.   Model based inference in the life sciences, a primer on evidence, 2nd ed., 184 p.   Springer, New York.
Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love.
    2004.   Fisheries sustainability via protection of age structure and spatial distribution of fish populations.   Fisheries 29:23–31.
Boreman, J., and R. R. Lewis.
    1987.   Atlantic coastal migration of striped bass.   Am. Fish. Soc. Symp. 1:331–339.
Brodie, W. B., S. J. Walsh, and D. B. Atkinson.
    1998.   The effect of stock abundance on range contraction of yellowtail flounder (Pleuronectes ferruginea) on the Grand Bank of Newfoundland in the Northwest Atlantic from 1975 to 1995.   J. Sea Res. 39:139–152.
Burnham, K. P., and D. R. Anderson.
    2002.   Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed., 496 p.   Springer-Verlag, New York.
Casini, M., T. Blenckner, C. Möllmann, A. Gårdmark, M. Lindegren, M. Llope, G. Kornilovs, M. Plikshs, and N. Stenseth Christian.
    2012.   Predator transitory spillover induces trophic cascades in ecological sinks.   Proc. Natl. Acad. Sci. USA. 109:8185–8189.
Chaput, G.
    2004.   Considerations for using spawner reference levels for managing single- and mixed-stock fisheries of Atlantic salmon.   ICES J. Mar. Sci. 61:1379–1388.
Clark, J.
    1968.   Seasonal movements of striped bass contingents of Long Island Sound and the New York Bight.   Trans. Am. Fish. Soc. 97:320–343.
Coutant, C. C.
    1985.   Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk.   Trans. Am. Fish. Soc. 114:31–61.
Crozier, W. W., P-J. Schon, G. Chaput, E. C. E. Potter, N. O. Maoileidigh, and J. C. MacLean.
    2004.   Managing Atlantic salmon (Salmo salar L.) in the mixed stock environment: challenges and consideration.   ICES J. Mar. Sci. 61:1344–1358.
Dahlgren, C. P., and D. B. Eggleston.
    2000.   Ecological processes underlying ontogenetic habitat shifts in a coral reef fish.   Ecology 81:2227–2240.
Dorazio, R. M., K. A. Hattala, C. B. McCollough, and J. E. Skjeveland.
    1994.   Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay.   Trans. Am. Fish. Soc. 123:950–963.
Dunning, D. J., J. R. Waldman, Q. E. Ross, and M. T. Mattson.
    2006.   Dispersal of age-2+ striped bass out of the Hudson River.   Am. Fish. Soc. Symp. 51:287–294.
Gillanders, B. M., D. J. Ferrell, and N. L. Andrew.
    2001.   Estimates of movement and life-history parameters of yellowtail kingfish (Seriola lalandi): how useful

are data from a cooperative tagging programme? Mar. Freshw. Res. 52:179–192.

Grüss, A., D. M. Kaplan, S. Guénette, C. M. Roberts, and L. W. Botsford.
    2011.   Consequences of adult and juvenile movement for marine protected areas. Biol. Conserv. 144:692–702.

Haeseker, S. L., J. T. Carmichael, J. T., and J. E. Hightower.
    1996.   Summer distribution and condition of striped bass within Albemarle Sound, North Carolina. Trans. Am. Fish. Soc. 125:690–704.

Hammer, C., and C. Zimmermann.
    2005.   The role of stock identification in formulating fishery management advice. *In* Stock identification methods: applications in fishery science (S. X. Cadrin, K. D. Friedland, and J. R. Waldman, eds.), p. 631–658. Elsevier Academic Press, Burlington, MA.

Hartman, K. J., and S. B. Brandt.
    1995.   Comparative energetic and the development of bioenergetics models for sympatric estuarine piscivores. Can. J. Fish. Aquat. Sci. 52:1647–1666.

Heifetz, J., and J. T. Fujioka.
    1991.   Movement dynamics of tagged sablefish in the northeastern Pacific. Fish. Res. 11:355–374.

Hilborn, R.
    1990.   Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish. Aquat. Sci. 47:635–643.

Hilborn, R., A. E. Punt, and J. Orensanz.
    2004.   Beyond band-aids in fisheries management: fixing world fisheries. Bull. Mar. Sci. 74:493–507.

Hutchings, J. A., and J. K. Baum.
    2005.   Measuring marine fish biodiversity: temporal changes in abundance, life history, and demography. Philos. Trans. R. Soc. Lond., Ser B: Biol. Sci. 360:315–338.

IPCC (Intergovernmental Panel on Climate Change).
    2007.   Climate change 2007: synthesis report. Contribution of working groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 104 p. [Available from http://www.ipcc.ch/publications_and_data/ar4/syr/en/contents.html, accessed October 2012.]

Link, J. S., J. A. Nye, and J. A. Hare.
    2011.   Guidelines for incorporating fish distribution shifts into a fisheries management context. Fish Fish. 12:461–469.

Longhurst, A.
    2002.   Murphy's law revisited: longevity as a factor in recruitment to fish populations. Fish. Res. 56:125–131.

MacCall, A. D.
    1990.   Dynamic geography of marine fish populations, 155 p. Univ. Washington Press, Seattle.

Macpherson, E., and C. M. Duarte.
    1991.   Bathymetric trends in demersal fish size: is there a general relationship? Mar. Ecol. Prog. Ser. 71:103–112.

Merriman, D.
    1941.   Studies on the striped bass (*Roccus saxatilis*) of the Atlantic coast. Fish. Bull. 50:1–77.

Overholtz, W. J.
    2002.   The Gulf of Maine–Georges Bank Atlantic herring (*Clupea harengus*): spatial pattern analysis of the collapse and recovery of a large marine fish complex. Fish. Res. 57:237–254.

Richards, R. A., and P. J. Rago.
    1999.   A case history of effective fisheries management: Chesapeake Bay Striped Bass. N. Am. J. Fish. Manage. 19:356–375.

Rulifson, R. A., and C. S. Manooch III.
    1990.   Recruitment of juvenile Striped Bass in the Roanoke River, North Carolina, as related to reservoir discharge. N. Am. J. Fish. Manage. 10:397–407.

Secor, D. H.
    1999.   Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fish. Res. 43:13–34.

Secor, D. H., and P. M. Piccoli.
    1996.   Age-and sex-dependent migrations of Striped Bass in the Hudson River as determined by chemical microanalysis of otoliths. Estuaries 19:778–793.
    2007.   Oceanic migration rates of upper Chesapeake Bay striped bass (*Morone saxatilis*), determined by otolith microchemical analysis. Fish. Bull. 105:62–73.

Secor, D. H., J. R. Rooker, E. Zlokovitz, and V. S. Zdanowicz.
    2001.   Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. Mar. Ecol. Prog. Ser. 211:245–253.

Shepherd, G. R., J. Moser, D. Deuel, and P. Carlsen.
    2006.   The migration pattern of bluefish (*Pomatomus saltatrix*) along the Atlantic coast determined from tag recoveries. Fish. Bull. 104:559–570.

Shepherd, T. D., and M. K. Litvak.
    2004.   Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. Fish Fish. 5:141–152.

Swain, D. P., and E. J. Wade.
    1993.   Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 50:725–733.

Waldman, J. R., D. J. Dunning, Q. E. Ross, and M. T. Mattson.
    1990.   Range dynamics of Hudson River striped bass along the Atlantic coast. Trans. Am. Fish. Soc. 119:910–919.

Welsh, S. A., D. R. Smith, R. W. Laney, and R. C. Tipton.
    2007.   Tag-based estimates of annual fishing mortality of a mixed Atlantic coastal stock of striped bass. Trans. Am. Fish. Soc. 136:34–42.

Werner, E. E., and J. F. Gilliam.
    1984.   The ontogenetic niche shift and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15:393–426.

Winters, G. H., and J. P. Wheeler.
    1985.   Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. 42:989–998.

Worm, B., R. Hilborn, J. K Baum, T. A. Branch, J. S. Collie, C. Costello, M. J. Fogarty, E. A. Fulton, J. A. Hutchings, S. Jennings, O. P. Jensen, H. K. Lotze, P. M. Mace, T. R. McClanahan, C. Minto, S. R. Palumbi, A. M. Parma, D. Ricard, A. Rosenberg, R. Watson, and D. Zeller.
    2009.   Rebuilding global fisheries. Science 325:578–585.

Zlokovitz, E. R., D. H. Secor, and P. M. Piccoli.
    2003.   Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. Fish. Res. 63:245–259.