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Partial migration of striped bass: revisiting the contingent hypothesis

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ABSTRACT: Partial migration, by which contingents within populations undertake divergent migrations, is common in marine fishes but remains poorly documented. Intrapopulation groups of fish with similar seasonal migration behaviors were noted early in the fisheries literature and have attracted increased interest for their role in population resilience to environmental change and fishing. Here, we used acoustic telemetry to test historical hypotheses on contingent structure for striped bass *Morone saxatilis* in the Hudson River, New York (USA), which harbors one of the largest populations of this species. Season and region of release were used as design elements to evaluate 3 principal contingents. In total, 51 implanted striped bass were detected in New York Harbor (NYH), Hudson River, and other estuarine and coastal receiver arrays from June 2010 through December 2011. Multivariate analyses of >500 000 recoveries confirmed predictions of 3 broad contingent behaviors, viz. those that principally utilized (1) the Upper Hudson River Estuary, (2) the NYH and Lower Hudson River Estuary, and (3) coastal waters, but commingled in upper Hudson River spawning habitats during late spring. All contingents occupied NYH, but their transit routes into and out of the harbor varied significantly. Further behavioral diversity was observed within contingents, including size-specific differential migration, multiple natal origins (natal divergence), and non-annual (skipped) spawning. Contingent structure within Hudson River striped bass likely distributes the influences of regional fisheries, pollution, and other environmental forces, promoting stability and persistence in the overall population.

KEY WORDS: *Morone saxatilis* · Partial migration · Striped bass · Hudson River · Telemetry · Behavioral diversity

INTRODUCTION

With recent advances in tracking technologies, scientists have begun observing migration at varying scales. Of particular interest, intrapopulation groups of individuals share similar seasonal migrations that persist over much of their lifespan. The term 'contingent' dates back to the origins of modern fisheries science (Hjort 1914, Gilbert 1915) but was recently revived by Secor (1999), who postulated that contingents of fish remain distinct by maintaining divergent migration pathways as systems of partial migration. These pathways intersect in ways that define population membership (i.e. on spawning grounds) and have consequences for fisheries and coastal stewardship.

Partial migration is classically defined by the simultaneous occurrence of resident and migratory contingents within the same population, sometimes as a result of early life responses to environmental conditions (Kerr et al. 2009, Chapman et al. 2011) and has been documented for diverse coastal species ranging

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from eels (Tsukamoto et al. 1998) to tunas (Fromentin & Powers 2005). Partial migration often produces multiple types of seasonal migrations that can bolster resilience, stability, and yield in populations (Kraus & Secor 2004, Kerr et al. 2010, Petitgas et al. 2010). Through partial migration, contingents are differentially exposed to sets of habitats that cause independent outcomes, resulting in an averaging or portfolio effect (Secor et al. 2009). For instance, in the Hudson River (New York, USA), resident striped bass *Morone saxatilis* receive a degree of protection from exploitation due to their higher exposure to pollution and human consumption advisories while the migratory contingents of striped bass encounter much higher rates of coastal exploitation (Secor 1999). Consequently, the resident contingent likely contributes stability to the overall Hudson River population.

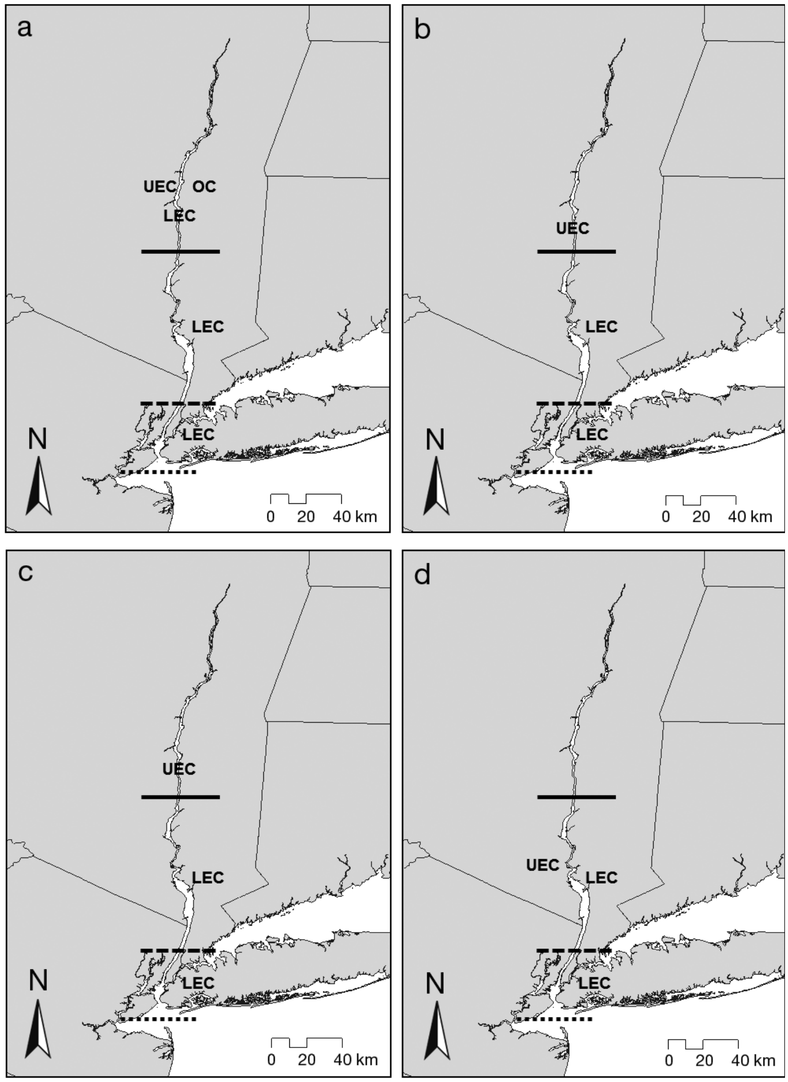

Fig. 1. Hypothesized distribution of the Upper Estuary (UEC), Lower Estuary (LEC) and Ocean (OC) Contingents of striped bass *Morone saxatilis* in the Hudson River Estuary during (a) spring, (b) summer, (c) fall, and (d) winter. Striped bass from the OC were expected to be present in the spring only. For the purposes of this study, the upper estuary is defined as the area above the solid black line. The lower estuary is located between the solid and dashed line, and New York Harbor is between the dashed and dotted lines

Striped bass are a long-lived anadromous species naturally ranging in North America from the Gulf of Mexico to the St. Lawrence River. In an extensive tagging study, Clark (1968) observed patterns of seasonal homing to certain regions of the Hudson River, New York (NY) Harbor, and NY Bight by individuals that had been tagged and released at similar times and places. This led him to hypothesize that separate seasonal patterns of migration persisted over the lifespan of Hudson River striped bass that were organized as contingents. Subsequent research using various techniques showed evidence for Clark's contingents (Secor & Piccoli 1996, Ashley et al. 2000, Secor et al. 2001, Zlokovitz et al. 2003), and a recent acoustic telemetry study resolved seasonal movements by the resident contingent (Wingate & Secor 2007).

Here, we tested contingent structure to better understand the practical implications of associated migration behaviors and also examined the role of NY Harbor as a seasonal habitat among contingents. Based on previous research, we hypothesized that (1) an Upper Estuary Contingent (UEC) primarily resides in the upper estuary and visits the lower estuary during winter months only, (2) a Lower Estuary Contingent (LEC) resides in the lower estuary and NY Harbor year round, and (3) an Ocean Contingent (OC) uses the river principally as a spawning migration corridor to upper estuary spawning grounds in the spring and spends the rest of the year in the coastal Atlantic (Fig. 1). During the period June 2010 to December 2011, 75 striped bass were captured, tagged, and assigned to 1 of 3 putative contingents based upon the season and location of capture. Acoustic telemetry data are often complex and diffi-

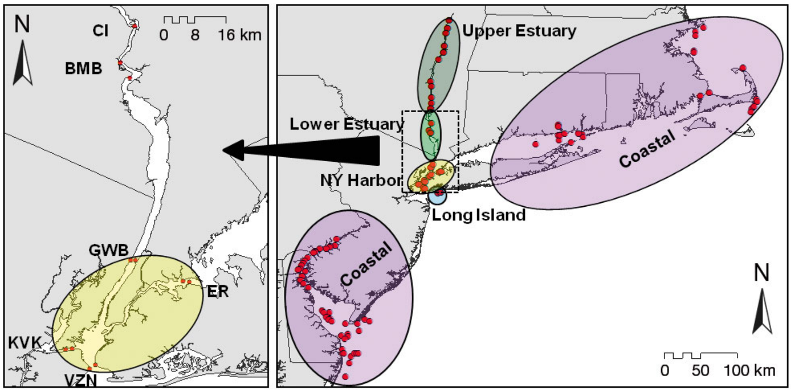

Fig. 2. Hudson River and Mid-Atlantic Bight, with approximate receiver locations and areal designations used in PCA and cluster analyses. Acoustic receiver locations are indicated by closed circles. Inset depicts deployment of acoustic receivers that acted as gates for New York Harbor (shaded in yellow) and Hudson River Estuary regions. From north to south the gates were Constitution Island (CI), Bear Mountain Bridge (BMB), George Washington Bridge (GWB), East River (ER), Kill Van Kull (KVK), and Verrazano Narrows (VZN)

cult to quantify, and methods to describe the movements of individuals over multiple spatial scales have not been well developed. We strategically placed acoustic receivers in the Hudson River and NY Harbor to test how classified contingents differed in their (1) overall and seasonal patterns of migration in the Hudson River estuary and coastal regions, (2) use of NY Harbor in particular, and (3) 'choice' of migration corridors into and out of NY Harbor and the Hudson River.

MATERIALS AND METHODS

Telemetry

During the period October 2009 to May 2010, 75 striped bass were captured, implanted with an acoustic transmitter, and released in specific regions to test whether contingent behaviors persisted among seasons and years. The contingents included (1) UEC (n = 15) caught with hook and line in tidal freshwater Hudson River in the Catskills-Athens region (river km 170–190) during fall 2009, (2) LEC (n = 40) caught with hook and line in the NY Harbor region (Fig. 2; confluence of Hudson River, East River, and NY Atlantic Bight) during fall 2009, and (3) OC (n = 20) of large (>700 mm total length, TL) ripe adults captured in the Hudson River (river km 165–190) during the 2010 spring spawning season. A few OC fish were captured by hook and line (n = 4); most were made available by NY State Department of Environmental Conservation (NYSDEC) scientists from their springtime 2010 haul seine monitoring program (Table 1).

Transmitters (VEMCO V16-4H-R64K; 67 mm, 10 g, 2.5 yr expected battery life) were surgically implanted following previously developed procedures (Wingate & Secor 2007). Transmitters were programmed with a random delay period of 20 to 69 s to decrease the possibility of code collision. In all instances, we monitored post implantation stress and mortality by holding fish in tanks or floating pens for 15 min prior to release. Transmitter performance was double-checked during this recovery period. Measurements of TL (mm), weight (kg), and if determined sex (e.g. running ripe fish in spring) of all released fish were recorded.

Fish were detected by remote receivers principally deployed by NYSDEC, Delaware State University, State University of NY at Stony Brook, and University of Maryland Center for Environmental Science. Smaller numbers of detections in Atlantic coastal regions were made available by other research groups through the Atlantic Coastal Telemetry Network (www.theactnetwork.com/). Together, these deployments provided broad detection coverage

Table 1. Summary of striped bass *Morone saxatilis* implanted with acoustic coded transmitters during fall 2009 and spring 2010 in New York Harbor (Lower Estuary Contingent) and Hudson River (Upper Estuary Contingent and Ocean Contingent). Only tagged fish that were detected beyond 31 August 2010 were assigned study codes and included in analyses. TL: total length

Contingent	Tagging season	Tagging location	Study IDs	TL (mm)	
				Mean	Range
Upper Estuary	Fall 2009	Upper Estuary	1–10	490	410–540
Lower Estuary	Fall 2009	New York Harbor and East River	11–40	607	435–960
Ocean	Spring 2010	Upper Estuary	41–51	896	820–975

(Fig. 2) in (1) upper and lower estuary regions of the Hudson River, (2) NY Harbor, (3) the South Shore of Long Island, (4) southern New England, and (5) Delaware Bay. In most instances, receivers (VEMCO VR2W) were moored through attachment to US Coast Guard buoys; however, to ensure complete coverage of inlets to NY Harbor, receivers were also attached to an acoustically triggered buoy (ORE Offshore Sub Sea Sonics©). Here, they were deployed to act as 'gates' that would allow broad regional placement of individuals within the Hudson River, the NY Harbor, and coastal approaches (Fig. 2). Receivers continuously monitored for transmitters and upon detection recorded the identification code, date, and time (UTC). Prior testing in the Hudson River indicated a detection range >1 km (Wingate & Secor 2007). Receivers were retrieved every 3 to 7 mo to download data and perform maintenance.

Data analyses

The primary study objective was to evaluate whether seasonal habitat use differed among contingents, focusing on seasonal homing by the LEC to NY Harbor. The term of the study was 1 June 2010 to 1 December 2011. The dataset was corrected for possible false detections by removing single detections from a given day. Fish not detected after 31 August 2010 were assumed to have died, and their records were removed from subsequent analyses to minimize potential bias. Detection records for the remaining 'active' individuals were summarized to a specific receiver station (e.g. GWB, VZN; see Fig. 2 for abbreviations) and a larger corresponding habitat region for each day an individual was detected. On occasions where fish transited between areas in a given day, they were assigned to where they spent the majority of that day according to the first and last detections. Habitat regions included Upper Hudson River, Lower Hudson River, NY Harbor, Long Island, and Coastal, the latter including Delaware Bay (Fig. 2). The resulting data were numbers of days in which an individual was detected at a certain receiver site or within a greater spatial area. These data were employed in analyses at 2 temporal levels, the entire study period and each of 6 seasons: June to August 2010, September to November 2010, December 2010 to February 2011, March to May 2011, June to August 2011, and September to November 2011. For all seasonal analyses, we expected that striped bass contingents would be found in separate regions, except for spring when contingents would converge in the upper Hudson River to spawn. For all tests, a p-value <0.05 was considered significant.

Tests of contingent behavior

Multivariate analyses of regional habitat incidence were conducted using principal component analysis (PCA; via SAS 9.2; SAS Institution, Inc.) and hierarchical cluster analysis (via SYSTAT13©). The first approach allowed reduction of a large dataset of daily records of individuals among regions, followed by *a posteriori* tests for contingent effects. The second approach was used to uncover additional structure that was not specified in the experimental design (i.e. groups in addition to the 3 tested contingents). All PCA procedures were run on the number of days an individual fish spent in a given area during the total study or during a specific season. These values were square root transformed to improve normality prior to the PCA. Tests for contingent differences on PCA scores used analysis of variance (ANOVA) or a non-parametric Kruskal-Wallis test (KWT) depending on whether scores met the assumptions of normality after transformation. Tukey's honestly significant difference (HSD) test was used to evaluate multiple comparisons following significant ANOVA results (Zar 1999). Individuals whose final detection occurred in a prior season were not included in analyses of later seasons.

For the cluster analysis, the total number of days an individual was detected in each of the 5 geographic areas over the course of the entire study was natural log transformed to reduce the effect of large outliers. These data were analyzed using combinations of the average or complete linkage methods with Euclidean or Mahalanobis distance coefficients (McGarigal et al. 2000). The best combination of linkage method and distance coefficient, as well as the appropriate number of clusters, was determined by visual inspection of clustering solutions and evaluation of pseudo-F, pseudo-t^2, Davies-Bouldin, and Dunn statistics.

Contingency table analysis was used to investigate differences in the regional incidence between contingents and seasons. For this analysis, habitat assignment was made according to where an individual was located the majority of the time within that season based on both detections and passage through gates. This led to reduced sample sizes for some region × season × contingent combinations and necessitated combining regions. We considered 3 broader areas: the Hudson River Estuary (upper and lower estuary regions), NY Harbor, and NY Bight

(Long Island), or Coastal (outside the Hudson River). Only individuals whose whereabouts could be determined through multiple detections in a region during a given season were included in that season's analysis. This criterion was more conservative than that used for the PCAs and led to different sample sizes for the 2 analyses in most seasons. All results were assessed via Pearson's chi-squared test except when average cell frequency was less than 6, in which case Fisher's exact test was used (Zar 1999).

Incidence in NY Harbor

Periods of continuous inhabitance and summed inhabitance in NY Harbor among contingents were calculated using methods described by Wingate et al. (2011). Each individual's daily record was tallied to calculate the number and length of 'continuous inhabitance' events in NY Harbor. We feel it is important to note that event lengths are conservatively biased because the harbor was not fully covered by receivers and detections may have been missed due to high levels of background noise. Event lengths should be interpreted to index relative durations of incidence in NY Harbor between contingents. Since NY Harbor was not completely saturated with receivers, days when fish were not detected were considered part of a continuous event as long as they had entered the harbor previously and the subsequent detection was at a gate or within the harbor. The aggregate number of days spent in NY Harbor by each individual was termed the 'summed inhabitance'. We calculated continuous and summed inhabitance for every fish over the course of the entire study and within each season. Individual inhabitance records were also used to generate the mean duration for each inhabitance event and the longest inhabitance event for each fish. To account for variability of time-in-study among individuals, summed inhabitance values for each fish were divided by the total number of days that an individual was present in the study or season. The resulting proportion was then arcsine transformed prior to ANOVA. Inhabitance data that were not normally distributed after arcsine transformation were analyzed as rank-transformed data using the KWT.

Detections at migration corridors

The number of days each fish was detected by a receiver stationed at 1 of the corridor sites (VZN, KVK, ER, GWB; see Fig. 2 for site abbreviations) was tabulated by contingent. The complete methodology can be found in the Supplement (available at www.int-res.com/articles/suppl/m525p185_supp.pdf).

RESULTS

In total, 75 striped bass (UEC = 15, LEC = 40, OC = 20) were captured and tagged in the fall of 2009 and spring of 2010. Individuals assigned to the putative contingents at the time of tagging differed in length (ANOVA; n = 75, $F_{2,72}$ = 47.9, p < 0.001). The UEC comprised the smallest fish (mean ± SD = 512.4 ± 48.3 mm; range = 410–584 mm), the LEC were larger and of variable size (614.9 ± 149.4 mm; range = 435–960 mm), and the OC were uniformly large due to targeted sampling of spawning-condition adults (880.5 ± 64.1 mm; range = 710–975 mm).

Fish tagged in this study were detected more than 550 000 times by receivers as far north as the Kennebec River in Maine and as far south as the Patuxent River, Maryland. Contingent samples exhibited varying rates of apparent mortality following their time of release. By the start of the designated study period (1 June 2010), the UEC and LEC were diminished by 13% (2/15) and 23% (9/40) since their fall release 7 mo prior. In contrast, the OC sample suffered 30% (6/20) loss during the first month after release (May to June 2010) and 45% (9/20) loss during the first 2 mo after release (May to July 2010). At the start of the final fall season (1 September 2011; 23 mo after release of UEC and LEC, 15 mo after release of OC), 75% of fish assigned to the UEC remained at large, as did 81% of LEC striped bass. In contrast, only 50% of OC individuals provided detections to this date. Losses prior to 31 August 2010 constituted nearly one-third of the tagged fish (n = 24; UEC = 5, LEC = 10, OC = 9) which were removed from the study, leaving 51 individuals for further analyses (Table 1).

Tests of contingent behavior

Regional differences were visually apparent from daily detections of individuals grouped by contingents (Fig. 3). The seasonality of movements was evidenced by high densities of detections during summer and fall months (May to December) and minimal detections during winter and early spring (January to April). Most individuals' movements conformed to the migration behavior hypothesized for their contin-

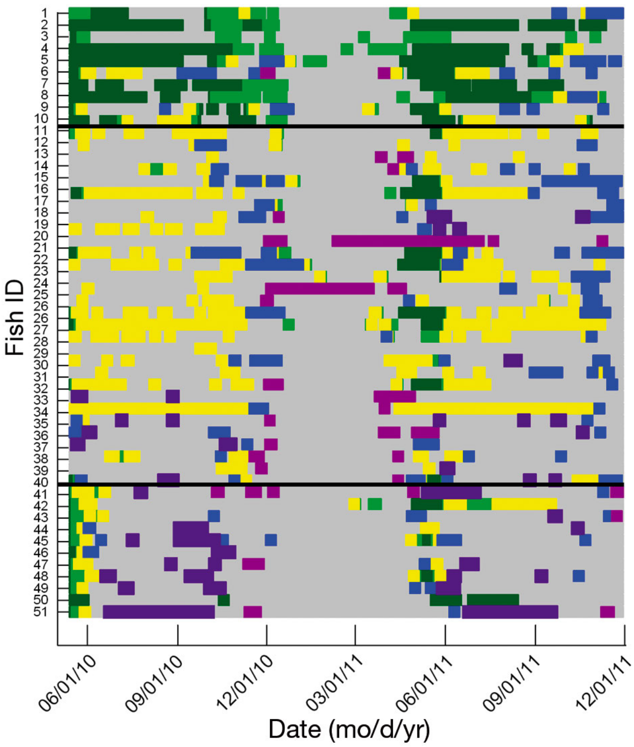

Fig. 3. Compilation of detections by area for 51 striped bass *Morone saxatilis* analyzed in the study. Individuals 1–10 represent the Upper Estuary Contingent, 11–40 the Lower Estuary Contingent, and 41–51 the Ocean Contingent. Within each contingent, fish are sorted by size with the smallest fish at the top. Each row's cells depict regional daily detections. Gray cells: no regional detection; dark green: upper Hudson River; light green: lower Hudson River; yellow: New York Harbor; blue: Long Island; dark and light purple: coastal detections north and south of the Hudson Canyon, respectively

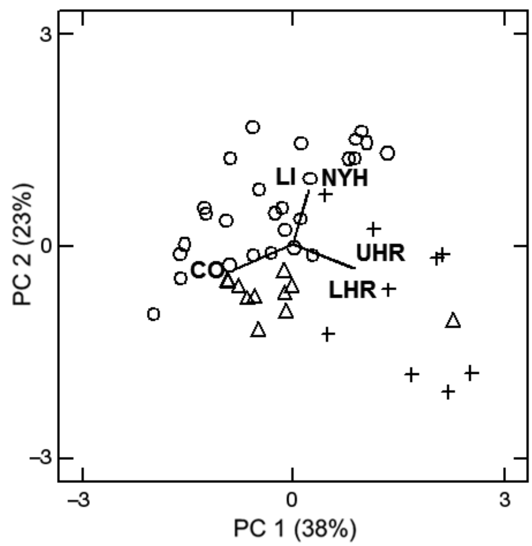

Fig. 4. PCA of daily detections of telemetered striped bass *Morone saxatilis* over the total length of the study. Upper Estuary Contingent fish are depicted as crosses, Lower Estuary Contingent fish as open circles, and Ocean Contingent fish as open triangles. Direction and strength of loadings for the 5 possible habitat classifications (UHR: upper Hudson River; LHR: lower Hudson River; NYH: New York Harbor; LI: Long Island; CO: Coastal) on the components are represented by solid lines

gent assignment, but within each contingent, some individuals displayed unexpected behaviors.

PCA supported expected seasonal migration patterns among contingents over the total study period. Most of the PCA variance (61%) was explained by the first 2 components (Fig. 4). Detections in the upper and lower stretches of the Hudson River were positively associated with the first component, while coastal detections were negatively correlated. These differences separated PCA scores of the UEC from the other 2 groups (ANOVA; $F_{2,48} = 15.92$, $p < 0.001$). The second component was positively associated with NY Harbor and Long Island detections and negatively associated with upper Hudson River detections, which differentiated LEC scores from those of the UEC and OC (ANOVA; $F_{2,48} = 12.9$, $p < 0.001$).

By season, PCAs showed the greatest segregation of contingents during both falls (Fig. 5b,f; Table 2). In the summer of 2010 (Fig. 5a), the LEC primarily resided in the lower Hudson River and NY Harbor, while the UEC was associated with the upper Hudson River. In the fall of 2010 (Fig. 5b), fish from the UEC began moving downriver and were detected in both the upper and lower Hudson River. Striped bass in the LEC shifted towards more marine environments and were primarily detected in NY Harbor and off Long Island, while OC fish were in coastal waters. Relatively few fish were detected (n = 20) during winter 2010 (Fig. 5c) and most were in the Hudson River, as evidenced by the wide overlap among contingent scores. As expected, fish from all contingents converged on the upper Hudson River spawning grounds during spring 2011 (Fig. 5d). Variability was observed on the second component, as not all LEC fish ascended the river and some OC individuals did not spawn in 2011 (see Table 4). Summer 2011 detections (Fig. 5e) resembled those of 2010, but LEC individuals were more widely dispersed. Most striped bass from the UEC again remained in the upper Hudson River. Fall 2011 (Fig. 5f), as in the previous year, featured pronounced differences in detections among contingents. Fish from the UEC again moved into the lower river, and LEC individuals occupied the area from the lower river to Long Island, while OC fish were in coastal waters.

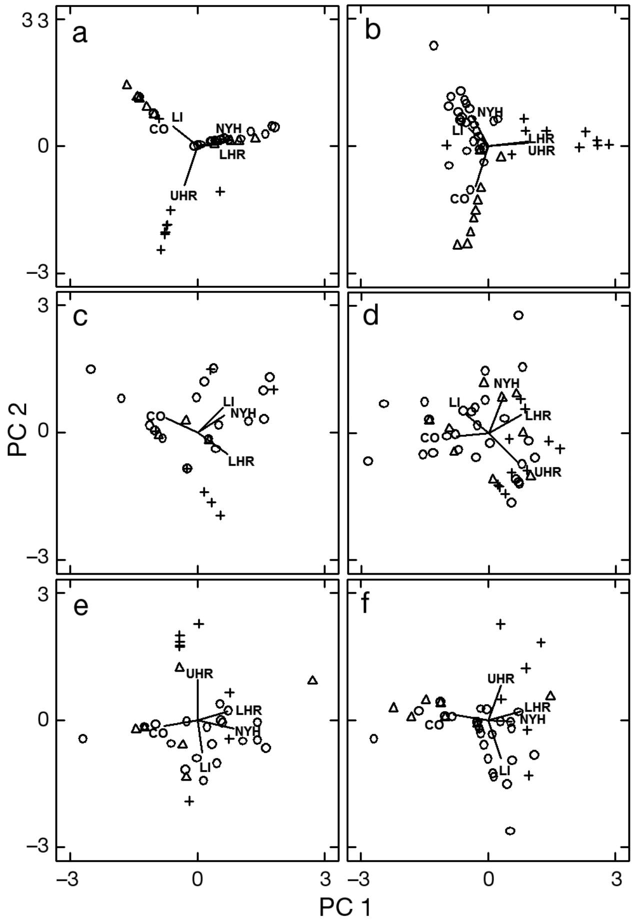

Fig. 5. PCAs on seasonal detections of telemetered striped bass *Morone saxatilis*: (a) Summer 2010, (b) Fall 2010, (c) Winter 2010/2011, (d) Spring 2011, (e) Summer 2011, (f) Fall 2011. Upper Estuary Contingent fish are depicted as crosses, Lower Estuary Contingent fish as open circles, and Ocean Contingent fish as open triangles. Direction and strength of loadings for the 5 possible habitat classifications (UHR: upper Hudson River; LHR: lower Hudson River; NYH: New York Harbor; LI: Long Island; CO: Coastal) on the components are represented by solid lines

Table 2. Summary of seasonal analyses of PCA scores. For each season of the study, the table reports the variation explained (VE) by each of the first 2 principal components, the number of individuals detected within that season (n), the results of ANOVA (F) or Kruskal-Wallis (χ^2) tests, and resulting p value. All p values < 0.05 were deemed significant

Season	Component	VE	n	Result	p
2010					
Summer	PC 1	0.32	37	$F_{2,34} = 3.32$	0.048
	PC 2	0.25		$\chi^2 = 13.31$	0.001
Fall	PC 1	0.36	47	$\chi^2 = 15.74$	<0.001
	PC 2	0.27		$\chi^2 = 22.19$	<0.001
Winter	PC 1	0.46	31	$F_{2,28} = 0.44$	0.651
	PC 2	0.22		$F_{2,28} = 5.61$	0.009
2011					
Spring	PC 1	0.33	48	$F_{2,45} = 4.13$	0.027
	PC 2	0.26		$\chi^2 = 3.38$	0.186
Summer	PC 1	0.31	36	$F_{2,33} = 0.12$	0.883
	PC 2	0.26		$\chi^2 = 6.31$	0.043
Fall	PC 1	0.28	41	$\chi^2 = 11.53$	0.003
	PC 2	0.25		$F_{2,38} = 6.70$	0.003

As tested through cross-tabulation, contingents were differentially represented across broad regional categories for most seasons (Table 3), corroborating results from the PCAs. Spatial segregation among contingents was maximized in the summer and fall. During summer and fall 2010, the UEC and LEC oriented to the upper Hudson River and NY Harbor/Long Island areas, respectively. The OC was detected predominately in northern coastal waters off Massachusetts during summer and fall, with fish being detected off the NY Bight and Delaware by late fall. The segregation of contingents repeated itself during summer and fall 2011, except for the UEC, which showed greater proportional representation in the NY Harbor region (Table 3). During the winter of 2010/2011, contingent segregation across broad regions was not detected. In spring 2011, there was a high degree of spatial overlap among contingents in the Hudson River, but some LEC and OC individuals were located in the NY Harbor/Long Island or coastal regions (Table 3). This pattern is likely attributable to Hudson River spawning migrations, which occurred for all contingents and caused some (but not all) OC fish to traverse the NY Harbor into the Hudson River.

A close examination of springtime detection patterns indicated that 21 of the 49 fish (43%) remaining in the study during the spring of 2011 presumably spawned in the Hudson River in both years, and an additional 11 fish spawned at least once (Table 4).

The cluster analysis on 51 individuals over the entire study period supported more diverse behavioral groups than the 3 tested in the study design (i.e. LEC, UEC, and OC). General consensus among validity measures supported an average linkage—Mahalanobis distance combination that included 8 clusters, which are represented here by their affinity for certain regions (Fig. 6; also see the Supplement). The first group (clusters 1 and 2) were composed of 22 striped bass (UEC = 1, LEC = 12, OC = 9) whose detections reflected a strong coastal affinity and infrequent detections upriver of NY Harbor. In contrast, the 9 members of Group II (cluster 3: UEC = 4, LEC = 5) all had multiple detections in every habitat area ex-

Table 3. Summary of the number of striped bass *Morone saxatilis* from each contingent that were located in a region during a given season and results of Pearson's chi-squared test for contingent habitat use by season. Totals for the number of striped bass from each contingent (n) and the total number of striped bass (N) are reported. All p values < 0.05 were deemed significant. UEC: Upper Estuary Contingent; LEC: Lower Estuary Contingent; OC: Ocean Contingent; NYH: New York Harbor; LI: Long Island

Season	Contingent	Habitat			n	N	p
		Hudson	NYH/LI	Coastal			
Summer 2010	UEC	7	2	0	9	39	<0.001
	LEC	0	16	4	20		
	OC	1	1	8	10		
Fall 2010	UEC	8	2	0	10	43	<0.001
	LEC	0	22	1	23		
	OC	1	0	9	10		
Winter	UEC	6	2	1	9	28	0.21
	LEC	8	2	7	17		
	OC	0	1	1	2		
Spring 2011	UEC	9	1	0	10	47	0.17
	LEC	14	6	8	28		
	OC	4	3	2	9		
Summer 2011	UEC	4	4	0	8	36	<0.001
	LEC	0	15	6	21		
	OC	1	1	5	7		
Fall 2011	UEC	3	7	0	10	36	<0.001
	LEC	0	16	4	20		
	OC	0	1	5	6		

cept Coastal, indicating that these fish showed strong affinity to the Hudson River Estuary, making use of the entire river, estuary, and immediate nearshore approaches. Group III (cluster 4) comprised 6 LEC striped bass that frequented the Long Island receiver array. Three of these individuals were detected in coastal arrays during the summer or winter, indicating that they visited the Hudson River seasonally but had stronger affinities to coastal habitats. Group IV (clusters 5 and 6) individuals were all detected on more days in NY Harbor than any other location. The 5 individuals in cluster 5 were assigned to the LEC at the time of tagging; 3 of the individuals showed annual fidelity to NY Harbor but also joined coastal migrants for a southerly winter migration. The 5 striped bass in cluster 6 (UEC = 2, LEC = 2, OC = 1) showed the greatest affinity to NY Harbor, with movement patterns centered on the harbor and the Hudson River; only 1 fish was detected for a few days outside of this area at the Long Island array. Group V (clusters 7 and 8: UEC = 3, OC = 1) approximated the hypothesized behavior of UEC individuals; these striped bass were not detected below the lower Hudson River.

Incidence in NY Harbor

Over the total duration of the study, LEC individuals spent the greatest proportion of time inside NY Harbor (ANOVA on summed inhabitance; $F_{2,48}$ = 5.84; p = 0.005; Fig. 7). Post hoc tests found a significant difference between the LEC and OC but not the LEC and UEC. Once fish entered NY Harbor, contingent membership affected the duration they continuously remained in the area. The longest con-

Table 4. Number of surviving (as of May 2011) tagged striped bass *Morone saxatilis* in each contingent that were presumed to spawn in 1 or both years of the study. Two individuals were lost to the study between the first and second spawning seasons

Spawning frequency	Contingent			Total
	Upper Estuary	Lower Estuary	Ocean	
Both years	8	9	4	21
One year	2	4	6	12
Did not spawn	0	16	0	16
Total	10	29	10	49

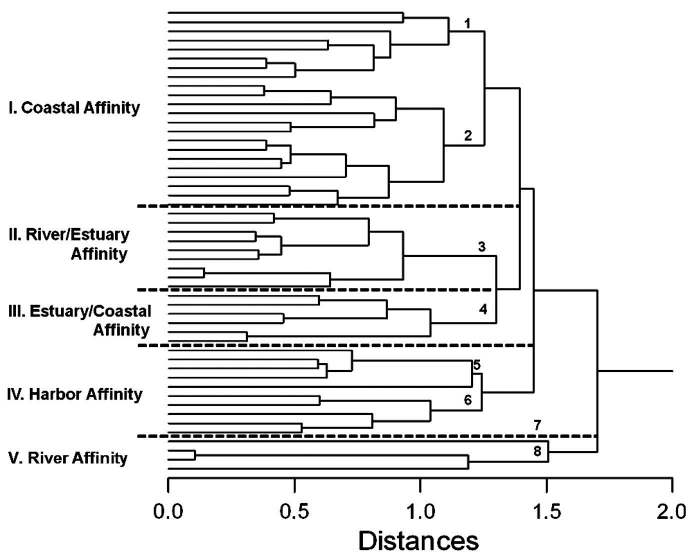

Fig. 6. Cluster analysis results from the average linking method and Mahalanobis distance coefficients. The analysis grouped the 51 individual striped bass *Morone saxatilis* into 8 clusters, which are demarcated on the separate branches. Labels were applied to the groups (left axis and horizontal dashed lines) based upon visual interpretation of the delineated clusters

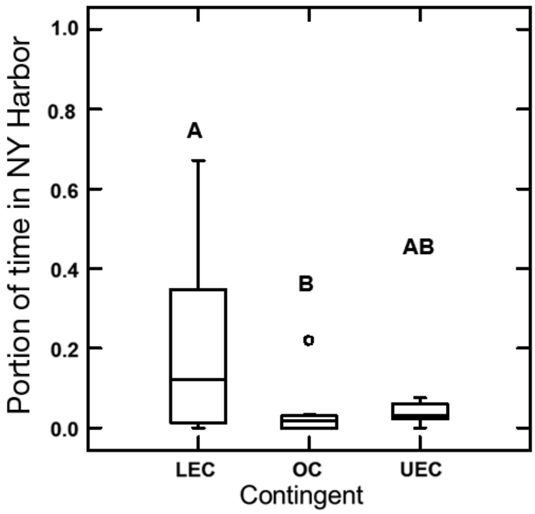

Fig. 7. Comparison of the proportion of days telemetered striped bass *Morone saxatilis* were detected residing in New York (NY) Harbor by members of each contingent. Contingents are specified on the *x*-axis (LEC: Lower Estuary Contingent; OC: Ocean Contingent; UEC: Upper Estuary Contingent), and the proportion of time a fish spent in NY Harbor out of that individual's overall time at large is on the *y*-axis. The limits of the boxes represent the 1st and 3rd quartiles and the interior solid line the median. The whiskers are 1.5 the interquartile range. Open circles represent values greater than 3 times the interquartile range. Letters above plots represent Tukey HSD groupings

tinuous inhabitance event for individuals differed significantly overall (n = 51; KWT; χ^2 = 6.73; df = 2; p = 0.03) among contingents; however, post hoc tests indicated no significant comparisons. A member of the LEC accounted for the longest continuous inhabitance event of 202 d and LEC individuals contributed 14 of the 15 longest events. Season as a main factor did not affect the amount of time spent in NY Harbor (2-way ANOVA on rank-transformed proportions of summed inhabitance; overall model $F_{17,272}$ = 5.25; p < 0.001; Contingent term $F_{2,278}$ = 17.55; p < 0.001; Season term $F_{5,278}$ = 0.70; p = 0.622; Contingent × Season interaction $F_{10,278}$ = 2.28; p = 0.014). Use of NY Harbor by the LEC, measured by summed inhabitance, was significantly greater than that of other contingents during the summers of 2010 (χ^2 = 7.99; df = 2; p < 0.016) and 2011 (χ^2 = 11.42; df = 2; p = 0.003), and fall 2010 (χ^2 = 18.33; df = 2; p < 0.001; Fig. 8b). Inhabitance of NY Harbor by UEC members was uniformly low (KWT; χ^2 = 6.03; df = 5; p = 0.303; Fig. 8a). Appearances by OC striped bass in NY Harbor were similarly rare and were weakly associated with presumed spawning periods, namely early summer of 2010 and spring of 2011 (KWT; χ^2 = 10.47; df = 5; p = 0.063; Fig. 8c).

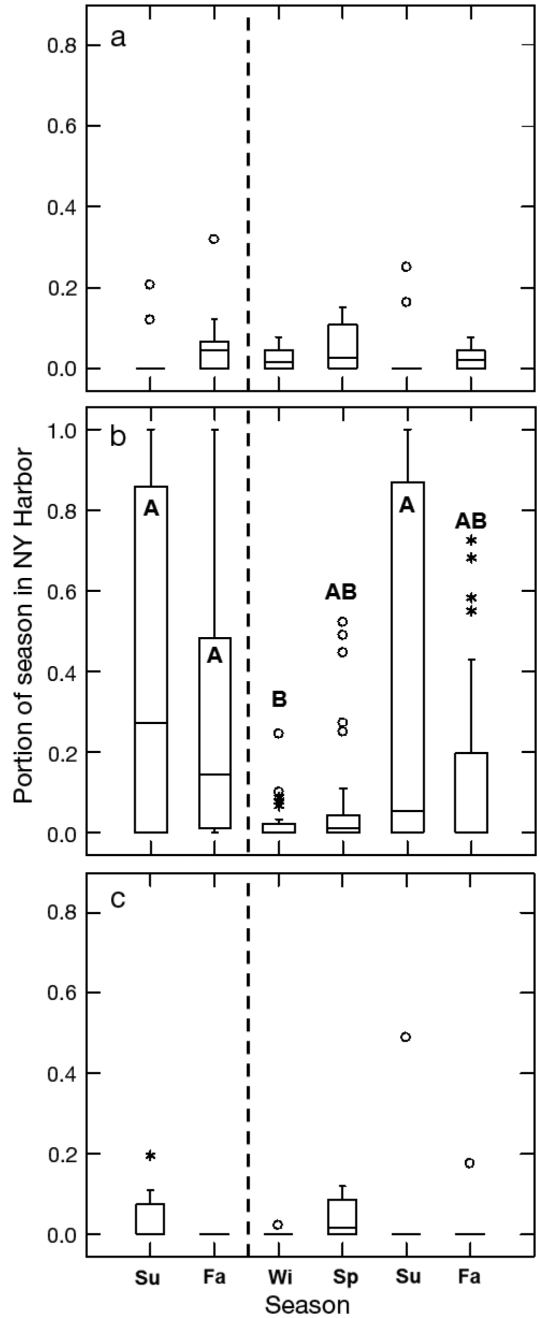

Fig. 8. Proportion of days telemetered striped bass *Morone saxatilis* spent in New York (NY) Harbor during each season (Su: summer, Fa: fall, Wi: winter, Sp: spring) by members of each contingent: (a) Upper Estuary Contingent, (b) Lower Estuary Contingent, (c) Ocean Contingent. The limits of the boxes represent the 1st and 3rd quartiles and the interior solid line the median. The whiskers are 1.5 the interquartile range. Values between 1.5 and 3 times the interquartile range and values greater than 3 times the interquartile range are represented by asterisks and open circles, respectively. Significant differences in seasonal occupation were found only for the Lower Estuary Contingent; Tukey-Kramer groupings are denoted by letters above seasons. Dashed line represents separation between 2010 and 2011

Detections at migration corridors

For the total study, corridor use (VZN, GWB, KVK, and ER; see Fig. 2) differed significantly (Pearson χ^2 = 302.33; df = 6; n = 892; p < 0.001) by designated contingents. The bulk of corridor detections (65%) were contributed by LEC individuals; UEC and OC individuals accounted for 20% and 15% of corridor detections. Telemetered striped bass showed different corridor use according to contingent membership during spring (KWT; χ^2 = 44.28; df = 6; n = 125; p < 0.001), summer (KWT; χ^2 = 299.56; df = 6; n = 449; p < 0.001), and fall (KWT; χ^2 = 147.05; df = 6; n = 254; p < 0.001), but not during winter (KWT; χ^2 = 7.27; df = 4; n = 60; p = 0.122). More detailed results can be found in the Supplement.

DISCUSSION

Contingent structure

This telemetry study on 75 tagged striped bass (51 analyzed) confirmed that at least 3 contingents exist within the Hudson River stock and that they follow divergent, but overlapping, migration pathways. These contingents shared similar seasonal migration behaviors, which likely have population-level consequences for how individuals encounter pollution, water quality, foraging and reproductive conditions, and fishing pressure (Secor 1999, Ashley et al. 2000, Able & Grothues 2007).

Previous studies (e.g. Secor & Piccoli 1996, Wingate & Secor 2007) have described the movement patterns of the UEC and OC; here, we confirmed a third seasonal lower estuarine 'contingent' (Figs. 3 & 4). These striped bass were tagged in NY Harbor during fall months and showed a propensity to reside in this region during most parts of the year. As previously demonstrated, the OC was composed of large spawning adults tagged on the spawning ground that showed wide ranging migration behaviors in coastal waters from the Delmarva Peninsula to Cape Cod. The UEC were smaller striped bass tagged in the upper estuary and showed homing behaviors to that region during summer and fall months.

Multivariate analyses indicated that the LEC exhibited greater variability in regional habitat use patterns than other contingents. This inference is biased by the sampling design, which emphasized fish tagged in NY Harbor. Nevertheless, from a broad regional perspective, the LEC showed a higher affinity for a mix of NY Harbor and coastal habitats than did the other 2 contingents (Figs. 5 & 7, Table 3). At finer resolution, apparent in the cluster analysis (Fig. 6), contingent sub-groups were identified with varying affinities for more exclusive NY Harbor incidence or increased reliance on either western Long Island or more distant coastal regions.

The UEC showed expected patterns of residency throughout most of the year (Wingate & Secor 2007), with the exception of winter where they occupied other regions including Haverstraw Bay (lower estuary), NY Harbor, and coastal areas (Table 3). No striped bass were observed to remain in the upper estuary during winter months. Previous findings of completely resident freshwater behaviors by Hudson River striped bass (Secor & Piccoli 1996, Ashley et al. 2000) were likely biased because they relied on otolith strontium and contaminant tracers, which incompletely represented winter migrations because tracers are not taken up during winter and other periods when fish are not growing (Zlokovitz et al. 2003). As in the telemetry study of Wingate & Secor (2007), the majority of UEC fish that displayed resident behaviors in both years (5 of 5 individuals) returned to the same stretch of river they occupied the previous year, via the same routes, indicating high seasonal site fidelity.

Also conforming to predicted behaviors, the OC spent the least amount of time in the upper or lower estuaries, appearing there solely during the spawning season (Figs. 3 & 5). This pattern supported the hypothesis that this contingent primarily uses the Hudson River and NY Harbor as migration corridors. High apparent losses by this contingent immediately following tagging were evident in the spring of 2010 (45% within 2 mo), the likely result of targeted recreational fishing on this contingent in the Hudson River. Another period of loss occurred 1 yr later (18%), again likely due to fishing mortality by anglers, as tagged fish were detected ascending the river and on the spawning grounds, but not exiting.

Receiver coverage limited our ability to characterize contingent migrations. In particular, when fish movement is reduced, or occurs in regions with limited coverage, biased inferences are expected. This is evident during winter months, when movement rates are expected to decline. Characterization of contingent migrations may have also been complicated by sudden shifts in contingent membership (Zlokovitz et al. 2003). If telemetered individuals shifted their behavior during the study period, our estimates of within-contingent complexity would be biased high.

Within-contingent diversity and partial migration

The multiple statistical approaches used in this study complemented each other to confirm general contingent behaviors while also documenting previously unknown levels of migratory diversity. The PCA (Figs. 4 & 5, Table 2) and contingency table analysis (Table 3) corroborated each other, providing a weight of evidence for contingent structure in the Hudson River striped bass population. Although each contingent can be described generally, the cluster analysis suggested a broader set of migratory patterns, particularly for the LEC (Fig. 6; also see the Supplement). These results do not invalidate contingent structuring; conversely, they demonstrate meaningful fine-scale diversity in individual movements.

There were several obvious misfits to the presumed contingent assignments. These fish are representative of the complex fine-scale behaviors described by the cluster analysis, but the broad patterns of behavior within contingents were detectable despite these influences. A single UEC fish (ID = 6) showed an affinity to NY Harbor and near coastal habitats and also migrated to Delaware Bay in winter. A single large spawning adult (ID = 50, TL = 940 mm) that was classified as an OC individual was clearly a resident UEC fish, supporting the results of Zlokovitz & Secor (1999) who found evidence for large resident individuals. Several LEC fish showed affinities to coastal habitats and undertook significant seasonal coastal migrations, akin to OC individuals. Many adult-sized fish (16/49) detected throughout the 18 mo study period did not partake in a spawning run and an additional 12 fish spawned in only 1 year (Table 4). However, several LEC striped bass (IDs = 13, 20, 24, 33) were detected during spring in the Delaware Estuary and were likely not natal to the Hudson River. A number of LEC fish (n = 13) resided in the harbor during the summer but migrated to coastal Delaware and Maryland in the winter (e.g. Fish IDs = 13, 21, 31, and 38), a behavior not documented in the literature but corroborated by conventional tagging data (K. Hattala pers. comm.).

The varied migration behaviors observed in this study likely represent the action of multiple types of partial migration that influences contingent structure. Theoretical explanations for partial migration have focused on early life condition thresholds (Dodson et al. 2013), which cause individuals to adopt resident or migratory behaviors, as evidenced by the white perch *Morone americana*, a sympatric congener of striped bass (Kraus & Secor 2004, Kerr & Secor 2009). Although not specifically demonstrated here, such mechanisms could underlie resident and migratory behaviors in Hudson River striped bass. One type of partial migration is differential or size- and sex-dependent migration (Chapman et al. 2012), which has often been ascribed to coastal striped bass (Waldman et al. 1990, Dorazio et al. 1994, Secor & Piccoli 2007). In this study, size differences existed among contingents, but fish that underwent coastal migrations came from as broad a range of sizes (460–975 mm) as those that did not (410–940 mm; Table 3; also see the Supplement), suggesting that partial migration influences contingent structure in ways not strictly attributable to size. Importantly, contingent membership is not static, as otolith tracer studies have shown that adult striped bass can shift their behaviors from resident to migratory or vice versa (Zlokovitz et al. 2003). The precise forces that influence contingent switching could be event driven (e.g. weather, abrupt food web changes) but remain unknown and should be the focus of further study.

Individual movements and migration behaviors can have important ramifications on population connectivity and dynamics (Frisk et al. 2013), and this is demonstrated by the contingent behaviors of Hudson River striped bass. In our study, the majority (55%; 28/51) of striped bass examined made excursions to coastal habitats and non-natal estuaries. Coastal migrations were diverse; 6 individuals were detected by receiver arrays both north and south of the Hudson River, but 12 fish were detected only to the north and an additional 10 fish only to the south. These movements provide an opportunity for differential environmental and anthropogenic pressures (e.g. harvest) on specific population segments. This is especially germane when considering striped bass, as some areas are open to commercial harvest while others are not. Due to PCB contaminants, no commercial harvest of striped bass is allowed within the Hudson River or nearby waters, so LEC individuals that remain solely within NY Harbor (i.e. striped bass in Group IV of the cluster analysis) would not be exposed to commercial harvest while those that occupied the area just east of the Long Island array would. Alternatively, an OC individual that migrates from the Hudson River to eastern Long Island Sound would not encounter a commercial fishery, while fish that forage off Massachusetts would be available to the largest commercial fishery in coastal waters (Kneebone et al. 2014).

During this study, telemetered fish demonstrated strong seasonal fidelity to habitat patches and migration pathways. For instance, striped bass made use of a wide variety of artificially structured habitats within NY Harbor (e.g. Belmont Island, anchorage areas), and telemetry results suggest that individuals are likely to home to these general areas year after year. Such 'conservative' movement behaviors are an emerging discovery general to telemetry studies for striped bass (Able & Grothues 2007, Ng et al. 2007, Wingate & Secor 2007, Pautzke et al. 2010, Wingate et al. 2011) and indeed to other marine fishes (Secor 2015). Stresses to striped bass, such as fishing hot spots and habitat alteration, are local in nature. When overlain by somewhat recalcitrant homing behaviors, these stresses are expected to have nonlinear effects (Petitgas et al. 2010).

Urban estuaries as striped bass habitat

In comparison to other estuaries that contribute to coastal mixed-stock striped bass fisheries (Delaware, Chesapeake, and Roanoke), NY Harbor and the lower estuary of the Hudson River are relatively small and highly urbanized, suggesting that the harbor may function more for transit than for feeding, growth, and survival. Telemetry results, particularly those for the LEC, strongly suggest otherwise. Estimates of extended seasonal habitat use in the harbor are likely biased low (due to patchy receiver coverage and periods of low movement), yet harbor receivers detected sustained habitat use ranging from 5 to 6 mo for multiple individuals (Figs. 3, 7, & 8). Here we provide unique information that a contingent of striped bass persists across seasons and recurs between years, confirming Clark's (1968) original inferences on NY Harbor striped bass and underscoring the importance of estuary habitat for striped bass.

Findings from this study suggest that despite dredging, channelization, hardened shorelines, and pollution, NY Harbor and the surrounding urban estuary functions as essential habitat for striped bass by connecting reproductive habitats to coastal foraging and overwintering habitats as well as providing year-round foraging and wintering habitat for a central component (contingent) of adult and subadult striped bass. Further, the harbor provides a foraging habitat for striped bass that spawned in other estuaries (Fig. 3). The Hudson River hosts large spawning populations of river herring *Alosa pseudoharengus, A. aestivalis*, and American shad *A. sapidissima*, and evidence exists that predatory gauntlets within the lower estuary and NY Harbor shape cohort abundance in those species (Limburg 2001). The overlap of small alosine prey with striped bass and other piscivores suggests that the harbor could function as a foraging arena, a role that may have been of greater importance when river herring and American shad were at higher historical abundance (Hall et al. 2012).

This examination of contingent structure demonstrated that the diverse behaviors of individual striped bass can be aggregated and together have potential impacts at a population scale. These conclusions were supported by an experimental design and quantitative methods that allowed specific hypotheses to be tested. Our approach emerged from an awareness of our desired questions and relied on multiple analyses to interrogate a complicated set of data. The study design and methods should be transferable to other species and locations where broad-scale movements are examined. Telemetry and other 'digital age' technologies (Secor in press) provide unparalleled detail on the movements of fishes, and as quantitative methods develop, these tools will become even more informative.

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LITERATURE CITED

Able KW, Grothues TM (2007) Diversity of estuarine movements of striped bass (*Morone saxatilis*): a synoptic examination of an estuarine system in southern New Jersey. Fisheries 105:426–435

Ashley JTF, Secor DH, Zlokovitz E, Baker JE, Wales SQ (2000) Linking habitat use of Hudson River striped bass to accumulation of polychlorinated biphenyl congeners. Environ Sci Technol 34:1023–1029

Chapman BB, Brönmark C, Nilsson JA, Hansson LA (2011) The ecology and evolution of partial migration. Oikos 120:1764–1775

Chapman BB, Skov C, Hulthén K, Brodersen J, Nilsson PA, Hansson LA, Brönmark C (2012) Partial migration in fishes: definitions, methodologies and taxonomic distribution. J Fish Biol 81:479–499

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

Dodson JJ, Abin-Horth N, Thériault V, Páez DJ (2013) The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biol Rev Camb Philos Soc 88: 602–625

Dorazio RM, Hattala KA, McCullough CB, Skjeveland JE (1994) Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. Trans Am Fish Soc 123:950–963

Frisk MG, Jordaan A, Miller TJ (2013) Moving beyond the current paradigm in marine population connectivity: Are adults the missing link? Fish Fish 15:242–254

Fromentin JM, Powers JE (2005) Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. Fish Fish 6:281–306

Gilbert CH (1915) Contributions to the life history of the sockeye salmon. British Columbia Fisheries Department, Vancouver, BC

Hall CJ, Jordaan A, Frisk MG (2012) Centuries of anadromous forage fish loss: consequences for ecosystem connectivity and productivity. BioScience 62:723–731

Hjort J (1914) Fluctuations in the great fisheries of Northern Europe. Conseil Permanent International Pour L'exploration de la Mer 20:1–228

Kerr LA, Secor DH (2009) Bioenergetic trajectories underlying partial migration in Patuxent River (Chesapeake Bay) white perch (*Morone americana*). Can J Fish Aquat Sci 66:602–612

Kerr LA, Piccoli PM, Secor DH (2009) Partial migration as exemplified by the estuarine-dependent white perch. Fisheries 34:114–123

Kerr LA, Cadrin SX, Secor DH (2010) Simulation modeling as a tool for examining the consequences of spatial structure and connectivity to local and regional population dynamics. ICES J Mar Sci 67:1631–1639

Kneebone J, Hoffman WS, Dean MJ, Armstrong MP (2014) Movements of striped bass between the Exclusive Economic Zone and Massachusetts state waters. N Am J Fish Manag 34:524–534

Kraus RT, Secor DH (2004) Dynamics of white perch *Morone americana* population contingents in the Patuxent River estuary, Maryland, USA. Mar Ecol Prog Ser 279:247–259

Limburg KE (2001) Through the gauntlet again: demographic restructuring of American shad by migration. Ecology 82:1584–1596

McGarigal KS, Cushman SA, Stafford SG (2000) Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York, NY

Ng CL, Able KW, Grothues TM (2007) Habitat use, site fidelity, and movement of adult striped bass in a southern New Jersey estuary based on mobile acoustic telemetry. Trans Am Fish Soc 136:1344–1355

Pautzke SM, Mather ME, Finn JT, Deegan LA, Muth RM (2010) Seasonal use of a New England estuary by foraging contingents of migratory striped bass. Trans Am Fish Soc 139:257–269

Petitgas P, Secor DH, McQuinn I, Huse G, Lo N (2010) What is a collapsed stock and what is required for its recovery? Mechanisms that sustain and establish life-cycle closure in space and time. ICES J Mar Sci 67:1841–1848

Secor DH (1999) Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fish Res 43: 13–34

Secor DH (2015) Migration ecology of marine fishes. Johns Hopkins University Press, Baltimore, MD

Secor DH, Piccoli PM (1996) Age- and sex-dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. Estuaries 19:778–793

Secor DH, Piccoli PM (2007) Determination of frequency of anadromous migrations by Chesapeake Bay striped bass based upon otolith microchemical analysis. Fish Bull 105: 62–73

Secor DH, Rooker JR, Zlokovitz E, Zdanowicz VS (2001) Identification of the riverine, estuarine, and coastal contingents of Hudson River striped bass based upon elemental fingerprints. Mar Ecol Prog Ser 211:245–253

Secor DH, Kerr LA, Cadrin SX (2009) Connectivity effects on productivity, stability, and persistence in an Atlantic herring metapopulation. ICES J Mar Sci 66:1726–1732

Tsukamoto K, Nakai I, Tesch WV (1998) Do all freshwater eels migrate? Nature 396:635–636

Waldman JR, Dunning DJ, Ross QE, Mattson MT (1990) Range dynamics of Hudson River striped bass along the Atlantic Coast. Trans Am Fish Soc 119:910–919

Wingate RL, Secor DH (2007) Intercept telemetry of the Hudson River striped bass resident contingent: migration and homing patterns. Trans Am Fish Soc 136:95–104

Wingate RL, Secor DH, Kraus RT (2011) Seasonal patterns of movement and residency by striped bass within a subestuary of the Chesapeake Bay. Trans Am Fish Soc 140:1441–1450

Zar J (1999) Biostatistical analysis, 4th edn. Prentice-Hall, Upper Saddle River, NJ

Zlokovitz ER, Secor DH (1999) Effect of habitat use on PCB body burden in Hudson River striped bass *Morone saxatilis.* Can J Fish Aquat Sci 56:86–93

Zlokovitz ER, Secor DH, Piccoli PM (2003) Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. Fish Res 63:245–259

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