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**Movements of Young Striped Bass out of the Hudson River  
in Relation to Age, Length, and Abundance**

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### Abstract

We investigated the relationship between the abundance of young striped bass *Morone saxatilis* of the Hudson River and their age- and size-related dispersion outside of the river. Results from a standardized recruitment index showed that between 1985 and 1990, the Hudson River experienced record low recruitment of striped bass, followed by record high recruitment, and ending with moderately high recruitment. From March 1986 through February 1992, subadult striped bass were recaptured by anglers within one year after these fish were tagged and released in the lower Hudson River. The annual distributions of recaptured striped bass ( $n = 2055$ ; ages 1 and 2) over this period of extreme fluctuation in abundance were examined to determine if there was evidence of density-dependence in two independent measures of dispersion: (1) the proportion of striped bass recaptured inside and outside of the Hudson River, and (2) the distance traveled from the river mouth for those fish recaptured outside of the river. Both the proportions of striped bass recaptured outside the Hudson River, and the mean distance at recapture from the mouth of the river increased significantly ( $P < 0.05$ ) for the age-1 cohorts as the number of young striped bass in the population increased; these measures decreased near the end of the study, possibly in response to the effects of moderating recruitment levels. However, the proportions of age-2 striped bass caught inside and outside the Hudson River did not vary significantly among years, whereas the mean distance from the mouth of the river did vary significantly, showing a similar pattern to the age-1 fish, but with a one year lag. Regression analyses among years of distances traveled outside of the Hudson River showed a stronger influence for fish length than for age. The most likely reason for the increased migration out of the Hudson River and of distances outside of the river from its mouth of subadult striped bass was a density-dependent lowering of the threshold at which a portion of the population adopted a migratory behavior.

### Introduction

Striped bass *Morone saxatilis* from the Hudson River estuary comprise one of the major Atlantic coast migratory striped bass stocks (Richards and Deuel 1987; Waldman and Fabrizio 1994). Mark-recapture (Raney et al. 1954; Clark 1968; McLaren et al. 1981) and chemical microanalysis of otoliths (Secor and Piccoli 1996) have shown that many of these striped bass move into and out of the Hudson River annually. Striped bass that exit the river range as far north as Nova Scotia and southward to North Carolina (Waldman et al. 1990).

The abundances of striped bass populations are known to fluctuate widely, due to changes in both environmental conditions and harvest rates (Richards and Deuel 1987); shifting abundances may affect the geographic distribution of a fish population across years (MacCall 1990; Swain and Wade 1993). In Chesapeake Bay, it has twice been observed that the proportion of striped bass that emigrated from the bay increased with an increase in

abundance (Merriman 1941; Kriete et al. 1979). When striped bass in the Hudson River became more abundant, their range along the Atlantic coast expanded (Waldman et al. 1990).

We examined movements between 1985 and 1992 of striped bass tagged annually in the lower Hudson River, a period in which the Hudson River experienced extremes in striped bass recruitment. Based on a standardized juvenile abundance survey (Figure 1) begun in 1976 (McKown and Young 1992), the striped bass population in the Hudson River experienced record low recruitment (1985) and the record third lowest year (1986), followed by a record high year (1987), the record second highest year (1988), and two more high indices (1989 and 1990; Young et al. 1993). Thus, we were able to examine the geographic distribution of recaptures of tagged fish for evidence of density-dependent effects on the dispersion of the population during a period of great variation in density.

#### Methods

From November 1985 through April 1990, striped bass were captured, marked with an internal anchor tag (Floy FTF-69 or Hallprint), and released from mid-autumn until early spring in the Hudson River between river kilometers (km) 0 and 23. Until the 1988-1989 release period, all fish marked were 200 mm total length or greater. During subsequent release periods the minimum size marked was 150 mm (all lengths reported are total length). Otter trawls were used to capture striped bass for tagging. Field procedures are outlined in Dunning et al. (1989) and Mattson et al. (1990). Scales were removed from the flank below the dorsal fins; they were later used to estimate the age of the individuals tagged, released, and later recaptured.

Minimum rewards of either \$5 or \$10 were paid for the return of tags. Anglers who completed a questionnaire, sent with the reward, were entered into an annual drawing for nine rewards ranging from \$100 to \$1000.

Our recapture year was 1 March through February of the following year. We categorized recaptures by their length when released because we believed that these data were more reliable than lengths at recapture reported by anglers, inasmuch as release data were collected using a quality assurance/quality control program (Geoghegan et al. 1990). We restricted our analysis to striped bass recaptured within the first year following release because we knew for certain the geographic location of these fish prior to the spring migration period and because we believed that growth differences among individuals would not yet be substantial.

Statistical analyses were conducted using a restricted data set ( $n = 2055$ ) in which particular variables were equivalent across recapture years. Thus, only striped bass greater than or equal to 200 mm TL that were successfully aged were included, and only those of age-1 or age-2 because

sample sizes of both younger and older age classes were too small for interannual comparison. Also, only angling recaptures were included because we believed that commercial or research-based recaptures were strongly biased geographically.

The Hudson River was delimited as the waters north of the southern tip of Manhattan Island (km 0). The relationship between fish length and month of recapture was analyzed with linear regression (PROC GLM; SAS 1987). Chi-square contingency table tests were used (with an alpha level of 0.05) to test for differences in the proportions of recaptures outside of the Hudson River to total recaptures within age categories (Sokal and Rohlf 1969).

We used analysis of variance (ANOVA) to test for differences among years in the distance from the mouth of the river of recaptures, by age class, and for the two age classes combined, and analysis of covariance (ANCOVA) in parallel fashion but with fish length as a covariate (PROC GLM; SAS 1987). Multiple comparisons were made with Scheffe's test and an alpha level of 0.05. Correlation analysis (PROC CORR; SAS 1987) was used to examine the relationship between distance traveled outside of the Hudson River and fish length by age and recapture year. Multiple regression was used to explore the relationship among years between distance from the mouth of the river of recaptures and both fish length and age (PROC GLM; SAS 1987).

#### Results

There did not appear to be a meaningful temporal effect on the lengths of fish recaptured within their first year at large. Among the six recapture years, there was a significant relationship between fish length and recapture month only for the 1989-1990 recapture year ( $F$ -value = 5.63;  $P$  = 0.018). However, the relationship between fish length and recapture month for only those striped bass recaptured outside of the Hudson River was not significant for the 1989-1990 recapture year or for any other recapture years.

The proportions of striped bass recaptured in the Hudson River among recapture years declined to their minima for both ages 1 and 2 in the 1988-1989 and 1989-1990 recapture years, before returning in 1990-1991 and 1991-1992 to approximately the same levels observed in the 1986-1987 and 1987-1988 recapture years (Table 1). The differences among years in the proportions of striped bass recaptured inside and outside of the Hudson River were significant for age-1 ( $\chi^2$  = 19.86;  $P$  = 0.001) but not for age-2 ( $\chi^2$  = 4.25;  $P$  = 0.499) fish.

For age-1 striped bass, the mean distance from the mouth of the Hudson River to recapture site only for individuals recaptured outside of the river more than doubled between the 1986-1987 and 1989-1990 recapture years, before declining over the two subsequent years (Table 2). Age-2 striped bass showed a similar pattern, but they demonstrated a peak in mean distance traveled one

year later (1990-1991) than age-1 fish (Table 2).

Differences among recapture years in distances traveled from the Hudson River by age class were also compared using ANOVA and ANCOVA (Table 2). Both tests were highly significant ( $P < 0.0001$ ) for both age-1 and age-2 fish, although the  $F$ -values obtained were greater with the effects of length removed using ANCOVA. The Scheffe multiple comparison test showed significant differences among recapture years within each of the two age classes (Table 2). When the two age classes were combined, both ANOVA ( $F = 9.67$ ;  $P = 0.0001$ ) and ANCOVA ( $F = 20.20$ ;  $P = 0.0001$ ) showed highly significant differences among recapture years in distances traveled outside the Hudson River.

Correlations between striped bass length and distance traveled outside of the Hudson River for age-1 fish were nonsignificant only for the 1986-1987 and 1987-1988 recapture years, and were highly significant thereafter (Table 3). For age-2 striped bass, these correlations were nonsignificant for the first three recapture years, but were significant over the subsequent three recapture years (Table 3).

Regression analyses of distances traveled among years from the Hudson River for the two age classes combined that involved fish length, age, and a fish length  $\times$  age interaction term alone, or in several combinations, showed a stronger influence for fish length than for age. Age alone had very little explanatory power ( $r^2 = 0.005$ ;  $F = 5.64$ ;  $P = 0.0177$ ), whereas length alone provided an increase in  $r^2$  to 0.012 and a highly significant  $F$ -value (13.81;  $P = 0.0002$ ). Addition of age or age and an length  $\times$  age interaction term resulted in slightly higher and equivalent  $r^2$  values (0.049) with high significance ( $P < 0.0001$ ). However, for the later Type III model, length alone was significant ( $P = 0.0006$ ), but not age alone ( $P = 0.7640$ ) nor length  $\times$  age ( $P = 0.1637$ ).

#### Discussion

During the six years of our study, the change in recapture proportions inside and outside of the Hudson River for age-1 and age-2 striped bass greater than 200 mm long may be attributable to a change in the proportion of these fish that exited the Hudson River. It is likely that the cause for this increased emigration is linked to density dependent factors. The abundance of juvenile striped bass in the Hudson River during 1987 was the highest recorded between 1976 and 1990 (Figure 1), the 1988 value was the second highest, and the 1989 value also was high (Young et al. 1991). Given these indices, the total abundance of striped bass of ages 0 - 2 during the 1989-1990 recapture period should have been extremely high, inasmuch as it would have included three consecutively large cohorts. This is supported by population estimates from this same mark-recapture study, i.e., CESI (1991) found that the record low juvenile abundance indices from 1985 and 1986 resulted in estimated cohort

sizes at age-2 of less than 300,000 fish, whereas the record high indices of 1987 and 1988 produced cohort sizes at age-2 of more than 1 million fish. Thus, we hypothesize that the increasing trend in movement out of the river observed between the 1988-1989 and 1990-1991 recapture years was due to intraspecific interactions that became more intense as the number of young striped bass built-up from several years of high recruitment that followed two years of very low recruitment.

These findings suggest that age-specific annual life history patterns for young Hudson River striped bass are not static, but instead are linked with abundance. Hudson River striped bass display contrasting life cycles across their age spectrum, i.e., complete residence within the river for young fish, and residence outside the river for large fish that only use the river briefly for spawning. Between these extremes, a portion of the stock migrates and returns to the river annually to winter, and a portion of these may have spawned before migrating. At any given time, younger Hudson River striped bass are clearly less migratory than older fish. However, the thresholds between the non-migratory and migratory modes, as defined by age- or size-classes, may not be constant among years.

Gross (1987) provided evidence that migration of populations is favored when the gain in fitness from using the second habitat minus the costs of migration, exceeds the costs of remaining in the first habitat. The most important variable influencing whether migration occurs is the relative availability of food in fresh- and seawater habitats (Gross 1987); intraspecific competition for food among young striped bass within the Hudson River should intensify as their numbers increase. Juvenile and yearling striped bass demonstrate considerable overlap in food habits (Gardinier and Hoff 1982) in the Hudson estuary, as do size classes of striped bass less than 350 mm in other estuaries (e.g., Stevens 1966; Manooch 1973; Rulifson and McKenna 1987). McKown and Young (1992) also observed a possible density dependent effect on young striped bass over this period. They examined the mean length of age-0 Hudson River striped bass by sampling week during the annual juvenile abundance survey. Mean lengths during the two low recruitment years (1985 and 1986) were significantly greater ( $P < 0.05$ ) than during the two high recruitment years (1987 and 1988). Also, the standardized index of age-1 striped bass in the bays outside of the Hudson River showed a high correlation ( $r = 0.95$ ;  $P < 0.003$ ) with the combined Hudson River seine and trawl recruitment indices over the period of 1984-1989 (Young et al. 1991).

The more than 250% increase in mean distance of recapture from the Hudson River of age-1 striped bass between the 1985-1986 and 1989-1990 recapture periods is also consistent with a greater total abundance of that length class and a higher proportion of these fish outside of the river. In his review, MacCall (1990) showed that for many species, the density dependent

expansion of their ranges at times of high abundance is accomplished at the expense of occupying suboptimal habitats. Moreover, Swain and Wade (1993) suggested that the geographic pattern of basic habitat suitability may be best inferred from regional variation in population density at low abundances. If the changes we observed in the dispersion of these fish is due to density dependent habitat selection (in the broad sense, including food availability), then we infer that habitat suitability for young striped bass decreases with distance from the river, and the river habitat is more optimal than habitat outside the river.

Observations from the Connecticut River (150 km east of the Hudson River) support the view that riverine habitat is the preferred habitat of young striped bass. The Connecticut River has an approximately equal freshwater flow to the Hudson River but it does not have a spawning population of striped bass. Nonetheless, the Connecticut River hosts large numbers of subadult striped bass (Kynard and Warner 1987) of almost certain Hudson River origin (Wirgin et al. 1990); during 1980-1982, 80-90% of these fish were age 2.

An alternative to account for the changing proportions of subadult striped bass caught inside and outside of the Hudson River between 1986 and 1993 are regional fluctuations in fishing pressure directed at that size class. However, no changes in fishing regulations occurred during this time that would be likely to foster such a shift. Between March 1986 and February 1992, the minimum length north of the George Washington Bridge (km 23) remained at 457 mm while the possession limit remained at one fish per day. In New York State's marine district (waters south of the George Washington Bridge and outside of the Hudson River), the only change in recreational length limits was an increase from 838 mm to 914 mm in 1989. Additionally, no commercial fishing was allowed for striped bass in New York between March 1986 and February 1991. Therefore, we conclude that the most likely reason for the increased migration out of the Hudson River of subadult striped bass was a density-dependent lowering of the threshold at which a portion of the population adopted a migratory behavior.

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TABLE 1.-Proportions of striped bass recaptured inside and outside of the Hudson River within first year following tagging, by age at release and recapture year.

Recapture year	Age-1 only			Age-2 only		
	Inside river	Outside river	N	Inside river	Outside river	N
1986-1987	25.7	74.3	70	34.2	65.8	76
1987-1988	35.8	64.2	67	28.2	71.8	206
1988-1989	20.3	79.7	197	25.0	75.0	100
1989-1990	19.0	81.0	336	20.6	79.4	63
1990-1991	23.6	76.4	279	31.2	68.8	112
1991-1992	32.7	67.3	211	29.3	70.7	338

TABLE 2.-Number and mean distance (km) from the mouth of the Hudson River of striped bass initially tagged and then recaptured outside of the river within one year of release. Scheffe test is a multiple comparison test; rows with the same letter for a given age group are not significantly different. ANOVA tested for among-recapture year differences within an age group; ANCOVA was performed identically but with fish length as a covariate.

Recapture year	Age-1			Age-2		
	N	Mean distance (km)	Scheffe test	N	Mean distance (km)	Scheffe test
1986-1987	52	30.3	B	50	22.4	B
1987-1988	43	36.1	B	148	31.5	B
1988-1989	157	56.3	A B	75	54.9	A B
1989-1990	304	79.9	A	50	64.0	A B
1990-1991	248	45.5	A B	77	85.8	A
1991-1992	151	42.2	B	239	76.9	A B
ANOVA						
F-value		9.27			5.41	
P		0.0001			0.0001	
ANCOVA						
F-value		17.01			10.11	
P		0.0001			0.0001	

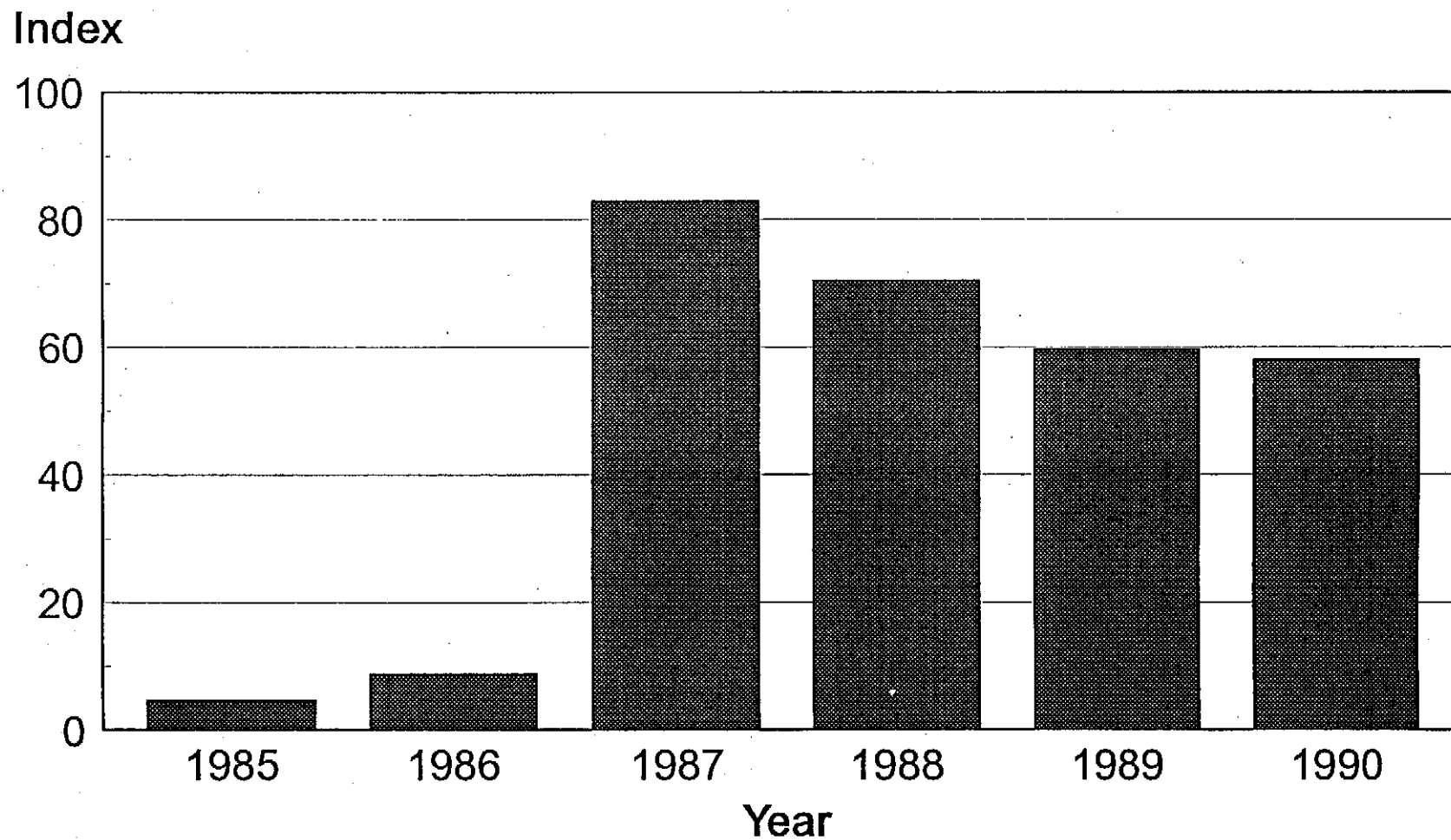
TABLE 3.--Levels of correlation between lengths of striped bass at release vs. distances traveled outside the Hudson River, by recapture year, for age-1 and age-2 fish.

Recapture year	Age-1			Age-2		
	N	Correlation coefficient	P	N	Correlation coefficient	P
1986-1987	52	0.198	0.1604	50	-0.006	0.9643
1987-1988	43	-0.011	0.9459	148	0.087	0.2910
1988-1989	157	0.208	0.0089	75	0.057	0.6256
1989-1990	272	0.272	0.0001	50	0.281	0.0494
1990-1991	213	0.261	0.0001	77	0.350	0.0018
1991-1992	142	0.280	0.0008	239	0.267	0.0001

**Figure 1.-Hudson River index of relative abundance (catch per seine haul; nine-week survey) of age-0 striped bass from 1985 - 1990.**

Year	Month	Index	Year	Month	Index
1985	May	10	1989	May	10
1985	June	10	1989	June	10
1985	July	10	1989	July	10
1985	August	10	1989	August	10
1985	September	10	1989	September	10
1985	October	10	1989	October	10
1985	November	10	1989	November	10
1985	December	10	1989	December	10
1986	May	10	1990	May	10
1986	June	10	1990	June	10
1986	July	10	1990	July	10
1986	August	10	1990	August	10
1986	September	10	1990	September	10
1986	October	10	1990	October	10
1986	November	10	1990	November	10
1986	December	10	1990	December	10

Figure 1.-Hudson River index of relative abundance (catch per seine haul; nine-week survey) of age-0 striped bass from 1985 - 1990.



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the 1990s, the number of people in the world who are illiterate has increased from 1.2 billion to 1.5 billion. The number of illiterate people in the world is expected to reach 1.7 billion by the year 2015. The number of illiterate people in the world is expected to reach 1.7 billion by the year 2015. The number of illiterate people in the world is expected to reach 1.7 billion by the year 2015.