

Abundance exchange models of fish assemblages along the Hudson River Estuary Gradient, New York

Nuanchan Singkran and Mark B. Bain

ABSTRACT

The spatially explicit abundance exchange model (AEM) was built for four fish species: winter flounder (*Pseudopleuronectes americanus*), Atlantic silverside (*Menidia menidia*), eastern silvery minnow (*Hybognathus regius*), and striped bass (*Morone saxatilis*) along the Hudson River estuary gradient, New York. The fish and habitat data during 1974–1997 were used to develop and calibrate the AEM; and the fish data during 1998–2001 was used to validate the model. Preference indexes of fish species for dissolved oxygen, salinity, water temperature, and bottom substrates along the gradient were estimated; and these were used to compute habitat preference (HP) of the associated fish species. The species HP was a key variable in the AEM to quantify abundance and distribution patterns of the associated species along the gradient. The AEM could efficiently predict abundance and distribution patterns of all modeled species except striped bass. The model ability for predicting a local distribution range of a fish species with broad tolerance on changing environment like striped bass should be improved.

Key words | distribution, habitat preference, modeling

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INTRODUCTION

In estuaries, gradients of change in physical factors (e.g., salinity, water temperature, and dissolved oxygen) often define the breadth of species distribution in space (Ray & Hayden 1992) and shape species abundance patterns in time. Abundance and distribution are influential features indicating population dynamics (Tilman & Kareiva 1997; Turchin 1998) and reflecting habitat utilizations of species (e.g., Winemiller & Leslie 1992; Willis & Magnuson 2000; Jackson *et al.* 2001; Martino & Able 2003). However, both abundance and distribution are rarely investigated in concert although they are elements of the same problem (Andrewartha & Birch 1954). Studies of species distribution ignore the temporal dimension of population dynamics by taking a snapshot of the spatial density of a population at a certain point in time or by averaging the population density over time. In contrast, studies of abundance ignore the spatial dimension and focus on temporal fluctuations in the number of organisms at a particular point, or the average over a large area (Turchin 1998).

In this study, an abundance exchange model was built for four fish species based on fish preferences on changing physical variables along the Hudson River estuary gradient, New York. The objectives of the study were to 1) use key physical habitat variables of the study gradient to model distribution and abundance patterns of fish species in space and time, respectively and 2) explore the local distribution range of each species on the gradient.

MATERIALS AND METHODS

Hudson River estuary gradient

The study gradient started from the river kilometer (RKM) 19 (region 1) in New York City to the RKM 246 (region 12) at Troy's Federal Dam in Albany, New York State (Figure 1). Water salinity is 18–30 ppt in the lowest zone

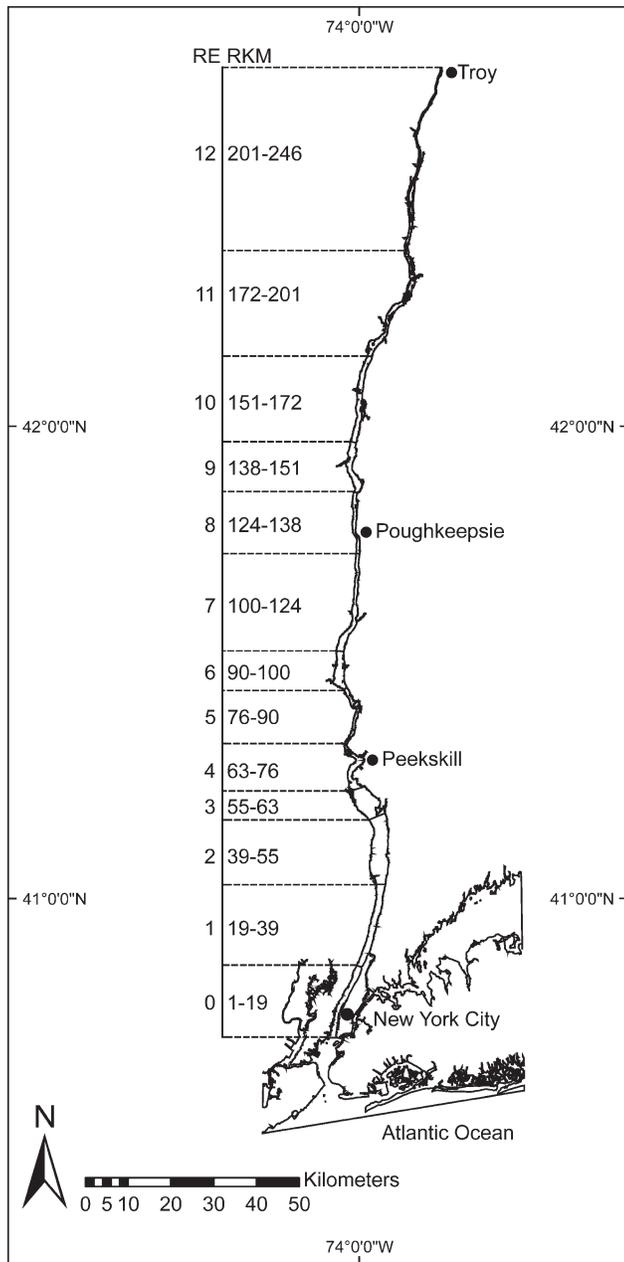


Figure 1 | The Hudson River estuary gradient. The gradient range was divided into 13 regions (RE) within 4 zones: the lowest (RKM 1–19), the lower (RKM 19–61), the middle (RKM 61–122), and the upper (RKM 122–246) zones.

(RKM 1–19) of the gradient; and it varies between mesohaline and oligohaline in the lower (RKM 19–61) and the middle (RKM 61–122) zones depending on tide and freshwater flow. Water is usually fresh in the upper zone (RKM 122–246, *Strayer et al. 2004*).

Data sources

Fish abundance and species richness, dissolved oxygen, salinity, and water temperature from the beach seine survey (BSS) of the five power plant utilities' Hudson River Estuary Monitory Program (HREMP) during 1974–2001 were used. Substrate data used were from a combination of the BSS during 1974–2001 and New York State Department of Environmental Conservation during 1998–2003.

Abundance exchange model development

The spatially explicit AEM was built based on the non-Fick's law of dispersion (*Johnson et al. 1992*). In the AEM, the migration rate (k) of each fish species varied in relation to the species habitat preference (HP) along the gradient. The HP of a modeled species at each life stage (i.e., 0 + year-and 1 + year-old) is estimated as:

$$HP = \left(\prod_{x=1}^N Pi_x \right)^{1/N} \quad (1)$$

Pi_x is a species preference index for each habitat variable x ($x = 1, 2, 3, \dots, N$) and can be written as:

$$Pi_x = \frac{(F_j/F_t)}{(E_j/E_t)} \quad (2)$$

F_j is the number of individuals of a modeled species observed at an intensity interval j of a habitat variable x . F_t is the total number of individuals of a modeled species observed from all intensity intervals j of a habitat variable x . E_j is the number of observations for a habitat variable x at an intensity interval j . E_t is the total number of observations for a habitat variable x from all intensity intervals j . N is the total number of the habitat variables. To obtain the index between 0 and 1, the Pi_x on each interval j is normalized (i.e., $Pi_{x,j}/Pi_{x,jmax}$). The species HP was then computed using the Equation (1), and it was the key variable in the main equations (Equation 3 and Equation 4 below) to simulate

the AEM for each modeled species

$$\begin{aligned} \frac{dA_n}{dt} = & (ak_{n-1,n} \times A_{n-1}) + (ak_{n+1,n} \times A_{n+1}) - (r_d \times A_n) \\ & - \left[\left(\frac{aHP_{n-1}}{aHP_{n-1} + aHP_{n+1} + \varepsilon} \right) \right. \\ & \left. + \left(\frac{aHP_{n+1}}{aHP_{n-1} + aHP_{n+1} + \varepsilon} \right) \right] \times (ak_n \times A_n) \end{aligned} \quad (3)$$

$$\begin{aligned} \frac{dY_n}{dt} = & (yk_{n-1,n} \times Y_{n-1}) + (yk_{n+1,n} \times Y_{n+1}) + f(Y_n) \\ & - \left[\left(\frac{yHP_{n-1}}{yHP_{n-1} + yHP_{n+1} + \varepsilon} \right) + \left(\frac{yHP_{n+1}}{yHP_{n-1} + yHP_{n+1} + \varepsilon} \right) \right] \\ & \times (yk_n \times Y_n) \end{aligned} \quad (4)$$

In Equation (3), A_n is the population of a fish species at 1 + year-old stage in habitat n , ak_n is a migration rate of A out of habitat n , whereas $ak_{n-1,n}$ and $ak_{n+1,n}$ are migration rates of A from habitat $n - 1$ and $n + 1$, respectively, to habitat n . In Equation (3), ak_n equals $(1 - aHP_n)$ over time t . The rest migration rates of A in habitats $n - 1$ and $n + 1$ are computed in the same way. The aHP_n , aHP_{n-1} , and aHP_{n+1} are the HPs of A in habitats n , $n - 1$, and $n + 1$, respectively. The natural mortality of A_n in the growing season is ignored, but it is considered in winter; and it is computed by multiplying the death fraction r_d of fish over the winter months by the fish population that survives winter in habitat n .

In Equation (4), Y_n is the population of a fish species at 0 + year-old stage in habitat n , yk_n migration rate of Y out of habitat n , whereas $yk_{n-1,n}$ and $yk_{n+1,n}$ are migration rates of Y from habitat $n - 1$ and $n + 1$, respectively, to habitat n . In Equation (4), yk_n equals $(1 - yHP_n)$ over time t . The rest migration rates of Y habitats $n - 1$ and $n + 1$ are computed in the same way. The yHP_n , yHP_{n-1} , and yHP_{n+1} are the HPs of Y in habitats n , $n - 1$, and $n + 1$, respectively. The birth of a fish species in habitat n , for example, is represented by a logistic growth model, $f(Y_n)$, where $f(Y_n)$ equals $r_b \times (A_n) \times (1 - Y_n/C_y)$. That is, the birth of Y_n depends on A_n abundance, birth fraction r_b , and carrying capacity C_y of Y_n . A small number ε (e.g., $\varepsilon \leq 10^{-6}$) is added to each equation to avoid zero denominators in case the species HP at each life stage in any habitat becomes zero at

a certain time t of simulation. The total population P of a fish species in habitat n equals $A_n + Y_n$.

Four modeled fish species were winter flounder (*Pseudopleuronectes americanus*), Atlantic silverside (*Menidia menidia*), eastern silvery minnow (*Hybognathus regius*), and striped bass (*Morone saxatilis*). Winter flounder is a valuable commercial and recreational marine species along the northwest Atlantic coast (Pereira *et al.* 1999). On the Hudson River estuary gradient, winter flounder were mainly observed at the river mouth where water is brackish. Atlantic silverside is an estuarine species; and it is ecologically important as forage for other fish and apparently a key member of the estuarine food web (Fay *et al.* 1983). On the Hudson River estuary gradient, Atlantic silversides showed a broader distribution range than winter flounder according to their higher tolerance on low salinity, but were rarely observed in the freshwater portion of the gradient. Eastern silvery minnow is a freshwater species and it was observed only at the upstream portion of the gradient where water is fresh. Striped bass is an anadromous species that spawns in tidal rivers and migrates to estuarine and marine coastal waters to feed and grow (McLaren *et al.* 1981). This species was observed throughout the Hudson River estuary gradient, but with varied abundance. Dissolved oxygen (DO), salinity, water temperature, and bottom substrates were used to estimate fish species HP. The model simulation was not done for region 0 because of the data unavailability from the HREMP at this region prior to 1996.

Model simulation and validation

The AEM was initiated by assigning individuals of each modeled fish species to certain Hudson regions (Table 1) where yearly average abundance of the associated species was frequently (>35%) observed over the 24-year period (1974–1997). Because of insufficient information to estimate carrying capacity C_y for each modeled species, the same value of C_y for all modeled species was assigned to all Hudson regions in the growing season (Table 1). Likewise, the same ranges of birth fraction r_b in the growing season and death fraction r_d in winter for each selected species were assigned to all Hudson regions (Table 1). From these initial conditions, the model generates a series of uniformly

Table 1 | Given initial values of necessary variables

Modeled fish	Initial no.of individuals	*Region	C _y	Population variables†	
				r _b	r _d
Winter flounder	50,000	1	8,000	0.20–0.40	0.05–0.08
Atlantic silverside	50,000	2	8,000	0.20–0.40	0.05–0.08
Eastern silvery minnow	25,000	11,12	8,000	0.40–0.60	0.05–0.10
Striped bass	50,000	1	8,000	0.30–0.35	0.10–0.15

*The regions where the modeled fish were observed > 35%.

†C_y = carrying capacity, r_b = birth fraction (month⁻¹), r_d = death fraction (month⁻¹).

distributed random values of population variables for each fish species in the associated seasons. To explore how the model would behave in a system in which a sharp change in each population variable might occur for some reason (e.g., food increase/decline, predator), $\pm 50\%$ changes in value of each population variable were assigned one at a time at all Hudson regions to rerun the model.

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The fish species P_{is} were estimated and calibrated from the fish and habitat data observed over the 24-year period (1974–1997, Table 2). Mean values of each habitat variable from the 1,632 samples during this period were classified into intervals using natural breaks (Jenks), one of the classification types in ArcGIS 9.1. Based on this method, the similar values for each habitat variable were grouped

together in the same interval, and the differences between intervals were maximized. A fish species P_i for each habitat variable at each classified interval was then estimated using Equation 2. Series of IF-THEN-ELSE statements (logical functions) were used to incorporate the species P_{is} at each interval for all habitat variables into the AEM for computing the species HP (Equation 1). The species migration rate *k* in the model was then converted from the species HP and used to quantify distribution pattern of that species over space.

Series of uniformly distributed random values of all dynamic habitat variables (except substrates) were generated based on the monthly mean values of the associated variables in each region over the 24-year observation (1974–1997). The distributed random values of each habitat variable along the gradient during January–March were generated from the observed values in December. The percentage substrate composition observed along the Hudson River estuary gradient was assumed to be constant over time (Hatzenbeler *et al.* 2000). The fish species P_{is} for gravelly mud and muddy gravel were not computed. These two substrate types were observed $\leq 2\%$ on the gradient.

The AEM was built and calibrated using monthly mean observed fish and habitat data along the Hudson River estuary gradient over the first 24-year period. Then, the model was validated against the monthly fish data available during July–October in the last 4-year period (i.e., 1998–2001). Briefly speaking, the AEM with its estimated P_{is} for each modeled fish species and the same assigned values of the fish population variables from the first 24-year period were used to predict the abundance and distribution patterns of the same species along the study gradient in the last 4-year period.

Table 2 | Preference index (Pi) for each habitat variable of each modeled fish species at two life stages (i.e., 0+ and 1+ yr-old) estimated from the 24-year beach seine fish and habitat data collected for the five power plant utilities' monitoring program along the Hudson River estuary gradient (regions 1–12) during 1974–1997

Habitat variables	Pi							
	Winter founder		Atlantic silverside		Eastern silvery minnow		Stripped bass	
	0 + yr	1 + yr	0 + yr	1 + yr	0 + yr	1 + yr	0 + yr	1 + yr
Dissolver oxygen (mg/L)								
4.6–6	1.00	0.53	0.28	1.00	0.00	0.02	1.00	1.00
6.1–8	0.14	0.36	1.00	0.58	1.00	1.00	1.79	0.36
8.1–12	0.16	1.00	0.81	0.49	0.19	0.40	0.44	0.80
12–17	0.02	0.00	0.15	0.01	0.00	0.01	0.12	0.05
Salinity (ppt.)								
<1	0.01	0.00	0.00	0.00	1.00	1.00	0.13	0.23
1–3.9	0.02	0.08	0.31	0.39	0.00	0.01	0.52	1.00
4–6.9	0.29	0.93	0.93	1.00	0.00	0.00	1.00	0.52
7–14	1.00	1.00	1.00	0.71	0.00	0.00	0.74	0.20
Water temperature (°C)								
1.1–8	0.18	0.03	0.00	0.00	0.00	0.01	0.01	0.00
8.1–15	0.51	1.00	0.05	0.18	0.01	0.36	0.15	0.02
15.1–22	0.74	0.70	0.32	0.73	0.03	0.41	0.42	0.07
22.1–27	1.00	0.28	0.45	1.00	1.00	1.00	1.00	1.00
27.1–29	0.60	0.07	1.00	0.78	0.17	0.70	0.84	0.00
Mud (%)								
5.1–15	0.00	0.00	0.00	0.00	1.00	1.00	0.09	0.13
15.1–27	0.68	0.80	0.74	0.92	0.00	0.02	0.41	0.37
27.1–31	0.01	0.06	0.06	0.00	0.01	0.01	0.49	0.23
31.1–38	1.00	1.00	1.00	1.00	0.00	0.00	1.00	1.00
38.1–69	0.01	0.00	0.14	0.10	0.00	0.00	0.25	0.44
Sandy mud (%)								
2.1–8	0.00	0.00	0.00	0.00	1.00	1.00	0.09	0.10
8.1–22	0.01	0.00	0.15	0.07	0.01	0.01	0.41	0.49
22.1–31	0.02	0.02	0.45	0.27	0.00	0.01	0.49	0.28
31.1–35	1.00	1.00	1.00	1.00	0.00	0.00	1.00	1.00
35.1–50	0.00	0.01	0.03	0.00	0.00	0.01	0.25	0.18
Sand (%)								
≤2	0.00	0.00	0.00	0.00	0.00	0.01	0.14	0.16
2.1–4	0.00	0.00	0.08	0.01	0.00	0.00	0.31	0.25
4.1–12	1.00	1.00	0.27	0.46	0.00	0.01	0.65	1.00
12.1–22	0.08	0.09	1.00	1.00	0.00	0.02	1.00	0.45
22.1–36	0.35	0.41	0.30	0.46	1.00	1.00	0.37	0.23
Muddy sand (%)								
<1	0.12	0.15	1.00	0.77	0.00	0.00	0.94	0.26
1.0–5	1.00	1.00	0.68	1.00	0.00	0.00	1.00	1.00
5.1–10	0.00	0.00	0.02	0.00	0.00	0.00	0.18	0.09

Table 2 | (continued)

Habitat variables	Pi							
	Winter founder		Atlantic silverside		Eastern silvery minnow		Stripped bass	
	0 + yr	1 + yr	0 + yr	1 + yr	0 + yr	1 + yr	0 + yr	1 + yr
10.1–23	0.00	0.00	0.00	0.00	1.00	1.00	0.13	0.07
23.1–37	0.00	0.00	0.00	0.00	0.42	0.42	0.19	0.07
Gravelly sand (%)								
< 1	0.11	0.13	1.00	0.68	0.00	0.00	0.85	0.24
1.0–2	0.00	0.00	0.01	0.00	0.01	0.02	0.22	0.11
2.1–3	0.00	0.00	0.00	0.00	0.25	1.00	0.19	0.07
3.1–5	1.00	1.00	0.77	1.00	0.00	0.00	1.00	1.00
5.1–12	0.00	0.00	0.00	0.00	1.00	0.77	0.08	0.05
Gravel (%)								
≤ 3	1.00	1.00	0.55	1.00	0.00	0.01	1.52	1.00
3.1–4	0.00	0.00	0.83	0.07	0.00	0.00	1.00	0.54
4.1–10	0.16	0.18	1.00	0.99	1.00	1.00	0.52	0.33
10.1–15	0.00	0.02	0.07	0.00	0.03	0.02	0.36	0.24
Sandy gravel (%)								
0	0.57	0.68	1.00	1.00	0.07	0.37	1.00	0.89
0.1–1	1.00	1.00	0.15	0.28	0.00	0.00	0.40	1.00
1.1–5	0.00	0.00	0.00	0.00	1.00	1.00	0.09	0.20
Cobble (%)								
≤ 1	1.00	1.00	0.54	0.84	0.00	0.01	1.00	1.00
1.1–2	0.03	0.03	1.00	0.92	1.00	1.00	0.83	0.28
2.1–3	0.27	0.33	0.76	1.00	0.10	0.55	0.83	0.40
3.1–5	0.00	0.00	0.00	0.00	0.02	0.01	0.37	0.25

STELLA® 7.0.3 Research (High Performance Systems Inc. 2002) was used to run the AEM for a long-term prediction (i.e., 100 hundred years for this study) starting with month 0 on December 1st and ending at 1,200 months on November 30th. In the model run, the interval of time between calculations (dt) was set to a small value of 0.0625 months to avoid artifactual delays and dynamics during the software calculation. These problems are unlikely to occur as long as dt is defined as a relatively small value or below 0.25 (High Performance Systems Inc. 2002). The chi-square (χ^2) statistic was used to test the goodness of fit between the monthly mean predicted abundance (%) from the 100-year simulation and the mean observed abundance (%) of the target fish species along the gradient in the associated time period.

RESULTS

Populations of the four modeled fish species showed seasonal patterns of variation in the inshore zone of the Hudson system over the 100-year simulation following results for Atlantic silverside (Figure 2). The fish populations declined in winter as a result of winter mortality and increased in the growing season owing to birth and growth of offspring. The populations were relatively stable for a certain time period in the growing season after the spawning period when no offspring were born (Figure 2A). As expected, the fish population size increased when higher value of either C_y (Figure 2B) or r_b (Figure 2C), or lower value of r_d (Figure 2D) was assigned one at a time for simulating the model. In contrast, the fish population size

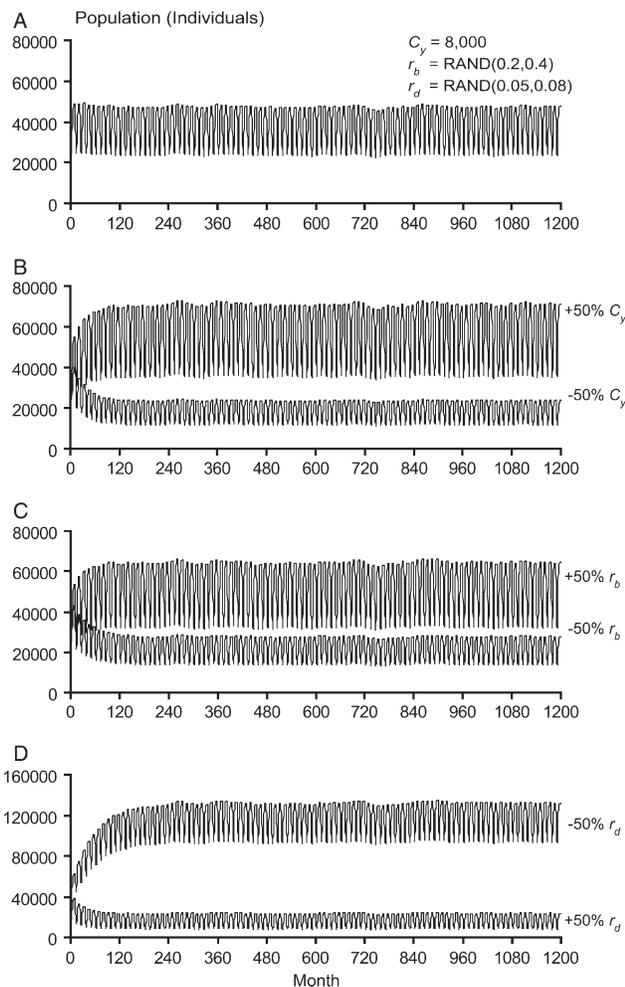


Figure 2 | A seasonal pattern of Atlantic silverside over the 100-year simulation (A). The population size decreased or increased for the first 12-year period of the simulation when 50% changes in carrying capacity C_y (B), birth fraction r_b (C), or death fraction r_d (D) were assigned to the model. The population size returned to a seasonal pattern over the long-term period.

declined when lower value of either C_y (Figure 2B) or r_b (Figure 2C), or higher value of r_d (Figure 2D) was used one at a time to run the model. The fish population sizes exponentially increased or decreased for short-term predictions (i.e., around the first 12 years of the simulation) when any one of the three population variables was disturbed. However, the fish population sizes returned to their seasonal patterns of distribution (Figure 2B–D) when the population growth reached the carrying capacity of the system.

The mean predicted abundance of winter flounder, Atlantic silverside, and eastern silvery minnow from the 100-year simulation agreed with the mean observed abundance of the associated species ($\chi^2_{\text{predicted}} < 19.68, p > 0.05$,

$df = 11$) over the 24-year period (1974–1997), along the gradient in all associated months (April–November). The predicted abundances of striped bass were significantly different from the observation ($\chi^2_{\text{predicted}} \geq 19.68, p \leq 0.05, df = 11$) in April, June, and July. According to the model validation results, the AEM could efficiently predict the abundance and distribution patterns of the first three species, but showed low efficiency of predicting striped bass in all modeling months (July–October). The example of the predicted and observed abundances of the four modeled species in August obtained from this study were shown in Figure 3.

DISCUSSION

Patterns of physical habitat changes across marine-estuarine-river transitions on the gradient could efficiently explain the distribution patterns of winter flounder, Atlantic silverside, and eastern silvery minnow on the Hudson River estuary gradient. In the AEM, while the population variables (C_y , r_b , and r_d) shaped the population size of the fish species in time, the model key variable (i.e., physical habitat preference, HP) accounted for the distributions of the associated species in space. As the geometric mean of the fish species Pis for the selected physical habitat variables, the species HP could capture the local distribution ranges of winter flounder, Atlantic silverside, and eastern silvery minnow, and reflect the influences of physical habitat changes on the species distributions within the associated local ranges (Morrison *et al.* 1985; Guay *et al.* 2000; Singkran 2007). However, with its broad tolerance of changing environment, the distribution pattern of the fourth modeled species (i.e., striped bass) was unable to be significantly quantified by the species preference for physical habitat changes only.

In the lower zone of the gradient, changes in salinity concentration influentially shape distribution patterns of fish species assemblages with different salinity tolerances (e.g., Winemiller & Leslie 1992; Marshall & Elliott 1998; Whitfield 1999; Martino & Able 2003; Jaureguizar *et al.* 2003). At this zone, both abundance in time and distribution in space of winter flounder among regions were significantly captured by the AEM. The model revealed that the local

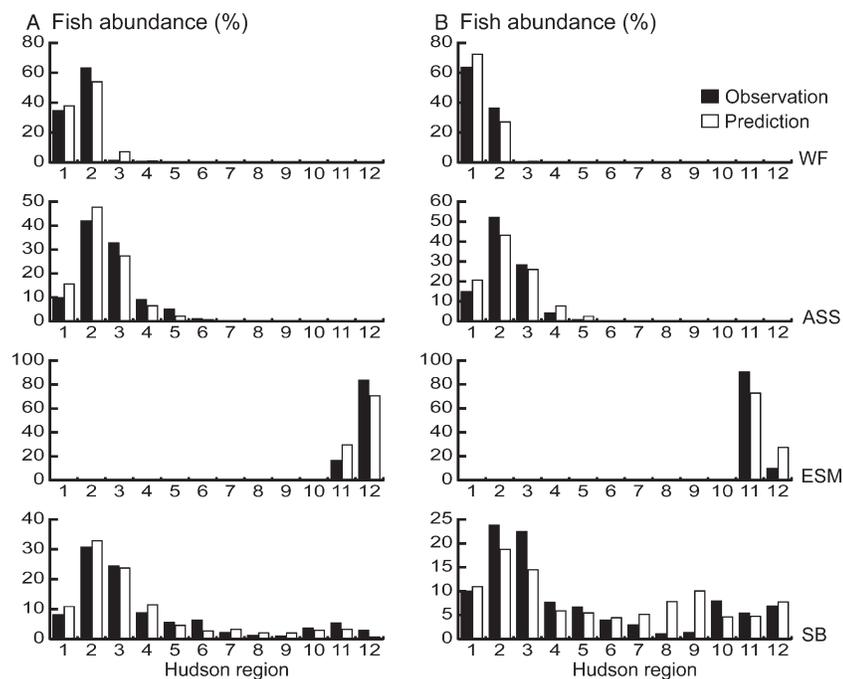


Figure 3 | The mean observed abundances of winter flounder (WF), Atlantic silverside (ASS), eastern silvery minnow (ESM) and striped bass (SB) along the study gradient in August over the first 24-year (1974–1997; A) and the latter 4-year (1998–2001; B) periods were compared with the mean predicted abundances of the associated species in the same month over the 100-year-simulation.

distribution range of this marine species on the gradient was defined by the species Pi for changing salinity and substrate composition. That is, the upriver distribution of winter flounder was limited by its very low-to-zero Pi for the salinity concentration < 1 ppt and its zero Pi for specific percentage composition of bottom substrates (Table 2). Within its local distribution range in the lower zone, the model also suggested that most winter flounder would migrate downriver of the gradient after December and until spring; this pattern closely followed the variation in salinity in and above region 1 during this time period. The absent to low ($< 0.5\%$) abundance of winter flounder observed on the gradient in May and April during 1974–1997 supported the predicted results. While water temperature is typically an important variable shaping winter flounder distribution in coastal zones (McCracken 1963; Olla *et al.* 1969), it was apparently not a key variable defining the local distribution range of this species on the Hudson River estuary gradient. The 0+ year-old winter flounder showed the optimal Pi ($P_i = 1$) for water temperature between 22 and 27°C, and its lower Pi varied above zero for the water temperature beyond its optimal range on the gradient (Table 2).

The 1+ year-old winter flounder showed the optimal Pi for lower water temperature (than the young) between 8 and 15°C, and its lower Pi varied above zero for the water temperature beyond its optimal range (Table 2).

As an estuarine species migrating within the gradient range from the lower zone to some portion of the middle zone, the abundance and distribution patterns of Atlantic silverside were significantly captured by the AEM. Like winter flounder, the upriver distribution of Atlantic silverside on the gradient was limited by its zero Pi for salinity < 1 ppt and its zero Pi for specific percentage composition of bottom substrates (Table 2). However, Atlantic silverside showed higher Pi for salinity between 1–6.9 ppt than winter flounder (Table 2). This may contribute to its broader range of distribution upriver than winter flounder.

In the upper zone of the gradient, the predicted abundance and distribution patterns of eastern silvery minnow were restricted within the narrow range between region 11 and region 12; and these significantly agreed with the observations. Based on its computed Pi for salinity over the 24-year period in this study, eastern silvery minnow showed zero-to-very low Pis (0–0.01) for salinity ≥ 1 ppt

and high compositions of mud (>27%) and sandy mud (>22%) on the Hudson River estuary gradient (Table 2). These physical habitat conditions in the lower and middle zones obviously inhibited the downriver migration of eastern silvery minnow below the upper zone (below region 7).

Unlike the first three modeled species, the AEM showed low efficiency to quantify abundance and distribution patterns of striped bass along the Hudson River estuary gradient. The species HPs in the AEM were estimated from the large data set observed during 1974–1997 with well-designed stratifying random samplings to cover different habitat conditions in the inshore zone. Consequently, it is believed that the measurement error of the data used in this study was minimal. However, the significant disagreements between the prediction and observation of striped bass at some regions in certain months might be due to several reasons. For example, first, striped bass have great ability to maintain populations in a wide range of habitat conditions in aquatic ecosystems (Bain & Bain 1982). This species is able to occupy marine, estuarine, and freshwater habitats. It has colonized and expanded population in inland river ecosystems and non-native coasts (Pacific, from Mexico to Washington). Second, other than the species preference for physical habitat conditions, the abundance and distribution patterns of striped bass along the Hudson River estuary gradient may also be shaped by complex relationships of estuarine productivity, prey distributions, and migration behaviors of the species at different life stages, ages, and sexes (McLaren *et al.* 1981; Bain & Bain 1982; Clark 1985; Waldman *et al.* 1990; Secor & Piccoli 1996; Able & Fahay 1998) that were not considered in the AEM. Thus, for such a fish species with broad tolerance of environmental conditions across different aquatic ecosystems like striped bass, both important biotic and abiotic factors influencing the species distribution should be considered in the modeling process to improve the model ability of prediction.

CONCLUSION

The AEM could efficiently predict abundance and distribution patterns of winter flounder, Atlantic silverside, and eastern silvery minnow, but showed low efficiency of

quantifying abundance and distribution patterns of striped bass at some portions of the gradient in certain months. The species Pis for both important biological and physical factors may be needed to consider in parallel for improving the accuracy of the model prediction for striped bass.

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REFERENCES

- Able, K. W. & Fahay, M. P. 1998 *The First Year in the Life of Estuarine Fishes in the Middle Atlantic Bight*. Rutgers University Press, New Brunswick, New Jersey, USA.
- Andrewartha, H. G. & Birch, L. C. 1954 *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, USA.
- Bain, M. B. & Bain, J. L. 1982 *Habitat Suitability Index Models: Coastal Stocks of Striped Bass, FWS/OBS-82/10.1 U.S. Fish and Wildlife Service*. Office of Biological Services, Washington, DC, USA.
- Clark, J. 1985 *Seasonal movements of striped bass contingents of long Island sound and the New York Bight*. *Trans. Am. Fish. Soc.* **97**, 320–345.
- Fay, C. W., Neves, R. J. & Pardue, G. B. 1983 *Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)–Atlantic silverside*. FWS/OBS-82/11.10. U.S. Army Corps of Engineers, TR EL-82-4 U.S. Fish and Wildlife Service, Division of Biological Services.
- Guay, J. C., Boisclair, D., Rioux, D., Leclerc, M., Lapointe, M. & Legendre, P. 2000 *Development and validation of numerical habitat models for juveniles of Atlantic salmon (*Salmo salar*)*. *Can. J. Fish. Aquat. Sci.* **57**, 2065–2075.
- Hatzenbeler, G. R., Bozek, M. A., Jennings, M. J. & Emmons, E. E. 2000 *Seasonal variation in fish assemblage structure and habitat structure in the nearshore littoral zone of Wisconsin Lakes*. *North Am. J. Fish. Manage.* **20**, 360–368.
- High Performance Systems, Inc. 2002 *STELLA^(R) Research, Version 7.0.3 for Windows*, (3). Hanover, New Hampshire, USA.
- Jackson, D. A., Peres-Neto, P. R. & Olden, J. D. 2001 *What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors*. *Can. J. Fish. Aquat. Sci.* **58**, 157–170.
- Jaureguizar, A. J., Mennic, R., Bremeca, C., Mianzan, H. & Lastaa, C. 2003 *Fish assemblage and environmental patterns in the Río de la Plata estuary*. *Estuar. Coast. Shelf Sci.* **56**, 921–933.

- Johnson, A. R., Wiens, J. A., Milne, B. T. & Crist, T. O. 1992 Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecol.* **7**, 63–75.
- Marshall, S. & Elliott, M. 1998 Environmental influences on the fish assemblage of the Humber Estuary. *Estuar. Coast. Shelf Sci.* **46**, 175–184.
- Martino, E. J. & Able, K. W. 2003 Fish assemblages across the marine to low salinity transition zone of a temperate estuary. *Estuar. Coast. Shelf Sci.* **56**, 969–987.
- McCracken, F. D. 1963 Seasonal movements of the winter flounder, *Pseudopleuronectes americanus*, on the Atlantic coast. *J. Fish. Res. Board Can.* **20**, 551–585.
- McLaren, J. B., Cooper, J. C., Hoff, T. B. & Lander, V. 1981 Movements of Hudson River striped bass. *Trans. Am. Fish. Soc.* **110**, 158–167.
- Morrison, K. A., Therien, N. & Coupal, B. 1985 Simulating fish redistribution in the LG-2 reservoir after flooding. *Ecol. Model.* **28**, 97–111.
- Olla, B. L., Wicklund, R. & Wilk, S. 1969 Behavior of winter flounder in a natural habitat. *Trans. Am. Fish. Soc.* **98**, 717–720.
- Pereira, J. J., Goldberg, R., Ziskowski, J. J., Berrien, P. L., Morse, W. W. & Johnson, D. L. 1999 Essential fish habitat source document: winter flounder, *Pseudopleuronectes americanus*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-138 U.S. Department of Commerce and National Oceanic and Atmospheric Administration, Woods Hole, Massachusetts, USA.
- Ray, G. C. & Hayden, B. P. 1992 Coastal zone ecotones. In: Hansen, A. J. & di Castri, F. (eds) *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer-Verlag, New York, USA, pp. 403–420.
- Secor, D. H. & Piccoli, P. M. 1996 Age- and sex-dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. *Estuaries* **19**, 728–793.
- Singkran, N. 2007 An abundance exchange model of fish assemblage response to changing habitat along embayment-stream gradients of Lake Ontario, New York. *Ecol. Model.* **201**, 453–467.
- Strayer, D. L., Hattala, K. A. & Kahnle, A. W. 2004 Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. *Can. J. Fish. Aquat. Sci.* **61**, 924–941.
- Tilman, D. & Kareiva, P. (eds) 1997 *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interaction*. Princeton University Press, Princeton, New Jersey, USA.
- Turchin, P. 1998 *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- Waldman, J. R., Dunning, D. J., Ross, Q. E. & Mattson, M. T. 1990 Range dynamics of Hudson River striped bass along the Atlantic Coast. *Trans. Am. Fish. Soc.* **119**, 910–919.
- Whitfield, A. K. 1999 Ichthyofaunal assemblages in estuaries: a South African case study. *Rev. Fish Biol. Fish.* **9**, 151–186.
- Willis, T. V. & Magnuson, J. J. 2000 Patterns in fish species composition across the interface between streams and lakes. *Can. J. Fish. Aquat. Sci.* **57**, 1042–1052.
- Winemiller, K. O. & Leslie, M. A. 1992 Fish assemblages across a complex, tropical freshwater/marine ecotone. *Environ. Biol. Fishes* **34**, 29–50.

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