

The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population

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Abstract. Understanding mechanisms that support long-term persistence of populations and sustainability of productive fisheries is a priority in fisheries management. Complex spatial structure within populations is increasingly viewed as a result of a plastic behavioral response that can have consequences for the dynamics of a population. We incorporated spatial structure and environmental forcing into a population model to examine the consequences for population stability (coefficient of variation of spawning-stock biomass), resilience (time to recover from disturbance), and productivity (spawning-stock biomass). White perch (*Morone americana*) served as a model species that exhibits simultaneous occurrence of migratory and resident groups within a population. We evaluated the role that contingents (behavioral groups within populations that exhibit divergent life histories) play in mitigating population responses to unfavorable environmental conditions. We used age-structured models that incorporated contingent-specific vital rates to simulate population dynamics of white perch in a sub-estuary of Chesapeake Bay, USA. The dynamics of the population were most sensitive to the proportion of individuals within each contingent and to a lesser degree to the level of correlation in recruitment between contingents in their responses to the environment. Increased representation of the dispersive contingent within populations resulted in increased productivity and resilience, but decreased stability. Empirical evidence from the Patuxent River white perch population was consistent with these findings. A high negative correlation in resident and dispersive contingent recruitment dynamics resulted in increased productivity and stability, with little effect on resilience. With high positive correlation between contingent recruitments, the model showed similar responses in population productivity and resilience, but decreased stability. Because contingent structure involves differing patterns of nursery habitat use, spatial management that conserves sets of habitats rather than the single most productive nursery habitat would be expected to contribute to long-term population stability.

Key words: Chesapeake Bay, USA; contingent; life history diversity; *Morone americana*; population dynamics; productivity; resilience; spatial structure; stability; white perch.

INTRODUCTION

In the past, the extensive range, abundance, and fecundity of many fish species had been thought to ensure that few populations were at risk of localized depletion or extinction (Huxley 1884). Today, the increased prevalence of stock collapse (e.g., Canadian stocks of Atlantic cod, *Gadus morhua*) and long recovery time of exploited populations (e.g., select *Sebastes* populations; Jacobson and Cadrin 2002, MacCall and He 2002) indicate that we do not fully understand mechanisms that contribute to stability and resilience in marine fish populations. Stability is the ability of a population to maintain its integrity and persist despite disturbance, and resilience is the ability of a population

to return to an equilibrium state after disturbance (adopted from McCann 2000). Increasingly, spatial structure within populations is viewed as an attribute that can contribute to population stability and resilience by buffering population-level responses to unfavorable environmental conditions and preventing recruitment failure (Hilborn et al. 2003, Berkeley et al. 2004, Ruzzante et al. 2006, Bradbury et al. 2008).

An important mechanism of stability within communities is the differential response of populations to environmental conditions (i.e., asynchronous dynamics; Doak et al. 1998, McCann 2000). The link made between asynchronous dynamics and stability is also recognized in metapopulation theory, which focuses on the impact that differences in demographics and dynamics of local populations have on regional population persistence (Hanski 1999). In fish populations, life history diversity was found to have a stabilizing effect on

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metapopulations due to differential responses of phenotypes to environmental fluctuations (e.g., differential response of spawning populations of sockeye salmon to environmental fluctuations; Hilborn et al. 2003). Thus, life history diversity, or biocomplexity, is viewed as important to the sustainability of fish stock complexes (collections of discrete spawning populations; Hilborn et al. 2003, Ruzzante et al. 2006). We believe these same ideas extend to intra-population dynamics with divergent spatial tactics within a population potentially contributing to overall stability.

Spatial structure within populations can affect overall dynamics, because the different habitats experienced by groups of individuals can impact their abundance, growth, reproduction, maturity, recruitment, and survival (Hayes et al. 1996). Contingent structure is a term used to describe a type of spatial structuring whereby portions of a population exhibit divergent life history tactics and consequently may use different habitats (Hjort 1914, Secor 1999). For example, resident and migratory contingents can exist within the same genetic population, a phenomenon termed partial migration (Berthold 2001, Kerr et al. 2009). Intrinsic differences, such as differences in growth rate independent of the influence of habitat, also exist between contingents based on the environmental conditions experienced during early life history (Jonsson 1985, Kerr and Secor 2009). Habitat-related or intrinsic differences in vital rates and productivity of contingents will have consequences for the contingent's response to the environment; as such each contingent carries its own risk of recruitment failure.

Depending on contingent-specific demographics and recruitment variability, contingent structure may have a positive or negative impact on stability, productivity, and resilience. Drawing from economic theory on investment strategy, consolidation of investment in high-risk stocks may increase chances of catastrophic loss, but potentially can produce more rapid and higher earnings, compared to diversification of investments, which reduces risk at the expense of profit. Likewise, diversification of a population into contingents may enhance stability of the population by dampening interannual variability in recruitment, but decrease productivity and result in a longer time to recover after disturbance. Alternatively, if a population that is relatively stable is diversified to include an episodically high-yield contingent, then contingent structure within populations may enhance resiliency through a phenomenon termed the "storage effect," whereby potential for strong recruitments during favorable environmental conditions is essentially stored in the adult population (Secor 2007). Thus, episodic high recruitment of a single highly productive contingent may promote rapid recovery of a population when appropriate environmental conditions are present. We hypothesize that the relative investment of the population in each contingent and degree of correlation in recruitment dynamics will affect

the stability, productivity, and resilience of the overall population.

The goal of this research was to incorporate complex spatial dynamics into a population model and examine the consequences of spatial structuring to stability (measured as variance in spawning-stock biomass), resilience (time to recover from disturbance), and productivity (long-term average spawning-stock biomass) of the population. Using white perch (*Morone americana*), a model species that exhibits contingent structure (Kraus and Secor 2004, Kerr et al. 2009) and a degree of asynchrony in contingent recruitment dynamics within some populations (Kraus and Secor 2005b), we illustrate the role that contingents play in buffering population-level responses against unfavorable environmental conditions. Using empirically derived parameters in our model, our goal was to evaluate the relative magnitude of population response (i.e., productivity, stability, and resilience) to (1) contingent representation (proportion of either contingent within a population) and (2) correlation in recruitment to each contingent under realistic simulations of environmental forcing.

METHODS

Model species

The white perch is an abundant fish in the Chesapeake Bay. Adults spawn in the tidal freshwater portions of estuaries in the spring, where eggs and larvae develop (Mansueti 1964). The white perch population in the Patuxent River is a partially migratory population, with a portion of the population remaining resident in natal freshwater environments (resident contingent) and the other portion dispersing down-estuary to inhabit brackish-water habitats (dispersive contingent; Kraus and Secor 2004, Kerr et al. 2009). Previous research, based on otolith strontium/calcium profile analysis, determined that this divergence in habitat use occurred during the juvenile stage, predominantly after the transition from larval to juvenile stage (Kraus and Secor 2004, Kerr et al. 2009). Contingent structuring within this population appears to be a behavioral response by individuals to conditions experienced during early life history that influence their growth (Kerr 2008). Prior to dispersal, larval growth rates of fish that became dispersive were significantly slower than those of fish that remained residents. Subsequent to dispersal, during juvenile and adult stages, growth rates of dispersive fish were faster than resident fish (Kraus and Secor 2004, Kerr and Secor 2009).

There is no indication that contingents are genetically distinct; no evidence supports assortive mating that could lead to such heritable differences in this population. Prior analysis of mitochondrial DNA of white perch from the Patuxent River did not reveal within-river genetic structure and grouped these fish into a larger population that included Upper Bay, Choptank, and Nanticoke River white perch based on genetic distance, indicating white perch in the Patuxent River

TABLE 1. Parameter estimates (and their sources) used in age-structured models of white perch (*Morone americana*).

Parameter	Definition	Value	Source
B_1	maximum number of recruits produced	1 985 000	Rothschild et al. (1992)
B_2	controls rate at which the maximum recruits per spawner is reached	1000	estimated Beverton Holt parameter
Z_1	total mortality over the larval period (total mortality was calculated from instantaneous mortality rates and stage-duration estimates; contingent-specific larval growth rates were used to estimate duration of larval-period-based size at transformation)	r, 1.54 (dry year), 1.54–0.50 (wet year); d, 1.54 (dry year), 0.50 (wet year)	Kerr and Secor (2009), Houde et al. (1989)
Z_a	mean total adult mortality (mortality held equal for both contingents and sexes)	0.59	Rothschild et al. (1992)
L_∞	asymptote (mm)	217	Kraus and Secor (2004)
k	rate (yr^{-1}) at which the growth model approaches the asymptote	r, 0.39; d, 0.69	Kraus and Secor (2004)
a_0	age at which length is zero	0	Kraus and Secor (2004)
α	length–mass parameter	6.42×10^{-6}	calculated from 2005 and 2006 Patuxent River adult white perch collections
β	length–mass parameter	3.28	calculated from 2005 and 2006 Patuxent River adult white perch collections

Note: Contingent-specific parameters are denoted as r (resident) and d (dispersive).

are not a unique genetic population (Mulligan and Chapman 1989). Additionally, collection of gravid adult white perch from both contingents in the freshwater region of the Patuxent River, as determined by retrospective analysis of habitat use based on otolith chemistry, suggests significant mixing between contingents during the springtime spawning period (Kraus and Secor 2004).

Kraus and Secor (2004, 2005a) documented differences in the rate of recruitment to contingents correlated with the strength of the spring freshet. The percentage of white perch recruits that were dispersive within a particular year class in the Patuxent River ranged from 0 in drought years and 85% in low-flow years to 96% in high-flow years (Kraus and Secor 2004, 2005a). Thus, the dispersive contingent dominated the population in both high- and low-flow years; the resident contingent was minimally present in high-flow years, increasingly represented in low-flow years, and exclusively present during drought years (Kraus and Secor 2004, 2005a). These findings led to the hypothesis that the resident contingent behavior contributes to long-term persistence, whereas the dispersive contingent contributes to population productivity and resilience (Kraus and Secor 2005a).

Age-structured model

Population dynamics of white perch in the Patuxent River was modeled as two contingent-specific, fully age-structured models that were linked through a common stock–recruitment relationship. The shared stock–recruitment relationship reflects the assumption that contingent structure is not heritable, which, although not tested directly, is supported by indirect evidence of

non-assortive mating and the appearance of genetic homogeneity. The model structure was designed to reflect two recruitment events: recruitment of individuals to the population (age 0) and recruitment of individuals to contingent (age 1). The parameters of age-structured models were derived from analysis of adult white perch otoliths from fish collections during the 2005 and 2006 springtime spawning seasons in the Patuxent River and previously reported literature values for this population (Table 1).

Age-structured models included 13 age groups (age 0 to age 12). Recruitment or abundance at age 0 (N_0) was calculated by

$$\text{Age 0: } N_0 = \frac{B_1 \times \text{SSB}_{\text{pop}}}{B_2 + \text{SSB}_{\text{pop}}} + \text{error} \quad (1)$$

where SSB_{pop} is the spawning-stock biomass of the overall population, B_1 is the maximum number of recruits produced, and B_2 controls the rate at which the asymptote, or maximum recruits per spawner, is reached (Table 1; Beverton and Holt 1957). The error term was modeled as a normally distributed deviation in abundance at age 0.

Spawning-stock biomass of the population was calculated as a function of the number at age, mass at age, and maturity at age of white perch in each contingent (SSB_{cont}) and summed across contingents to calculate SSB of the overall population:

$$\begin{aligned} \text{SSB}_{\text{cont}} &= \sum_{a=1}^{12} N_{t,a} M_a p_a \\ \text{SSB}_{\text{pop}} &= \sum \text{SSB}_{\text{cont}} \end{aligned} \quad (2)$$

where M_a is the average spawning mass (in kilograms)

TABLE 2. Length at age, mass at age, and proportion of female white perch (*Morone americana*) mature at age for the resident and dispersive contingents in the Patuxent River, a sub-estuary of Chesapeake Bay.

Age (yr)	Resident			Dispersive		
	Length (mm)	Mass (kg)	Proportion mature	Length (mm)	Mass (kg)	Proportion mature
0	0	0.00	0.00	0	0.00	0.00
1	70	0.01	0.00	108	0.03	0.00
2	118	0.04	0.73	162	0.11	0.73
3	150	0.09	0.98	190	0.19	0.98
4	171	0.14	1.00	203	0.24	1.00
5	186	0.18	1.00	210	0.26	1.00
6	196	0.21	1.00	214	0.28	1.00
7	203	0.24	1.00	215	0.29	1.00
8	207	0.25	1.00	216	0.29	1.00
9	211	0.27	1.00	217	0.29	1.00
10	213	0.28	1.00	217	0.29	1.00
11	214	0.28	1.00	217	0.29	1.00
12	215	0.29	1.00	217	0.29	1.00

of an age a fish, p_a is the average fraction of age a fish that are mature, and $N_{t,a}$ is the average number of fish of age a at time t (Brodziak et al. 1998). A common length–mass relationship was used to estimate mass at age (M_a) of white perch in each contingent:

$$M_a = \alpha L_a^\beta \quad (3)$$

where L_a is length at age a , α is a proportionality constant, and β is the exponent. Length and mass from collections of spawning white perch made in the spring of 2005 and 2006 in the Patuxent River were used to develop the length–mass relationship for white perch (Table 2). Length at age was estimated from contingent-specific von Bertalanffy growth equations (Tables 1 and 2; Kraus and Secor 2004):

$$L_a = L_\infty [1 - e^{-k(a-a_0)}] \quad (4)$$

where L_∞ is the asymptotic size, k defines the rate at which the curve approaches the asymptote, and a_0 is the hypothetical age at which the size of the fish is zero. The proportion of fish mature at age was assigned based on mean standard length at age (Mansueti 1961; Table 2).

Contingent structure was initiated at age 1 and contingent-specific population abundance at age 1 was calculated by

$$\begin{aligned} \text{Resident:} \quad N_{1(t+1),r} &= N_0(1-D)e^{-Z_{1,r}} \\ \text{Dispersive:} \quad N_{1(t+1),d} &= N_0(D)e^{-Z_{1,d}} \end{aligned} \quad (5)$$

where N_0 is initial population size, D is the proportion of the population that are dispersive (i.e., disperse out of the freshwater natal habitat), and Z_1 is contingent-specific (r, resident; d, dispersive) larval mortality. Larval mortality was modeled as a function of stream flow, with the dispersive contingent having specific values for high-flow years (daily instantaneous mortality rate = 0.04 d⁻¹) and low-flow years (daily instantaneous mortality rate = 0.11 d⁻¹; Tables 1 and 3). Daily instantaneous larval mortality rate of the resident

contingent was assumed to be 0.13 d⁻¹ in low-flow years and ranged from 0.04 to 0.13 d⁻¹ in high-flow years, according to the specified simulation (see *Simulations* description; Tables 1 and 3). Total larval mortality rates were calculated using stage-duration estimates based on contingent-specific larval growth rates (dispersive contingent = 0.5 mm/d, resident contingent = 0.6 mm/d; Kerr and Secor 2009; Table 3). Subsequent post-larval mortality rates were assumed to be equivalent between the contingents. The magnitude of dispersive contingent recruitment (D) was varied to explore a range of realistic scenarios (see *Simulations* description). Abundance-at-age for ages 2 to 12 yr (N_2 to N_{12}) was calculated for each contingent by

$$N_{a+1(t+1)} = N_{a(t)}e^{-Z_a}$$

where N_a is the age-specific abundance and Z_a is the total adult annual mortality. Adult annual mortality rate (Rothschild et al. 1992) was held constant at 0.59 across sex and contingent (Table 1).

Environmental stochasticity

Stochasticity was included in age-structured models as variability around the average proportion of the population that is dispersive (D) each year (standard deviation = 0.03) in the Patuxent River, independent of environmental forcing. Additionally, drought years, in which there are no dispersive recruits (age 1) within the population and larval survival is variable in resident contingent fish (Table 3), were simulated at a frequency of 20% (based on observations from Kraus and Secor 2004). Stochasticity was also incorporated into simulated recruitment as a normally distributed random deviate ranging up to 10% of the maximum number of recruits (from the Beverton-Holt stock recruit function).

Simulations

We used simulations to evaluate the response of population productivity, stability, and resilience to

changes in (1) contingent representation (average proportion of the population that recruits to each contingent each year) and (2) correlation in interannual age 1 abundances between contingents (i.e., recruitment synchrony). A series of 500 stochastic model runs, each conducted over a 150-year time period, were performed for each model simulation (only the last 100 years were used in analyses to allow the model to eliminate transient effects of initial conditions). To examine the consequence of changes in the proportion of the population that was dispersive (D), three simulations were constructed with differing degrees of contingent structure (0.25, 0.50, and 0.75 dispersive contingent representation). Additionally, two simulations were generated in which the population was modeled without contingent structure: a model in which all fish were dispersive ($D = 1$) and a model with all resident fish ($D = 0$). Contingent representation simulations were run with no correlation (ρ) in recruitment between contingents ($\rho = 0$).

Recruitment of fish to each contingent is likely to be correlated because of either a similar (positive correlation) or different (negative correlation) response to the same environmental conditions during early life. A range of interannual correlations in year 1 recruitments, ranging from highly positive ($\rho = 0.9$) to highly negative ($\rho = -0.9$) correlations, was simulated by changing the larval mortality rate (Table 3). We focused on changing the recruitment dynamics of the resident contingent to vary either in opposition or in synchrony with the dispersive contingent to examine the consequences of the resident contingent exhibiting a similar or unique response to environmental conditions as the dispersive contingent. Correlation simulations were run with equal representation of contingents ($D = 0.5$) in the population.

The response variables of interest to us were productivity, stability, and resilience. Mean SSB_{pop} was calculated as a metric of population productivity. Mean coefficient of variation ($CV_{pop} = SD/\mu \times 100$) of SSB_{pop} was calculated as a measure of stability. We also calculated mean productivity and stability measures of each contingent (CV_{cont} and SSB_{cont}). Resilience was quantified as the number of years to rebuild a population above mean SSB_{pop} after a sequence of five poor recruitment years, during which recruitment was 10% of maximum number of recruits (B_1 from the stock-recruit model). Additionally, simulations that encompass all pairwise combinations of contingent representation and recruitment correlation were run to examine simultaneous effects on productivity, stability, and resilience.

RESULTS

Contingent representation simulations

The overall productivity (SSB_{pop}) of white perch populations was sensitive to the proportion of the population composed of the dispersive contingent.

TABLE 3. Contingent-specific larval mortality in high- and low-stream-flow years across varying levels of contingent representation (dispersive fraction) and correlated recruitment dynamics (correlation).

Dispersive fraction	Correlation	Larval mortality			
		Dispersive		Resident	
		High	Low	High	Low
0	0			1.54	1.54
0	0.25			1.46	1.54
0	0.50			1.35	1.54
0	0.75			1.20	1.54
0	0.90			0.50	1.54
0	-0.25			1.54	1.45
0	-0.50			1.54	1.35
0	-0.75			1.54	1.00
0	-0.85			1.54	0.50
0.25	0	0.5	1.54	1.54	1.54
0.25	0.25	0.5	1.54	1.47	1.54
0.25	0.50	0.5	1.54	1.38	1.54
0.25	0.75	0.5	1.54	1.20	1.54
0.25	0.90	0.5	1.54	0.5	1.54
0.25	-0.25	0.5	1.54	1.54	1.45
0.25	-0.50	0.5	1.54	1.54	1.34
0.25	-0.75	0.5	1.54	1.54	1.00
0.25	-0.85	0.5	1.54	1.54	0.50
0.5	0	0.5	1.54	1.56	1.54
0.5	0.25	0.5	1.54	1.47	1.54
0.5	0.50	0.5	1.54	1.37	1.54
0.5	0.75	0.5	1.54	1.20	1.54
0.5	0.90	0.5	1.54	0.50	1.54
0.5	-0.25	0.5	1.54	1.54	1.43
0.5	-0.50	0.5	1.54	1.54	1.33
0.5	-0.75	0.5	1.54	1.54	1.00
0.5	-0.85	0.5	1.54	1.54	0.50
0.75	0	0.5	1.54	1.54	1.54
0.75	0.25	0.5	1.54	1.43	1.54
0.75	0.50	0.5	1.54	1.30	1.54
0.75	0.75	0.5	1.54	1.00	1.54
0.75	0.90	0.5	1.54	0.50	1.54
0.75	-0.25	0.5	1.54	1.54	1.41
0.75	-0.50	0.5	1.54	1.54	1.26
0.75	-0.75	0.5	1.54	1.54	0.80
0.75	-0.85	0.5	1.54	1.54	0.50
1	0	0.5	1.54		
1	0.25	0.5	1.54		
1	0.50	0.5	1.54		
1	0.75	0.5	1.54		
1	0.90	0.5	1.54		
1	-0.25	0.5	1.54		
1	-0.50	0.5	1.54		
1	-0.75	0.5	1.54		
1	-0.85	0.5	1.54		

Note: Larval mortality in drought years is 100% for the dispersive contingent and equal to low-flow-year mortality for the resident contingent.

Mean productivity increased as the relative abundance of dispersive white perch increased within populations (Fig. 1a). Across simulations, ranging from 0 (entire population is resident in freshwater natal region) to 100% dispersive contingent representation, mean SSB_{pop} ranged from 50 626 kg ($D = 0$) to 120 966 kg ($D = 1$). Thus, the modeled SSB_{pop} of a fully resident population was only 42% that of a fully dispersive population.

Interestingly, although more productive, populations characterized by high dispersive contingent representation were less stable (i.e., higher CV_{pop}). Mean CV_{pop} of

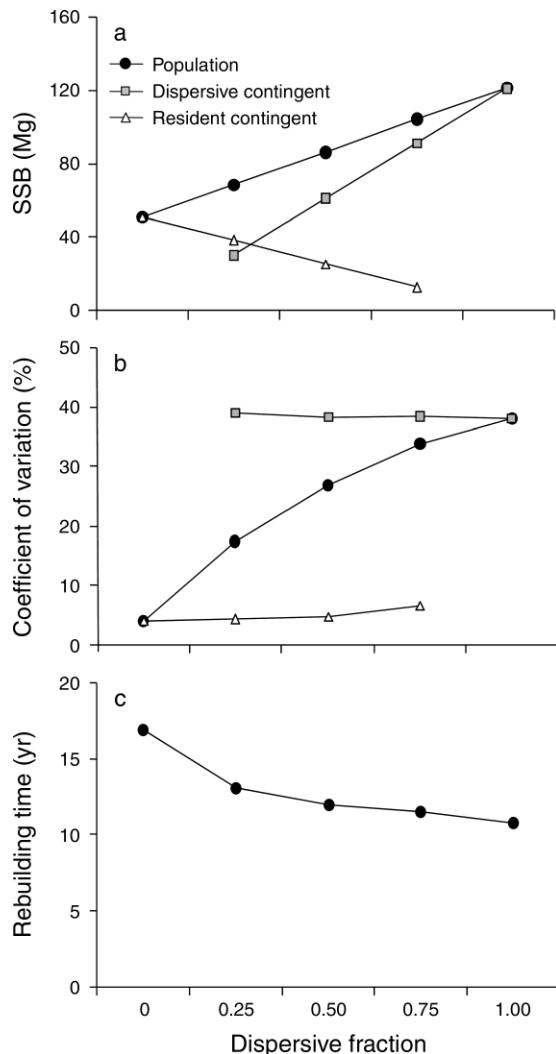


FIG. 1. (a) Spawning-stock biomass (SSB) and (b) the coefficient of variation of spawning-stock biomass of the resident and dispersive contingents and overall white perch (*Morone americana*) populations with varying levels of contingent representation (shown as the dispersive fraction) in the Patuxent River, a sub-estuary of Chesapeake Bay. (c) Population rebuilding time, the number of years it takes for spawning-stock biomass of a population to rebuild above mean SSB after a perturbation. Across scenarios, there is no correlation in recruitment dynamics between contingents ($\rho = 0$) for these simulations.

a fully resident population was $\sim 10\%$ that of a fully dispersive population ($CV_{pop} = 4\%$ at $D = 0$; $CV_{pop} = 38\%$ at $D = 1$; Fig. 1b). Thus, contingent structure, through increased representation of the resident contingent, had a positive effect on stability of a population by dampening variation in SSB_{pop} . Relative to a fully dispersive population, variation in SSB_{pop} was dampened by 4–21%, depending on resident contingent representation ($D = 0.75$ and $D = 0.25$, respectively).

Coincident with the trend of increased productivity, resilience was higher (i.e., decreased time to recover

from disturbance) in populations with high dispersive contingent representation. Across dispersal scenarios, the number of years to rebuild the population above mean SSB after perturbation ranged from 11 ($D = 1$) to 17 years ($D = 0$; Fig. 1c). Rebuilding time of fully resident populations was 57% longer than fully dispersive populations.

Correlation simulations

Productivity (SSB_{pop}) was highest in populations with the highest level of negative correlation in recruitment to contingents ($\rho = -0.9$; Fig. 2a). Productivity was also high in populations with the highest positive ($\rho = 0.9$) correlation. In populations wherein contingent recruit-

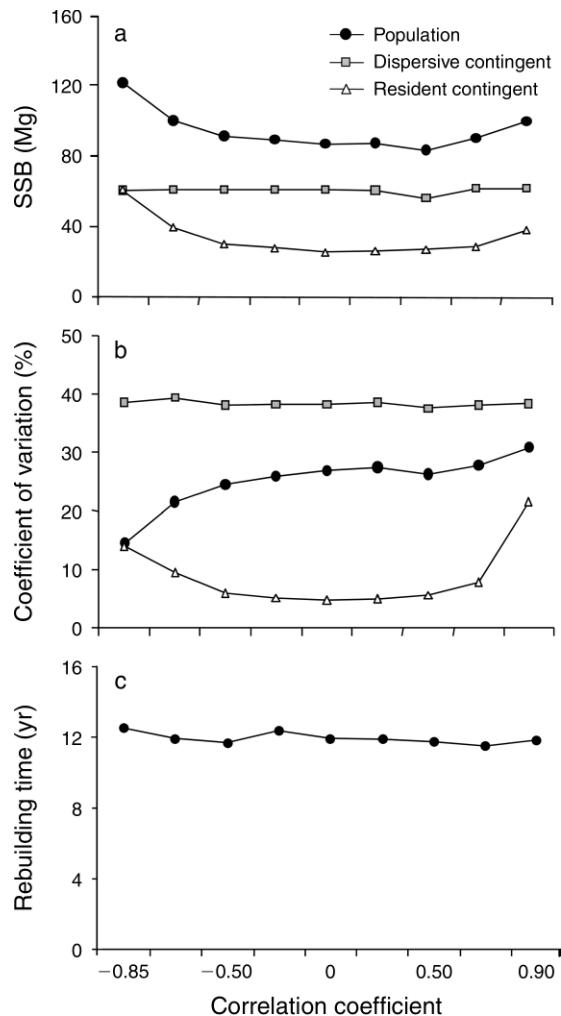


FIG. 2. (a) Spawning-stock biomass (SSB) and (b) the coefficient of variation of spawning-stock biomass of the resident and dispersive contingents and overall white perch populations with varying levels of correlation in recruitment to contingent. (c) Population rebuilding time, the number of years it takes for spawning-stock biomass of a population to rebuild above average SSB after a perturbation. Across correlation scenarios, the representation of contingents is equal (dispersive fraction within population, $D = 0.5$).

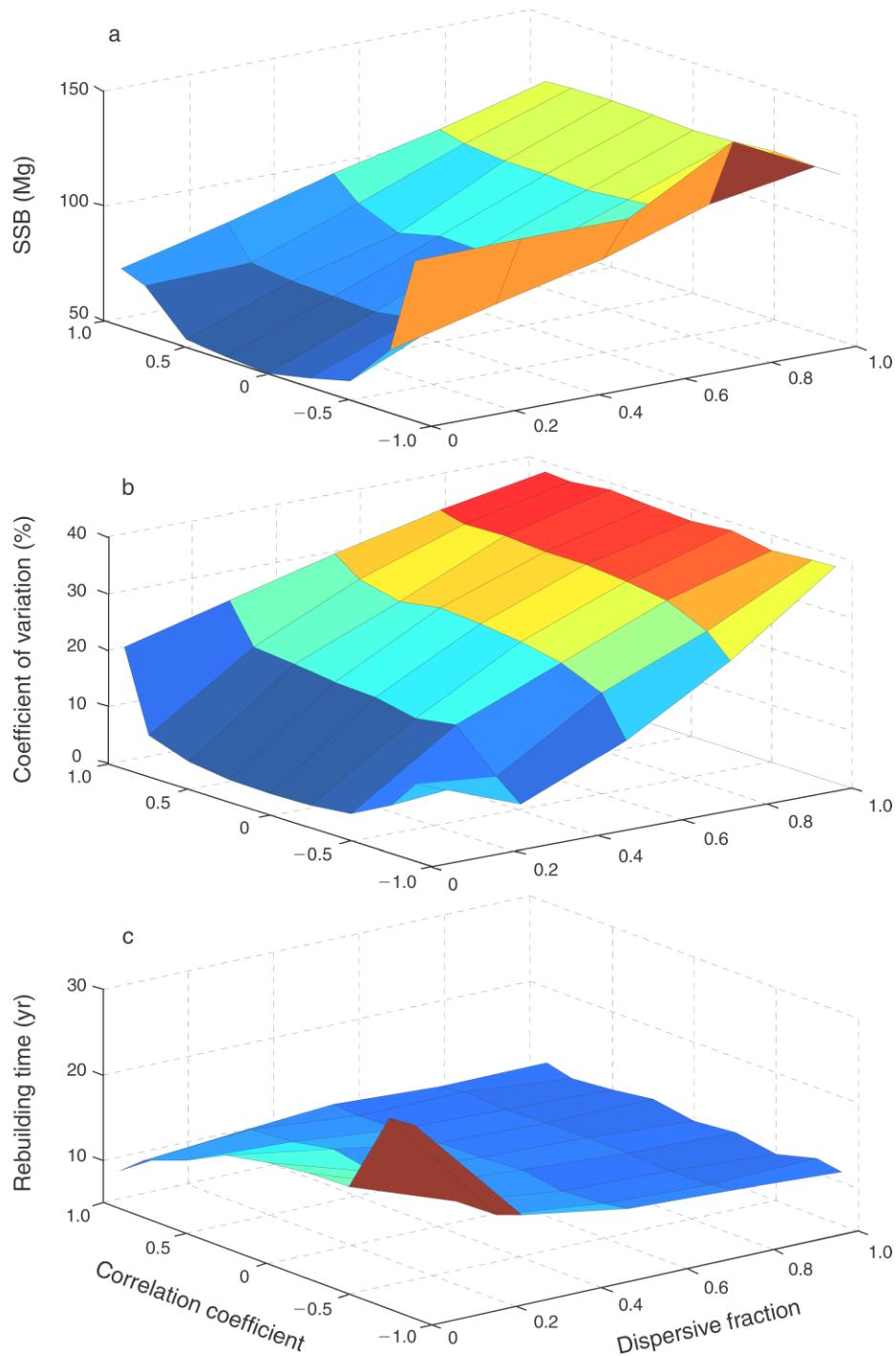


FIG. 3. (a) Productivity, (b) stability, and (c) resilience across all pairwise combinations of contingent representation and between-contingent recruitment correlation. Colors indicate the magnitude of response in the respective population metrics (spawning-stock biomass [SSB], coefficient of variation, rebuilding time), with red being the highest-magnitude response and dark blue being the lowest response value.

ment was negatively or positively correlated at lower levels, the population was less productive, with little variation in productivity across levels of correlation (Fig. 2a).

High positive and negative correlations between contingent recruitment resulted in similar high productivity within populations, but inverse responses with respect to stability. High negative correlation in

recruitment between contingents dampened variance in population fluctuations (e.g., 12% decrease in CV_{pop} at $\rho = -0.9$ relative to $\rho = 0$), whereas high positive correlation increased CV_{pop} of the population (e.g., 4% increase in CV at $\rho = 0.9$ relative to $\rho = 0$). Overall, changes in the degree of correlation in recruitment to contingents did not have a large effect on resilience of the population (Fig. 2c).

Contingent representation–correlation pairwise combinations

The response surface for productivity (SSB_{pop}) was steep and linear with changes in the representation of contingents in populations, whereas the surface was more subtle and concave in response to changes in between-contingent correlation (Fig. 3a). The highest productivity occurred in populations with high representation of dispersive individuals and a high negative between-contingent correlation. The response surface of stability was steeper in response to changes in contingent representation compared to correlation levels, which exhibited an s-shaped response (Fig. 3b). Populations with high representation of the dispersive contingent and high positive between-contingent correlation were characterized by the lowest stability (i.e., highest CV_{pop}). Overall, the response surface for resilience was relatively flat, with the exception of a peak in rebuilding time in a scenario in which the population was composed entirely of residents ($D = 0$) and exhibited relatively low productivity and stability due to larval dynamics (i.e., high larval mortality in high-stream-flow years and lower mortality in low-flow and drought years; Table 3; Fig. 3c). The relative higher steepness of productivity and stability response surfaces to contingent representation compared to between-contingent correlation indicated higher sensitivity of both population productivity and stability to contingent representation.

DISCUSSION

Simulations revealed that stability, resilience, and productivity measures were most sensitive to shifts in the proportion of the white perch population that dispersed from the freshwater natal habitat (D) and, to a lesser degree, the level of interannual correlation (ρ) in recruitment between contingents in response to the same set of environmental factors (i.e., stream flow). Increased representation of the dispersive contingent within populations resulted in increased productivity and resilience, but decreased stability (Fig. 4). The resident contingent, however, appeared to contribute uniquely to dynamics by enhancing the stability of populations through reduced interannual variability in recruitment (Fig. 4). A high negative correlation in resident and dispersive contingent recruitment dynamics resulted in increased productivity and stability, with little effect on resilience (Fig. 4). We identified similar responses in population productivity and resilience with a high positive correlation between contingent recruit-

ments, but stability was decreased. Thus, the periodic high recruitment and higher productivity of the dispersive contingent contributed disproportionately to rebuilding the overall population, whereas the consistent recruitment of the less productive resident contingent conferred stability to the population. These simulations support the view that contingent structure, specifically contingent-specific differences in demography and response to the environment, may contribute to population persistence.

The basic structure and parameter estimates of simulation models were informed by in-depth research of the white perch population in the Patuxent River of the Chesapeake Bay. The dispersive contingent was significantly more productive (i.e., higher growth rates, higher levels of recruitment), but a more variable contingent, with occasional recruitment failure due to environmental conditions (i.e., drought). The resident contingent showed lower productivity but relatively stable recruitment over time. Recent empirical estimates for the Patuxent River contingent system support an average D of 0.93 and correlations in recruitment to contingent of $\rho = 0.82$ – 0.94 . A large dispersive contingent coupled with high positive correlation (Kraus and Secor 2004, 2005b) in recruitment between contingents would indicate this is a population with relatively high productivity, high resilience, and low stability. Because dynamics of the population are sensitive to the relative abundance of contingents and the fraction that disperse is highly correlated with stream flow, changes in climate regime (i.e., periodicity of drought, high- and low-flow years) could dramatically alter contingent dynamics of the Patuxent River white perch population beyond that observed during the past decade (Kraus and Secor 2004, 2005a). The simulations of the age-structured model allowed us to more fully evaluate the roles contingent representation (i.e., fraction dispersive vs. resident) and the degree of independence in contingent response to the environment play in the regulation of population dynamics.

Empirical data

Contingent representation and correlation simulations were designed to cover a range of realistic population states, encompassing scenarios identified in other white perch populations within sub-estuaries of the Chesapeake Bay. Stable isotope ($\delta^{18}O$) analysis of adult white perch otoliths from the Upper Bay, Potomac, Choptank, Nanticoke, James, and York Rivers (2005–2006) revealed evidence of contingent structure across estuaries, with varying levels of contingent representation ($D = 0.31$ – 0.82 ; Kerr 2008). High levels of interannual variation in contingent representation were identified within these systems and are likely driven by environmental variability; thus oscillations or episodic shifts in climate could result in corresponding changes in contingent representation within these populations. Between-contingent correla-

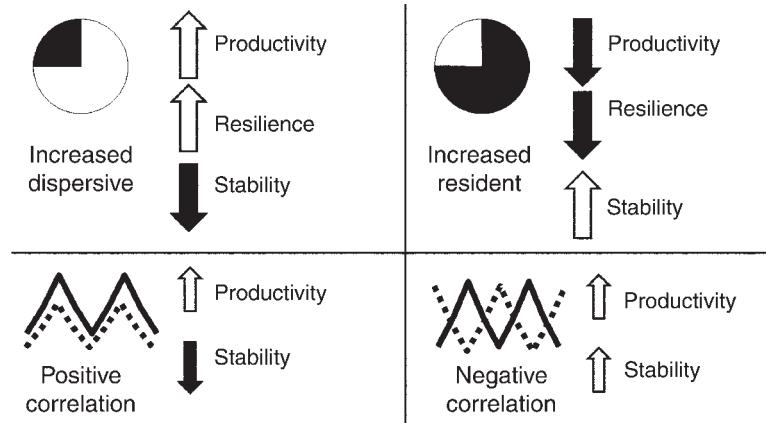


FIG. 4. Summary of simulation modeling results. The fill of arrows indicates the direction of change (open arrows, increased; solid arrows, decreased). The size of the arrows indicates the relatively greater response of population productivity, stability, and resilience changes in contingent representation compared to between-contingent recruitment correlation.

tions, as determined from trends in juvenile abundance in freshwater and brackish water habitat, also varied across and within systems ($\rho = 0.21\text{--}0.96$; Kraus and Secor 2005). Thus, the results of our simulations will inform our understanding of white perch population dynamics across sub-estuary populations within Chesapeake Bay.

Empirical data from other sub-estuaries was consistent with modeling results and trends for the Patuxent River population, where variability in adult catch per unit effort (CPUE) was more closely associated with juvenile abundances from brackish habitats (dispersive contingent) compared to freshwater habitats (resident contingent; Kraus and Secor 2005b). Kraus and Secor (2005b) used 1980–2001 commercial CPUE data to generate an index of spawning-stock biomass and the number of juveniles surveyed in brackish and freshwater littoral habitat as an index of contingent membership (D). In the Patuxent River, Upper, Bay, and Nanticoke Rivers, field data support the view that the dispersive contingent drives variability in adult productivity of the overall population.

Similar to the Patuxent River population, other estuaries exhibit higher CVs of juvenile abundance in brackish water as compared to freshwater (Kraus and Secor 2005b). Thus, across populations the more consistent recruitment of resident contingent fish likely results in dampened CV in overall juvenile recruitment. We hypothesized that mean adult CPUE (index of productivity) and CV of adult CPUE (index of stability) would be positively correlated with the mean proportion of populations that was dispersive within each estuary. Indeed, there was a positive, although nonsignificant, association between adult CPUE and CV of CPUE and the mean proportion of the population that is dispersive (L. A. Kerr, *unpublished data*). Thus, across estuaries there was a tendency for increased productivity and decreased stability with increased representation of the

dispersive contingent. Still, in the best-studied estuarine system to date, the Patuxent River, interannual changes in contingent contributions to adult age classes indicates an important role for both contingents.

Management implications

Management strategies to promote stability, productivity, or resilience of populations that exhibit contingent structure would require management of either the relative abundance of or level of correlation in recruitment between contingents. It is difficult to envision managing the correlation between contingents because correlation dynamics are structured during early life history in response to the environment. A more feasible option would be to manage the relative abundance of each contingent through habitat or other conservation efforts aimed at a specific contingent or spatial management of exploitation in the fishery (i.e., focused fishing effort on the more productive contingent; Ricker 1958). The results of the model simulations also support managing for the relative abundance between contingents, because the dynamics of the population were more sensitive to this factor. The largest survival difference between contingents occurs during the first year of life, so it would follow to target actions that affect these rates. As an example, severe degradation of the freshwater environment would prevent successful recruitment of the resident contingent and increase the extinction probability of the population. Measures to protect a portion of freshwater littoral habitats could offset this risk. This strategy is substantially different from a current paradigm that would promote protection of only the most productive nursery habitats (Beck et al. 2001). We argue that this strategy inadequately considers population stability (persistence) as an important management goal.

An important issue in management strategies that emphasize population persistence will be how to rank

performance indicators of productivity, stability, and resilience. Undoubtedly, different interest groups will give divergent weights to these performance indicators. Steele (2006) addressed this same problem in the context of weighting the importance of ecosystem metrics, suggesting that “we must accept that there is a societal or nonscientific element in assigning these weights—and work out a way to do this equitably.” For white perch populations, the best management practice could be a balance in conserving contingent structure that would support both population growth and stability.

Conclusions

In this study, we examined the consequences of intra-population spatial structure to the persistence of an estuarine fish population. Spatial structuring within populations has been documented extensively within diadromous fish populations (i.e., Salmonidae and Anguillidae). More recently, the importance of spatial structuring has been recognized in several marine fish populations (e.g., Atlantic cod, Smedbol and Wroblewski 2002, Ames 2004; Atlantic herring, McQuinn 1997; Atlantic bluefin tuna, Fromentin and Powers 2005) and is probably more widespread than previously recognized in marine and estuarine species (Kerr and Secor 2009; Secor and Kerr, *in press*). The degree to which the results of the white perch model can be generalized to other fish populations will be explored in future work through tailoring the model structure and parameters (e.g., Secor et al., *in press*). This type of model structure has been applied to examine the consequences of differences in demography and dispersal between populations in a metapopulation context (e.g., Gerber et al. 2005), but this is the first example we are aware of that applies this model framework to examine the consequences of within-population spatial structure.

Overall, the results of this modeling exercise suggest the need to consider finer-scale management of fish populations and to reevaluate the concept of population integrity (i.e., the “unit stock”; Harden-Jones 1968, Cushing 1975). Partial migration has been accounted for in management of some salmonid populations (e.g., Pacific salmon, Knudsen et al. 1999), but has not been considered for other coastal fish populations. The importance of persistent representation of resident and migratory phenotypes, without genetic differentiation, as an evolutionary adaptation to a heterogeneous environment should be recognized as possibly common to coastal fishes. Including contingent structure in population assessments and fishery management plans may require higher resolution spatial surveys and more sophisticated population models. Despite the increased costs of these efforts, benefits to management will include more explicit performance indicators related to stability and resilience and increased efficiency of spatial management of fisheries, such as protection of essential fish habitat (Cadrin and Secor 2009).

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