Partial Migration of Fishes as Exemplified by the Estuarine-Dependent White Perch

ABSTRACT: Partial migration defines the phenomenon of coexisting groups exhibiting migratory and resident behavior within the same population. In avian ecology, partial migration is a fundamental behavior that underlies the evolution of migration in general. Among fish taxa, the terminology and theory associated with partial migration has predominantly been used to describe salmon ecophenotypes, but the behavior is more widespread. Here, we document partial migration for the estuarine-dependent white perch (*Morone americana*), in the Patuxent River estuary (Chesapeake Bay, Maryland), wherein a portion of the population resides in freshwater natal habitats and another portion migrates down-estuary into brackish water (salinities > 3) habitats. Life-time migration histories were examined using otolith strontium:calcium profile analysis. Alternative life history tactics, initiated during the juvenile period in response to individual physiological condition, persisted over the lifetime of the individual and had population-level consequences, including differences in growth rate and productivity. Based upon a review of recent literature, we argue that partial migration is more widespread among fishes than previously recognized, and such population structure has important implications for population dynamics and persistence.

La Lobina Blanca como Ejemplo de Migración Parcial en Peces

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RESUMEN: La migración parcial sirve para definir patrones intra-poblacionales de comportamiento migratorio y residente. En ecología de aves, la migración parcial constituye una conducta fundamental dentro del contexto general de la migración. En peces, la terminología y teoría asociadas a la migración parcial se han utilizado principalmente para describir los ecofenotipos del salmón, sin embargo el comportamiento tiene un carácter más general. En la presente contribución se documenta la migración parcial de la lobina blanca (*Morone americana*) una especie estrictamente estuarina del Rio Patuxent (Bahía Chesapeake, Maryland) en donde una parte de la población es residente de hábitats de agua dulce y la otra migra hacia aguas salobres del estuario; un hábitat con salinidades > 3. Se examinaron las migraciones durante la historia de vida de la especie mediante un análisis de perfiles estroncio:calcio en los otolitos. Las tácticas alternativas de la historia de vida, que inician durante el periodo juvenil como respuesta a la condición fisiológica individual, persistieron durante toda la vida del organismo y tuvieron repercusiones a nivel poblacional que incluyen diferencias en las tasas de crecimiento y productividad. Sobre la base de una revisión de la literatura reciente, se argumenta que la migración parcial es un fenómeno más ampliamente distribuido de lo que se había reconocido, y que tal estructura poblacional tiene implicaciones importantes en la dinámica y persistencia de las poblaciones.

INTRODUCTION

The high capacity for dispersal of birds, insects, and fishes has led to theories that seek to generalize sedentary and migratory behaviors among and within species. In the study of bird populations, partial migration (also referenced as obligate partial migration) is

a central idea, wherein one portion of a population is migratory and another portion is sedentary, remaining resident on the breeding ground over its lifetime (Lack 1943; Berthold 2001). By comparison, fish ecology contains few organizing theories related to intra-population diversity in life cycles. Indeed, a central idea (member-vagrant hypothesis; Sinclair 1988) argues against selection for divergent migrations within populations of marine fishes, despite evidence that life cycle diversity is common (McQuinn 1997; Secor 1999; Fromentin and Powers 2005). The concept of partial migration has primarily been adopted from the avian literature to describe salmon ecophenotypes (phenotypes expressed in response to environmental conditions; see review by Jonsson and Jonsson 1993), but has not been widely applied outside this family (Kitamura et al. 2006; Brodersen et al. 2008). Partial migration in fishes has been overlooked due to the emphasis on closed population assumptions that are required in traditional fisheries stock assessment (Secor 1999; Cadrin and Secor in press), or obscured by the use of multiple terms to describe the phenomenon (Secor and Kerr in press). We propose that partial migration is a widely applicable and useful concept for understanding the life cycle diversity of fishes, because it provides a mechanistic understanding of the evolution, control, and adaptability of migratory behavior (Berthold 2001).

Proposed mechanisms for the maintenance of partial migration within bird and salmon populations include (1) a conditional strategy, whereby an individual's genetic makeup allows for the adoption of resident or migratory behavior based on an interaction between individual physiological condition and the environment (Gross 1996; Gross and Repka 1998; Lundberg 1988), (2) frequency-dependent selection of the migratory tactic (i.e., an evolutionary stable strategy; Lundberg 1988; Gross 1996), and (3) genetic polymorphism, whereby the two morphs represent reproductively isolated sub-populations (Lundberg 1988; Verspoor and Cole 1989).

The most widely accepted mechanism across taxa for partial migration is a conditional strategy, a concept rooted in the ideas of individual fitness and life history tradeoffs. The preponderance of evidence from salmonid studies supports the idea of partial migration as a conditional strategy, with the degree of migratory behavior expressed within the population based on an individual's physiological condition, as influenced by the environment, relative to a genetically-defined threshold (Jonsson and Jonsson 1993). Specifically, within brown trout (*Salmo trutta*; Forseth et al. 1999; Cucherousset et al. 2005) and Atlantic salmon populations (*Salmo salar*; Metcalfe et al. 1995; Bujold et al. 2004) growth rate (or

metabolism) early in life has been identified as the developmental threshold that triggers migratory behavior.

Theory on the evolution of partial migration in birds can enhance our understanding of the expression of migratory behavior across fish populations. In the wild, the expression of migratory behavior within a population is specific to the regional selection regime with shifts in the relative abundance of migratory and resident morphs occurring from year to year (Berthold 2001). Experimental evidence in bird populations, such as blackcaps, indicates shifts from partially migratory to fully migratory or sedentary populations were possible in only a few generations through selection (Berthold 1999). This flexibility in the expression of migratory behavior allows partial migration to be a widespread, highly adaptable, and successful behavioral strategy among birds. Here, we speculate that similar to birds, partial migration is common across fish species as a behavioral strategy, but to date is most frequently described in populations wherein it is morphologically expressed and readily observed (i.e., salmonid populations which exhibit morphological differences between resident and migratory individuals).

The white perch (*Morone americana*) is a dominant and ubiquitous estuarine species in the Chesapeake Bay that has been classified as semi-anadromous, completing its life cycle in fresh and brackish tidal waters. The conventional thinking was that all white perch move into brackish waters during the late-juvenile to adult stage, and adults return to freshwater habitats in the spring to spawn, with eggs and larvae developing in this environment (Figure 1; Mansueti 1964). Recently, chemical tracers in otoliths of white perch from the Patuxent River estuary identified divergent habitat use during the first year of life, with a portion of the population remaining resident in the natal freshwater region and a second portion of the population dispersing into brackish water (salinities > 3) environments (Kraus and Secor 2004b). The divergence in habitat use within the population occurred after the transition from larval to juvenile stage and the representation of

Figure 1. The life cycle of white perch. Gray arrows represent movement into brackish water and white arrows represent residence in freshwater. The life cycle depicted under the heading Dispersive Contingent was formerly assumed to represent the behavior of all white perch in the Chesapeake Bay.
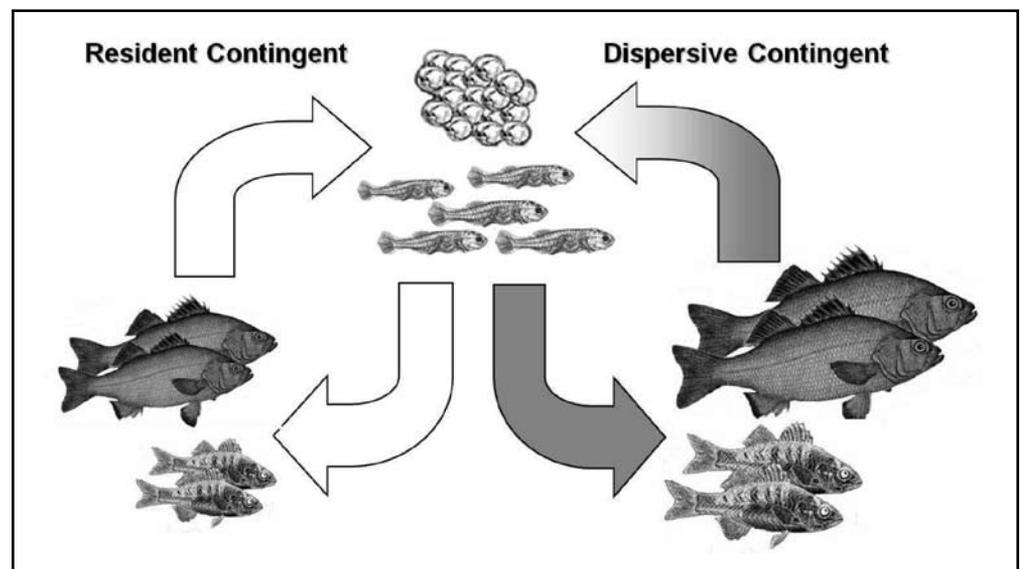
contingents, portions of the population that exhibit divergent migratory behaviors or habitat use, varied across years in response environmental conditions (i.e., streamflow, Kraus and Secor 2004a). Within a particular year-class, the percentage of white perch that remained resident during their first year of life ranged from 4% in high flow years, 15% in low flow years, and 100% in drought years (Kraus and Secor 2004b). The location of peaks in summer catch rates (2002–2005) of young-of-the year white perch within the tidal freshwater portion of the river ranged from river km 53 to 72 (Figure 2) and within the brackish water habitat ranged from river km 33 to 45, indicating this down-estuary movement averaged 16 river km (L. Kerr, unpublished data). Little was known regarding the permanence of freshwater residency within the population or whether all fish ultimately exhibit movement down-estuary and subsequent spawning migrations into freshwater.

Here, we provide evidence of divergent lifetime migratory patterns within a white perch population, a principal tenet in demonstrating partial migration. A review of the recent literature is presented to support the contention that par-

tial migration is likely a widespread phenomenon in fishes. Additionally, we address the impact partial migration may have on the dynamics and long-term persistence of populations, directing attention to this behavior as it relates to management and conservation goals.

METHODS

Sample Collection

Adult white perch were collected by fyke net in the tidal freshwater and oligohaline portions of the Patuxent River estuary where adults in the population were aggregated for spawning in the spring of 2001 and 2002 (Figure 2). A collection of adult otoliths (N = 363) was previously classified by juvenile habitat use (freshwater or brackish) based on strontium:calcium (Sr/Ca) measurements during the year-1 period of growth in the otolith (Kraus and Secor 2004b). We used these same prepared otoliths for age estimation and to conduct profile analyses of Sr/Ca (terminology after Elsdon et al. 2008) during the late juvenile and adult phases of life

Figure 2. Location of freshwater habitat in the Patuxent River estuary wherein adult white perch were collected (shaded box). Location of peaks in summer (2002–2005) catch rates of young-of-the year white perch within the tidal freshwater portion of the river (river km 53 to 72; dashed line) and within the brackish water habitat (river km 33–45, solid line).
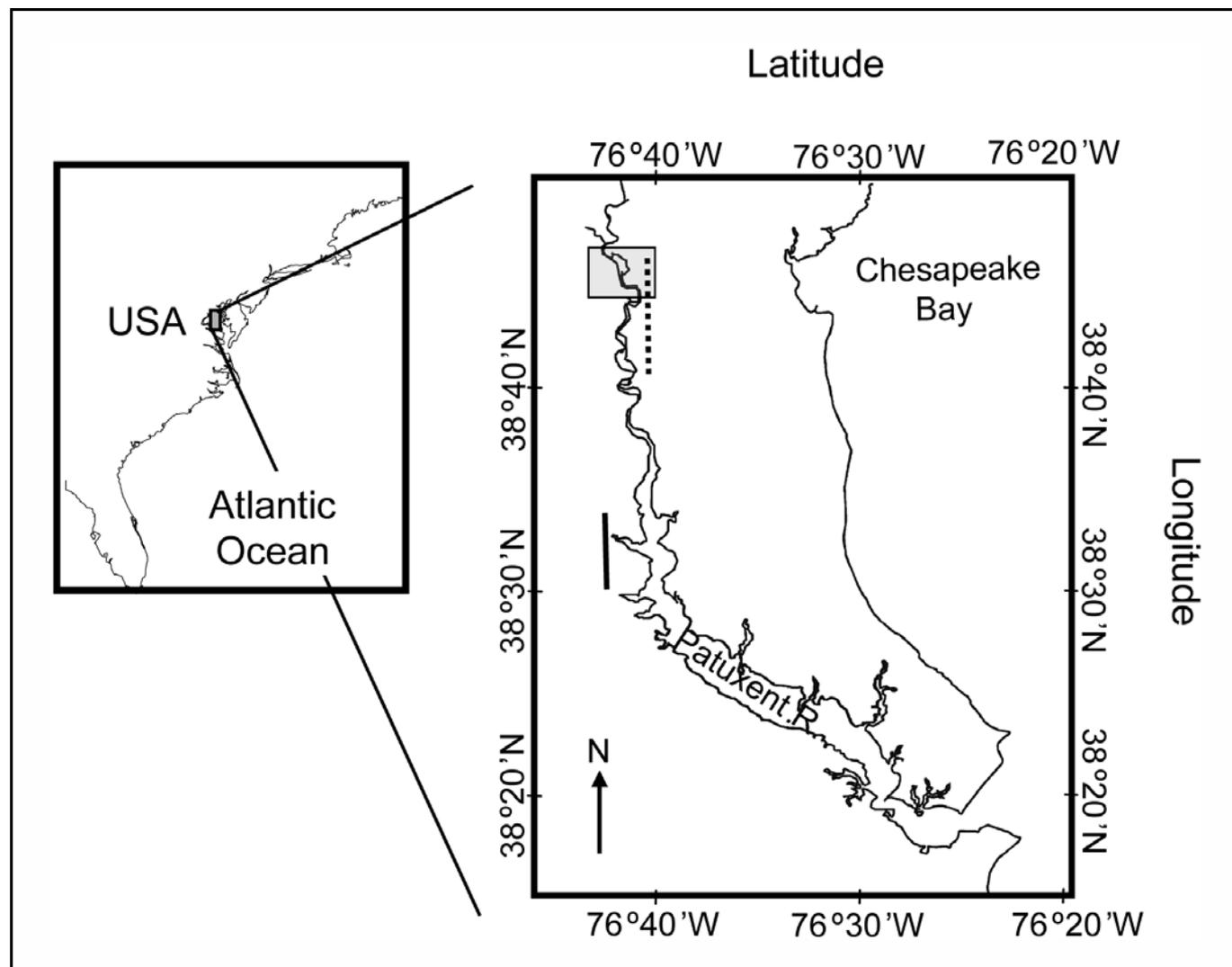
history. Annual growth zone formation of mature white perch otoliths was previously validated by oxytetracycline injection (Casey et al. 1988).

Sixty otoliths were sub-sampled from this collection. All fish characterized as freshwater residents during the first year of life (n = 27), and a random sub-sample of fish that dispersed (n = 33) during year-1 were analyzed for Sr/Ca profiles according to Kraus and Secor (2004b). Points were measured at 25 μm intervals from the first opaque zone (year 1) to the otolith edge. Backscatter electron micrographs were taken after microprobe analysis to assign the location of points to annual growth increments. Mean Sr/Ca values were calculated for each year of growth in the otolith. Width of annual growth increments was measured along the ventral side of the sulcal ridge from photos using ImageJ software (W. S. Rasband, ImageJ, U.S. National Institutes of Health, Bethesda, Maryland, http://rsb.info.nih.gov/ij/, 1997–2007).

Statistical Analysis

We classified individuals into migratory or resident contingents based on mean annual Sr/Ca values. Previous research in the Patuxent River estuary (Kraus and Secor 2004a) showed that brackish water (salinity > 3) habitat use corresponded to Sr/Ca values > 2 mmol/mol and freshwater habitat use corresponded to Sr/Ca values < 2 mmol/mol. Mean fish age, mean length at age, and sex ratio were compared between contingents respectively with a Wilcoxon rank sum test, two-sample t-test, and chi-square. We estimated growth rate using back-calculated fish length at age from the widths of otolith growth increments using the Biological Intercept Method (Campana 1990). The biological intercept of 3.2 μm at 3 mm TL was used (Kraus and Secor 2004b). We compared mean back-calculated length between resident and migratory fish at age 1, 2, and 3 years. Diagnostics were employed to test for univariate normality, equal variance, and influential observations. Statistical analyses were performed with SAS Version 9.0 (SAS Institute 1999, Cary, NC); α = 0.05 was used as a critical level of significance.

Generalized estimating equations were used to analyze otolith Sr/Ca values because mean Sr/Ca values were autocorrelated across annuli of individuals and the assumption of a normal distribution was not reasonable for this data (Liang and Zeger 1986). We analyzed data using the GENMOD procedure in SAS Version 9.0 (SAS Institute 1999, Cary, NC). The distribution of the data was specified as binomial and fit with a logistic link function. Repeated measures analysis was used to test whether lifetime patterns of habitat use, based on mean annual Sr/Ca values, were dependent on the individual's age, sex, or the interaction of the terms. This analysis

was constrained to ages 1–7 years based on the representation of ages in the sample and concerns of potential bias due to low representation of older age classes. The deviance ratio, a goodness of fit measure, was used to assess model adequacy.

RESULTS

The mean lifetime Sr/Ca value of fish classified as residents was low and showed little variability across individuals (mean lifetime Sr/Ca: 1.0 ± 0.2 mmol/mol), whereas fish classified as migratory had elevated mean Sr/Ca value with a higher degree of variability (mean lifetime Sr/Ca: 2.9 ± 0.8 mmol/mol). Otolith Sr/Ca values increased with age in migratory contingent fish, whereas individuals classified as resident exhibited stable mean annual Sr/Ca values during their lifetime (Figure 3). The majority of the subsample of fish examined in this study was classified as migratory (85%). Because the sample represented a sub-sample from a larger collection (N = 363) of fish, the sample-weighted representation within the overall population equates to 97% migratory and 3% resident fish across year-classes.

Resident fish in the sample ranged in age from 2 to 8 and migratory fish ranged from 3 to 10 years. The mean age of fish was similar between contingents (Wilcoxon rank sum test: Z = -1.83, P = 0.07). Significantly larger length at age was observed in migratory fish at age 2 and 3, but not at age 1 (t-tests: age 1: df = 58, t-test statistic = -1.43, P = 0.16; age 2: df = 58, t-test statistic = -2.26, P = 0.03; age 3: df = 54, t-test statistic -2.30, P = 0.03; Figure 4). There was a tendency for migratory individuals to be female (55%) and resident individuals to be male (78%), but the sex ratio for resident and migratory

Figure 3. Mean annual Sr/Ca (mmol/mol) of adult white perch grouped based on contingent classification (open circles = resident contingent, closed circles = migratory contingent). Error bars represent standard deviations. The black hatched line delineates brackish water (salinity > 3) habitat use corresponded to Sr/Ca values > 2 mmol/mol and freshwater habitat use corresponded to Sr/Ca values < 2 mmol/mol.
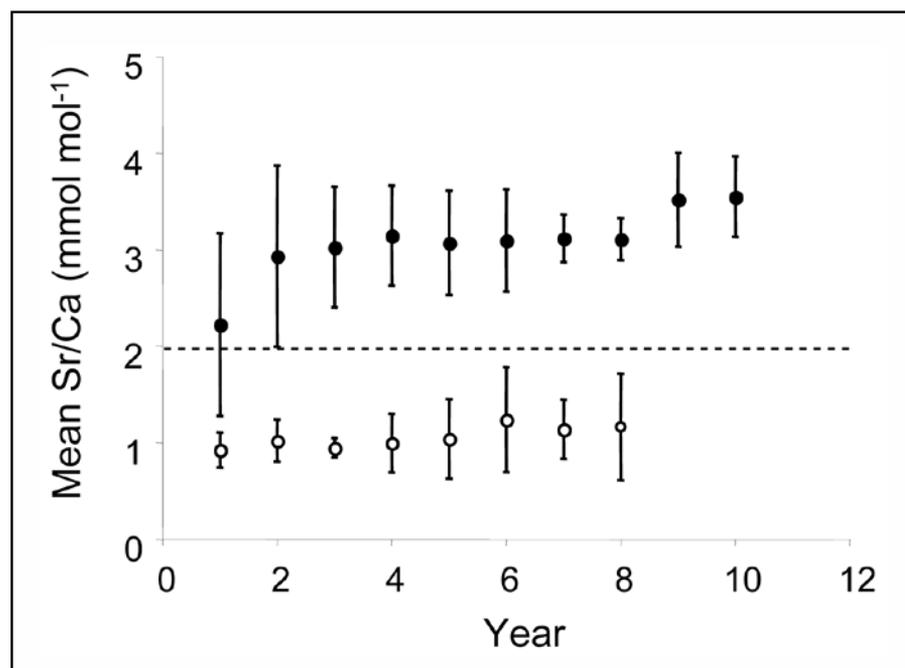
contingents was not significantly different from the 50:50 ratio of the overall sample (chi-square tests: $P \geq 0.1$; Table 1). Significant variation occurred in habitat classifications at ages 1 and 2 (repeated measures, age 1: $P = 0.01$; age 2: $P = 0.03$) but not at older ages; nor were there significant differences detected between sexes or the interaction between age and sex (all $P > 0.5$) in habitat classification. Significant variation is expected at age-1 as samples were chosen based on prior classification of age-1 habitat use (~50:50 representation of freshwater resident and dispersive fish). Still, the lack of significant difference in habitat use at older ages indicated that once a juvenile established a migratory or resident behavior, this persisted later in life.

Examination of Sr/Ca profiles showed that individuals that dispersed from the freshwater natal habitat did so primarily at age 1 (65%), and to a lesser extent at age 2 (18%), 3 (10%), and 4 (6%), with one individual dispersing at age 7 (Table 1). Thus, contingent behavior was generally initiated during the juvenile period (100% sexual maturity is reached by age 2 [males] and age 4 [females]; Mansueti 1961) and persisted over the lifetime of individuals (Figure 5). There were a few cases of resident individuals ($n = 3$) becoming migratory following maturity. Profiles of migratory individuals exhibited periodic decreases in Sr/Ca indicative of recurring movements into low salinity environments for short periods of time, but once a migratory tactic had been initiated, no reversion to a resident behavior was detected (Figure 5).

Figure 4. Back-calculated length at age (age-1 to -3) of white perch contingents (resident and migratory). Sample size is indicated above each box. The center vertical line marks the median, the length of each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. Asterisks are datapoints outside this range.
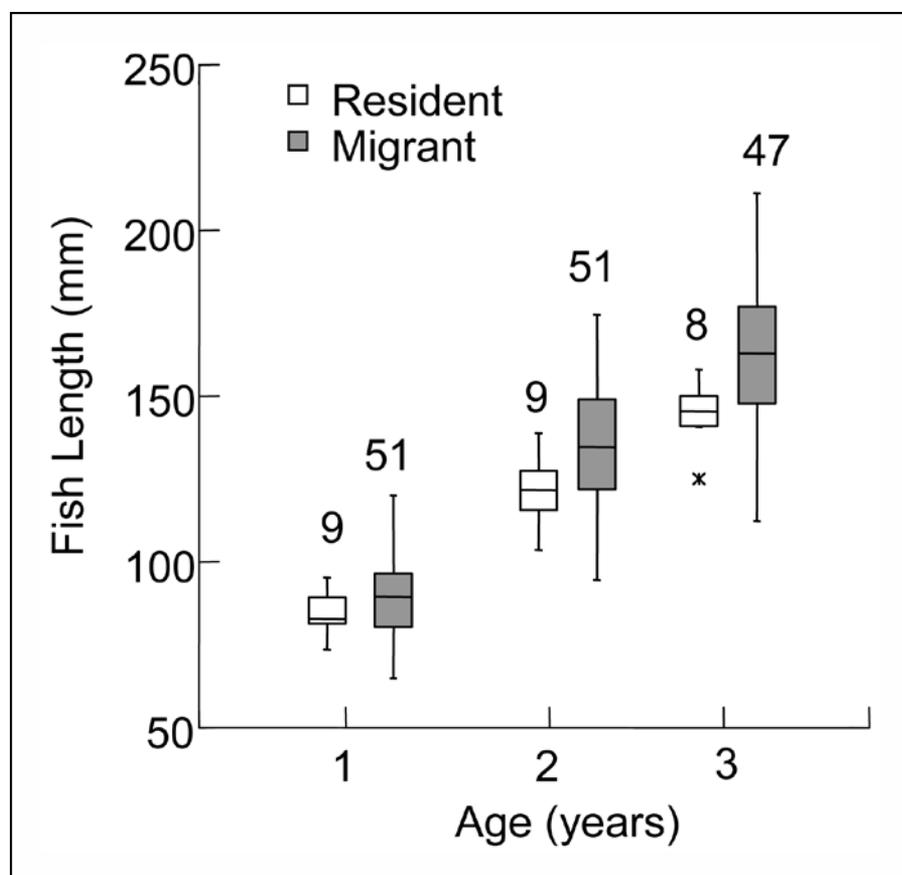

DISCUSSION

Based on microchemical analysis of otoliths, we determined that white perch exhibit partial migration, with a portion of the population remaining in the natal habitat (resident contingent) and another portion exhibiting denatant migration (migratory contingent). The majority of individuals were migratory, moving into brackish waters during the juvenile stage, remaining in this environment into the adult stage, and returning to freshwater to spawn. Still, a detectable minority of individuals remained in their freshwater natal habitat throughout their lifetime (Figure 5). Findings by Kraus and Secor (2004b) support the view that the resident contingent shows increased representation during low flow and drought conditions.

The flexibility in life history identified in white perch is consistent with obligate partial migration and is similar to that identified in several species of Salmonidae (e.g., Arctic char *Salvelinus alpinus*, Nordeng 1983; brown trout, Jonsson 1985; brook trout *Salvelinus fontinalis*, Thériault and Dodson 2003). The maintenance of alternative life history tactics is thought to be governed by the tradeoffs between the costs of migration (e.g., increased predation, physiological costs) balanced against the benefits of migration (e.g., higher food availability, increased growth potential; Jonsson and Jonsson 1993; Metcalfe 1998; Mangel and Stamps 2001). Over a lifetime, resident contingent fish exhibit slower growth (Kraus and Secor 2004b; this study), and are expected to have lower reproductive rates and fitness compared to the migratory portion of the population. Although not tested in this study, evidence from other studies indicates that the benefits of migration into higher salinity waters may be offset by higher predation risk in these deeper estuarine environments (Ruiz et al. 1993; Miltner et al. 1995; Paterson and Whitfield 2000). Additionally, faster juvenile growth rates exhibited by migratory individuals may be offset by physi-

Table 1. Summary of samples classified as members of the resident or migratory contingent by sex and, within the migratory contingent, by age at dispersal from the freshwater habitat. The percentage of individuals that dispersed at each age is indicated.

Contingent	Age @ dispersal	Count	Female	Male	% dispersal
Migratory	1	33	16	17	65
	2	9	5	4	18
	3	5	5	0	10
	4	3	1	2	6
	7	1	1	0	2
Resident	NA	9	2	7	0

Figure 5. Time series of Sr/Ca (mmol/mol) values sampled across the growth zones of adult white perch otoliths. Individuals are grouped based on lifetime habitat use, and classified as resident (a) or migratory (b) contingent members. The black hatched line delineates the threshold between brackish water (salinity > 3) habitat use corresponded to Sr/Ca values > 2 mmol/mol and freshwater habitat use corresponded to Sr/Ca values < 2 mmol/mol. Switching of life history tactic (resident to migratory behavior) later in life occurs in a small number of individuals as evidenced by Sr/Ca profiles (b). Photo insert shows electron micrograph with points indicating the location of microprobe analysis across otolith growth zones.
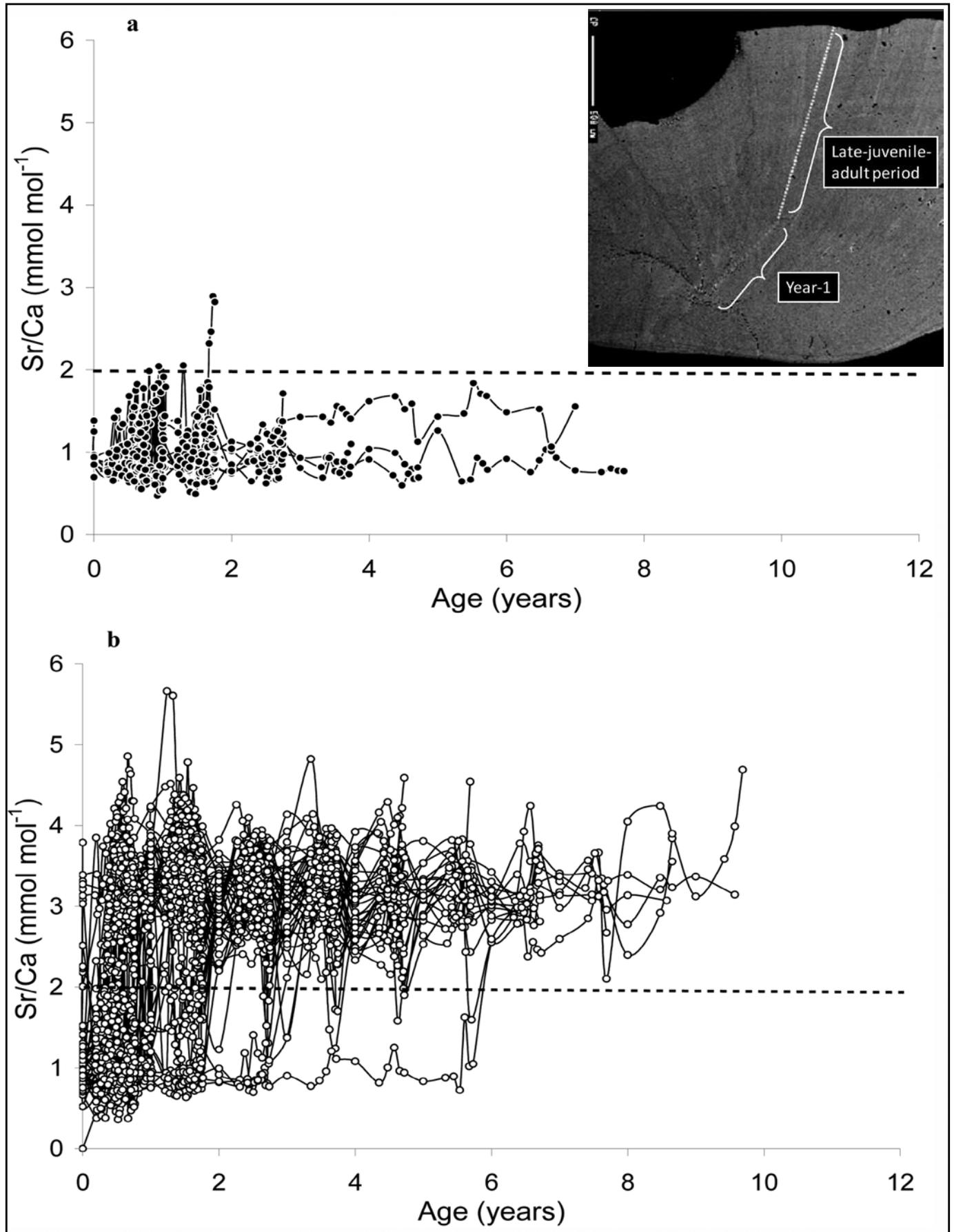
ological costs of accelerated growth such as reduced predator evasion (Metcalfe 1998; Billerbeck et al. 2001; Mangel and Stamps 2001).

The question of which fish within a population migrate has been examined in several salmonid populations. Overall, males tend to dominate the composition of resident fish, whereas females are more likely to migrate (Jonsson and Jonsson 1993). The tendency for females to migrate is linked to the growth advantage conferred to migrants within these populations and its consequences to reproductive success, such that larger females produce more eggs and thus have higher fitness (Fleming and Gross 1990; Jonsson and Jonsson 1993). No significant trend in females exhibiting migratory, rather than resident behavior, was observed in the Patuxent River white perch population.

Under the view that individuals maximize fitness, behavior should depend on the present condition of an individual and tradeoffs in future expected growth and probability of survival as a resident or migratory fish (Forseth 1999). Growth rate early in life has been identified as a controlling factor in the expression of migratory behavior in a number of fish species. In some cases, faster growing fish (e.g., Atlantic salmon, Metcalfe and Thorpe 1992; brown trout, Forseth et al. 1999; brook charr, Thériault and Dodson 2003) migrate and in other cases it is the slow growing fish that are migratory (e.g., sockeye salmon *Oncorhynchus nerka*, Ricker 1938; Arctic charr *Salvelinus alpinus,* Nordeng et al. 1983, Näslund et al. 1993). Faster growing fish may disperse because they have the energy reserves necessary to migrate or in response to limited food availability relative to their high energetic needs (Jonsson and Jonsson 1993). Alternatively, in some populations, slow-growing or poor condition individuals initiate migration in response to low food availability or high population density that limits them from growing at an optimal or threshold level (Jonsson and Jonsson 1993; Näslund et al. 1993).

Conditions experienced early in life appear to trigger migration in the white perch population. Initiation of migratory behavior in white perch occurred primarily in year-1 and secondarily in year-2 of life. Examination of the physiological basis of migratory behavior within this white perch population indicated that migratory fish grew slower early in life (larval period) compared to resident fish and, subsequent to dispersal, migratory juveniles had higher growth rates (Kraus and Secor 2004b; Kerr and Secor in press). Evidence supports the hypothesis that the conditions experienced by white perch early in their life history (e.g., temperature and prey density) have consequences to individual growth rates, and are the proximate factor determining migratory or resident behavior of white perch (L. Kerr, unpublished data).

Within bird and fish populations that exhibit partial migration, individuals can shift between resident and migratory behavior within their lifetime. This behavioral change is thought to be related to changes in individual fitness (Lundberg 1985; Dingel 1996; Zimmerman and Reeves 2002) and may be associated with changes in the relative productivity of habitats (Naslund et al. 1993). Mid-life shifts between migratory and resident behavior have been documented in Arctic charr (Radtke et al. 1996; Nordeng 1983) and striped bass (*Morone saxatilis,* Zlokovitz et al. 2003). Evidence of switching migratory behavior supports the hypothesis that this phenomenon is not genetically programmed, but represents alternative phenotypes. There was no evidence within the white perch population of migrants becoming residents later in life. Thus, it appears that the benefit of a migratory lifestyle outweighs advantages associated with remaining resident. We did, however; find evidence of resident fish initiating migratory behavior later in life. We hypothesize that, for these individuals, conditions in the freshwater habitat became less advantageous to individual fitness later in life. Alternatively, resident fish may have become entrained into schools of migratory individuals during spawning season when resident and migratory individuals mix (McQuin 1997).

Consequences of partial migration

A link between environmental conditions experienced during early life history and migratory behavior in white perch (L. Kerr, unpublished data), would suggest that inter-annual variation in the environment will likely lead to inter-annual differences in the expression of life history tactics within the population (Mangel 1994). For white perch, recruitment to the migratory contingent dominates in high flow years, with the resident contingent increasingly represented in low flow years, and exclusively present during drought years (Kraus and Secor 2004b). A corollary to this idea is that anthropogenic perturbation of the environment will have a significant effect on the expression of partial migration through its influence on both individual condition (e.g., growth rate) and the environment (e.g., relative productivity between habitats; Näslund et al. 1993). For instance, eutrophication within freshwater habitats may promote increased residency due to high productivity (Gross 1987). Similarly, increased water temperature in the natal freshwater habitat may increase energetic demands by white perch, potentially increasing the migratory portion of the population. Partial migration also has consequences to pollution ecology. For example, striped bass classified as freshwater residents had greater levels of PCBs than migrants (Zoklovitz and Secor 1999). King et al. (2004) identified a positive association between PCBs in white perch and the level of development in the Chesapeake Bay watershed. Because urbanization and development in the Chesapeake Bay watershed is centered in freshwater regions of the estuary, we expect that this relationship would translate to high PCB levels in resident fish.

For white perch, partial migration can play a role in population production and stability dynamics. Years of high flow are related to high recruitment and greater production of migratory juveniles and adults; the resident contingent, although less productive, may be important to the stability of the population during successive years of low flow, when its production is favored (Kraus and Secor 2004b). The different roles contingents play in mediating population dynamics and persistence highlights the potential importance of managing for conservation of partial migration within fish populations.

Partial migration could be widespread across fish taxa but insufficiently recognized due to the lack of ecophenotypes associated with migratory and resident tactics, as they are in salmonids. Further, the current language of fish migration (e.g., anadromous, catadromous, amphidromous) generalizes migratory behavior of populations and tends to be taxa-specific, obscuring the general recognition of partial migration as a central phenomenon in describing complex life cycles. In a review of the recent literature, Secor and Kerr (in press) observed that increased application of approaches that hind-cast an individual's spatial history and reconstruct migration patterns (e.g., otolith microchemistry and electronic tagging) has resulted in a geometric increase in papers describing life-cycle diversity. Importantly, although a large set of terms is used to describe this diversity, many of the terms center on a pattern of resident versus

Table 2. Lexicon of terms and phrases used to describe life cycle diversity within species and populations. Terms and phrases that apply to alternate life cycles were searched using Cambridge Scientific Abstracts © Aquatic Sciences and Fisheries Abstract (adapted from Secor and Kerr in press). Usage indicates the overall number of times a term was used. Usage is further broken down by taxonomic family and the ecosystems connected by migration (number in parentheses indicates usage when > 5 citations).

Mode	Term	Usage	Families	Ecosystem
Dispersive modes (4)	Stray(s)	70	Salmonid (60), Acipenserid, Clupeid, Cyprinid, Gadid, Moronid, Scombrid	River-Coast (57), Coast, River, River-Lake
	Ocean type(s)	35	Salmonid (34), Gadid	River-Coast (34), Coast
	Sea type(s)	4	Salmonid	River-Coast
	Dispersers	1	Gadid	Coast
Retentive modes (15)	Non-anadromous	30	Salmonid (29), Coregonid	River-Coast (29), River
	Non-migratory	21	Salmonid (14), Anguillid, Clupeid, Cyprinid, Osmerid, Sparid	River-Coast (15), Coast, River-Coast, River-Lake
	Sedentary	16	Anguillid, Centrarchid, Cottid, Cyprinid, Ecosid, Engraulid, Gadid, Osmerid,	River (8), Coast, Lake-Coast, River-Coast, River-Lake
	Resident form(s)	12	Salmonid (10), Osmerid	River-Coast (9), River-Lake
	Stream type(s)	8	Salmonid (8)	River, River-Coast
	Freshwater type(s)	5	Osmerid, Gasterosteid	River-Coast
	Resident type(s)	4	Gasterosteid, Salmonid, Anguillid	River-Coast, River-Estuary
	River type(s)	4	Salmonid, Plecoglossid	River-Coast, River-Lake
	Lake type(s)	3	Salmonid	River-Coast, River-Lake
	Resident behavior(s)	2	Moronid, Salmonid	River-Coast
	Non-amphidromous	2	Gobiid, Plecoglossid	River-Lake, Estuary-Coast
	Non-catadromous	1	Anguillid	River-Coast
	Non-diadromous	1	Eleotrid	River-Estuary
	Resident ecotype	1	Salmonid	River-Lake
	Retentive	1	Review	Review

migratory behavior, consistent with our expectation that partial migration could be widespread (Table 2). For example, resident and migratory components have been recognized in the Atlantic bluefin tuna (*Thunnus thynnus*) population, whereby a portion of the population completes its life cycle within the Mediterranean Sea and others migrate into the Western Atlantic (Rooker et al. 2007). Additionally, Gulf of Maine cod (*Gadus morhua*) exhibit resident and migratory morphs (Wroblewski et al. 1994) that may be structured through partial migration.

Migratory behavior has evolved independently many times and there appears to be commonalities governing its expression across taxa (Dingle 1996). The developments in avian literature on the expression of migratory behavior can inform our understanding of the genetic and environmental factors regulating migration thresholds of fish. As there is a potential for rapid change in the expression of migratory behavior within populations in response to environmental change, a mechanistic understanding of migration could improve forecasts of behavioral responses to future climate variability. Notably, partial migration points to the idea that individuals exhibiting minority behaviors—in the past discounted as anomalies—can play an important role in population dynamics.

ACKNOWLEDGMENTS

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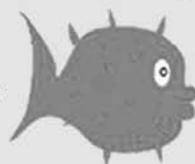hemistry. Fisheries Research 63:245–259.