

## ABSTRACT

Title of Document: ALTERNATIVE MIGRATORY PATHWAYS OF JUVENILE STRIPED BASS IN THE PATUXENT RIVER ESTUARY, MARYLAND

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Although highly migratory striped bass *Morone saxatilis* utilize spatially diverse and dynamic estuarine systems as nurseries, early dispersal behaviors have remained largely unknown. Using otolith chemistry, we identified consistent migratory and residence behaviors in juvenile striped bass year classes. Migrants were further separated by size and age into contingents that shared similar ontogenetic dispersal thresholds. We identified a small group of larval dispersers that moved to mesohaline waters prior to reaching 6 mm. Resident juveniles experienced better early growth than migrants. Small migrants had the lowest growth rates prior to dispersal, but afterward showed enhanced growth rate. Positive growth inflections were also observed for a group of migrants that reinvaded freshwater at larger sizes. Striped bass migration seems to be controlled by individual growth trajectories, where movement is driven by poor growth in the natal habitat.

ALTERNATIVE MIGRATORY PATHWAYS OF JUVENILE STRIPED BASS IN  
THE PATUXENT RIVER ESTUARY, MARYLAND

By

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## Introduction

### *Partial Migration and Persistence*

Migration, the movement of organisms between habitats over distances greater in scale than those employed during routine motion, is one of the most recognized of all animal behaviors. Although generally thought of as individually consistent and recurring (OED, 2012), migration takes many forms, occurs over many distances, and may transpire with varying frequencies (Chapman *et al.*, 2011b). One of the most interesting aspects of migration is that it is not ubiquitous within the populations of organisms that undertake this behavior. Indeed, most migrations may be “partial,” whereby a portion of a population refrains from the large scale movements undertaken by their peers (Lack, 1943). Dynamics that drive migration are diverse and may include differences in size, growth, condition, social status, and vulnerability to predation (Chapman *et al.*, 2011a). However, the causes and consequences of partial migration remain poorly understood, particularly for marine fishes.

In this thesis, we concentrated on how juvenile ecology contributes to partial migration, which has been explored in Salmonidae (salmon, trout, and charr species) but not thoroughly outside of this family. The ontogenetic development of partial migration in fishes has been shown to have large consequences on population resilience (Kerr *et al.*, 2010). As demonstrated in salmonids, early differences among individuals in intrinsic physiological condition and growth together with extrinsic environmental factors can lead to divergent spatial behavioral tactics (Jonsson and Jonsson, 1993). In natal (spawning and nursery) habitats, especially those with diverse spatial characteristics, these

behavioral differences may result in the physical separation of portions of the population, termed contingents (Secor, 1999). In an evolutionary context, authors have suggested that young-of-the-year (YOY) juvenile fish may weigh the costs incurred by movement, including predation and energy expenditures (Standen *et al.*, 2002; Skov *et al.*, 2011), against the costs of remaining in place, with the possible benefits of moving, such as improved foraging and growth (Boyle, 2008; Kerr and Secor, 2009). The interactions of fish with the environments in which they reside then leads to propensities to migrate or remain where they are (i.e. remain resident); this “conditional” decision on early migration is inherently plastic and may result in the maintenance of individual fitness in unpredictable and changing environmental settings (Lundberg, 1988).

The plasticity of partial migration fits into a larger ecological theme on the role of intrapopulation diversity to persistence. In a natural world filled with constant and random perturbations, a diversity of responses to these disturbances aids population persistence (McCann, 2000). The “insurance effect” imparted by diversity extends to behaviors like migration. A population not fully predestined to either migrate or remain resident, but rather to react through individual variation to conditions as they develop is better equipped to persist through, or recover from, potentially catastrophic circumstances. The importance of these diverse behaviors in young fishes has been indicated for Salmonidae, Clupeidae (herrings), and Moronidae (temperate sea bass) (Hilborn *et al.*, 2003; Ruzzante *et al.*, 2006; Kerr *et al.*, 2010).

A particularly instructive model for partial migration is the ontogenetic migratory behaviors of white perch *Morone americana*. This species spawns in the fresh and near fresh headwaters of coastal estuaries along the North American Atlantic coast (Mansueti,

1964). Following early larval residence in freshwater, a portion of YOY migrate to higher salinity habitats over a narrow distribution of ages while the remainder stay in freshwater (Kraus and Secor, 2004). YOY that remain resident tend to have higher early growth rates than those that migrate, while this latter group experiences higher growth following dispersal (Kraus and Secor, 2004; Kerr and Secor, 2009). The importance of the resident and migrant contingents to their fully recruited populations differs between estuaries, indicating the influence of local dynamics as well as inherent characteristics of growth to population persistence (Kerr and Secor, 2011). Considering the large number of fishes that utilize diverse estuarine habitats during ontogeny (Able, 2005), such important diversity in early migratory behaviors could well be widespread.

### Striped Bass

This thesis investigation seeks to better understand partial migration in estuarine fishes in general by focusing on the early ecology of striped bass *Morone saxatilis*. Striped bass is an anadromous species found throughout estuaries along the North American Atlantic coast from the St. Lawrence River, Canada in the north to northern Florida in the south, as well as along the northern Gulf of Mexico; this species has also been introduced to the US Pacific coast (Setzler-Hamilton and Hall, 1991). This species has long been an important resource to both the economies of the Chesapeake Bay region and states along the US Atlantic east coast from NC to ME (Norton *et al.*, 1984; Buerger and Kahn, 1989). Associated fisheries during the past 40 years have experienced a cycle of decline, strong management actions, and recovery (Richards and Rago, 1999). During this period the commercial importance of striped bass has waned somewhat while the



recreational fishery has expanded to support important local tourism and fishing industries (Lipton and Hicks, 2003).

Adult striped bass are anadromous and their movements are generalized as migrations from Atlantic coastal waters and higher salinity habitats to fresh and near fresh tidal reaches of coastal estuaries to spawn in the spring, prompted by environmental signals such as increasing water temperatures (Dovel, 1971; Secor and Houde, 1995). Striped bass are iteroparous capital spawners (females annually release eggs all at once), and as a result, waves of billions of eggs are released in day- to several day-spawning bouts that occur over a 1-2 month period. This results in cohorts of larvae and juveniles that can be differentiated by their hatch dates. Most of the newly hatched larvae are retained above the salt front in portions of the estuarine turbidity maximum (ETM). Under preferable environmental conditions, chiefly high freshwater flow, retentive forces are strong and the ETM offers higher concentrations of zooplankton prey, greater refuge from predation, and favorable environmental conditions for survival and development (Winger and Lasier, 1994; North and Houde, 2001; 2003). Regardless of the environmental conditions, mortality is very high during the larval stage, resulting in the loss of upwards of 99% of hatched larvae (Secor and Houde, 1995). Following the early larval period, metamorphosed juveniles disperse throughout the estuary, occupying a large extent of available mesohaline, oligohaline, and tidal freshwater regions of the natal estuary (Robichaud-Leblanc *et al.*, 1998).

Throughout most of their lifetime, striped bass undertake long migrations between estuarine spawning grounds and the coastal waters of the eastern United States (Secor and Piccoli, 1996; 2007). Although large proportions of fully recruited adults undertake

ocean migrations (as many as 75% of older females and 50% of older males), some adults remain in the Chesapeake Bay throughout the year; this proportion varies with age, size, and maturity (Dorazio *et al.*, 1991; Secor and Piccoli, 2007). The importance of early life history to these migrations remains unresolved, although work by Secor *et al.* (2001) did identify early movement within Hudson River estuarine habitats as potentially influential to adult behaviors. The similar reproductive ecology of striped bass and white perch, their shared ancestry, and their shared use of natal estuarine habitats suggest similar roles between the two species of early dispersal to later juvenile and adult migratory behaviors, and possibly population dynamics.

### Objectives and Goals

The importance of the timing of hatch, early growth, and subsequent ontogenetic migratory behaviors in the congeneric white perch to juvenile and adult behaviors and year-class strength suggests a role for similar behaviors in striped bass. The goals of this thesis were to 1) characterize the early migration of striped bass YOY over two year-classes and assign individuals to migratory contingents based on the characteristics of their specific dispersal histories, 2) identify proximate causes and apparent consequences of migratory behavior by measuring early vital rates that preceded and followed dispersal, and 3) identify important differences in growth and trophic status of juveniles that occupy specific estuarine salinity habitats.

### *Objective 1 (Chapter 1)*

In Chapter 1 we used otolith elemental analysis to hind-cast the intra-estuarine movements of juvenile striped bass in 2009 (n=71) and 2010 (n=34). The ratio of otolith concentrations of strontium and calcium (Sr/Ca) was used as a proxy for the

environmental salinities experienced by individual juveniles throughout ontogeny, allowing us to reconstruct lifetime histories of habitat use. We used Campana's (1990) biological intercept method to determine the sizes (total lengths, from otolith radii) at which individuals dispersed and, where possible, aged juveniles (2009 n=43; 2010 n=37) to determine dispersal ages (in weeks after hatch) and dates over which dispersal occurred. Length- and age-based profiles underwent a multi-step classification procedure that employed size- and age-specific Sr/Ca to characterize longitudinally-stratified movement histories over small sizes (total lengths 6-35 mm) and early ages (3-9 weeks after hatch) using principal component analysis (PCA). Individual juveniles were organized by their PCA scores using a hierarchical cluster analysis (CA). The resulting clusters were identified as size- and age-based migratory contingents: residents, larval dispersers, small/young migrants, and intermediate migrants. In a secondary analysis on a smaller sample that included larger individuals (total lengths 6-50 mm), additional contingents were identified: large migrants and returning migrants. The discreteness of PCA/CA-identified contingents was corroborated using repeated measures mixed models, which further allowed us to test the sizes and ages at which dispersals occurred. Resident and migratory contingents were consistently identified in both years indicating an underlying system of partial migration. Still, extrinsic factors were implicated: in 2009, dispersal by a slight majority of migrant contingent members (55%) was associated with a high flow event. Most individuals that dispersed did so during the early juvenile period (15-40 mm TL). A small incidence of juveniles that had dispersed as larvae (<5% of analyzed samples) was unexpected based on past field studies and experiments. Slight but significant differences in proportional representation of contingents between years

suggests annual variation in migratory behaviors and contingent success as has been observed in white perch (Kraus and Secor, 2004; Kerr and Secor, 2011). Disappearance of most residents and returning migrants between July and October 2009 signaled the possibility of contingent-specific differences in mortality.

*Objective 2 (Chapter 2)*

Using the contingent affiliations identified in Chapter 1, we investigated proximate causes and apparent consequences of partial migration in striped bass YOY in 2009 (n=71) and 2010 (n=34). We explored the importance of early growth, the timing of hatch, and environmental conditions preceding and following dispersal. Early growth influenced contingent membership in both years, with residents experiencing higher rates of growth during the larval and earliest juvenile periods. Although subtle, a gradient in growth was identified among migratory contingents where pre-dispersal growth rates increased with size-at-dispersal. This suggested the existence of a continuum of migratory tendencies linked to early growth rather than a specific threshold controlling dispersal. Although the timing of hatch did not specifically influence contingent membership, residents tended to be hatched later than other contingents. Hatch date did, however, affect early growth, with later hatched juveniles experiencing higher early growth rates. For larval dispersers, highly variable patterns of growth rates and hatch date representation suggested that passive transport led to their dispersal. As indicated above (see *Objective 1*) most migrants departed freshwater habitats during the same week as a major flow event in 2009. This suggested the possibility of flow influencing the timing, if not the likelihood, of dispersal. The combination of hatch date and early growth as factors determining migratory behavior and flow influencing the timing of

dispersal indicates that striped bass YOY employ a conditional strategy in decisions on migration. Following dispersal, growth rates tended to decline between hatch and 30 mm TL, but then stabilized and even increased for some contingents. Only small migrants, the slowest growing juvenile contingent in both years, experienced a subsequent increase in growth following initial dispersal; a similar increase in growth was experienced by the returning migrant contingent upon retreating back to freshwater. This shift from low to higher growth rates associated with dispersal for these two contingents may indicate a compensatory behavior (i.e. moving away from a poor growth habitat). At the time when juveniles were sampled (varying periods following dispersal) there were no differences in recent growth rate or physiological condition between contingents indicating that any post-dispersal growth differences likely dampen with time in the new habitat.

### *Objective 3 (Chapter 2)*

In Chapter 2 we explored the importance of salinity-based habitat variation on growth, condition, and feeding ecology. Recent growth (over 5 mm TL prior to collection) was higher for inhabitants of brackish habitats than freshwater habitats. Despite this enhanced growth, physiological condition did not differ between inhabitants of either salinity region. Fresh and brackish water food webs differed predictably, as carbon sources in freshwater displayed evidence of terrestrial, freshwater phytoplankton, and emergent vegetation input based on carbon stable isotope analysis. With increasing salinity, this signature graded to levels indicating a marine phytoplankton based food web. Despite habitat differences in food webs, trophic position (based on nitrogen stable isotope analysis) did not differ between the habitats. Although previous work suggested better feeding conditions for striped bass juveniles in brackish habitats, the breadth of

habitat-specific trophic niches did not differ. Further, in contrast to earlier studies, freshwater diets (based on stomach contents) were richer in larval fish prey items. That brackish habitats did not show obvious benefits in terms of improved feeding and growth could indicate that dispersals in part were driven more by current status (energy needs not being met) rather than an “informed” choice between two habitats. This departure from the well-documented increase in growth associated with dispersal for the congeneric white perch suggests increased variability in the ontogenetic spatial dynamics of striped bass. Additional analysis of the early behaviors of yearling and adult striped bass might shed light on any potential connection between early partial migration, year class strength and adult migration behaviors.

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# Chapter 1: The size and age dynamics of early migratory behaviors in striped bass

## Introduction

Freshwater, estuarine, and marine populations are subject to disturbances in the form of harvesting, pollution, habitat degradation, climate change, and food web disruptions (Lodge *et al.*, 2006; Carpenter *et al.*, 2008). The particular characteristics of populations that make them more or less resistant to decline and, ultimately, extirpation are an important area of ecological research. McCann (2000) used “insurance effect” to emphasize the ultimate importance of the *diversity of responses* to disturbances as what makes systems truly robust. McCann’s work is apropos to managing exploited populations. It may not be sufficient to merely regulate the number of individuals removed from an exploited population or to protect a certain territory of known residence. To ensure the persistence of a population, the diversity of behavioral responses to exploitation and other stresses should be preserved.

Species that rely on estuaries may face particularly acute disturbances, since their habitats are dynamic and greatly affected by weather events (Davis *et al.*, 2004). The effects of climate change, including sea-level rise (Morris *et al.*, 2002), intensified storm activity, and rising temperatures (Lovelock and Ellison, 2007) will likely increase the unpredictable nature of estuarine dynamics (Michener *et al.*, 1997) and lead to disruptions of fish populations and fisheries (Roessig *et al.*, 2004). A greater number of behavioral responses that are readily “available” to a population (i.e. already existing) can reduce the realized effects of these pressures. Hilborn *et al.* (2003) showed the

importance of diversity in spawning behavior within the Bristol Bay stock of sockeye salmon *Oncorhynchus nerka*. Diversity in the location, habitats, timing of spawning, and migration behaviors of young-of-the-year (YOY) juveniles helped to ensure a productive fishery buffered against climate change. In the North Sea, Atlantic herring *Clupea harengus* populations maintain diverse reproductive behaviors and a complex spatial structure that enhance persistence, even though as adults they co-aggregate on feeding grounds (Ruzzante *et al.*, 2006). Reich and DeAlteris (2009) concluded that the substantial loss of spawning behaviors and utilized spawning habitat due to the mismanagement of the Gulf of Maine Atlantic cod *Gadus morhua* fishery was partly to blame for the population's very slow and incomplete recovery. The common thread through these studies is that diversity in spatial behaviors within populations contributed to population stability (resistance to disturbance, from McCann 2000) and resilience (capacity for and rate of recovery from disturbance, from McCann 2000).

The importance of spatial structure to the stability and resilience of fish populations has brought renewed interest to the study of fish migrations. Clark (1968) proposed that the Hudson River population of striped bass was comprised of groups of similarly migrating fish, which he termed contingents. Although he speculated about the mechanism underlying contingent behaviors, Clark did not have the tools to further explore his contingent hypothesis. Secor and Piccoli (1996) and Zlokovitz and Secor (1999) reconstructed the lifetime movements of Hudson River and Long Island striped bass using otolith elemental analysis and their findings supported the existence of contingents – i.e. groups of fish with differing life-time migration patterns. Secor (1999) revisited the idea of contingents, suggested that contingent structuring was common

among fishes, and proposed a principal mechanism based on early ontogenetic thresholds, which are reinforced by periodic, episodic, or stochastic variations in habitat quality.

These contingent behaviors are first observed during the juvenile period, when individuals occupy nurseries both proximate and distant to spawning habitats. Based on local environmental conditions, individuals in different habitats may experience different vital rates (Hayes *et al.*, 1996), indicating unequal realized habitat conditions (i.e. growth representing habitat quality; MacCall, 1990). Members of contingents experiencing better habitats would be expected to experience higher survival and/or growth over other contingents occupying sub-optimal habitat. The importance of migratory contingent behavior in juveniles was well illustrated by work on white perch *Morone americana*, which completes its life cycle in estuaries. Kraus and Secor (2004a) established the existence of juvenile contingents in a natal estuary (Patuxent River, Chesapeake Bay) using otolith elemental analysis. A retentive contingent consisted of individuals that remained in freshwater spawning habitats, while a dispersive contingent was composed of individuals that moved down-estuary to higher salinity habitats around the time of metamorphosis from the larval to juvenile stages. A third, less numerous contingent consisted of individuals that returned to freshwater after having spent time in brackish water. Kerr *et al.* (2009) summarized the differences in realized habitat quality as measured by growth rate, with members of migratory contingents often experiencing higher growth potential than resident, non-migratory fish. Despite higher growth rates for the retentive contingent prior to dispersal, the dispersive contingent was better represented in the adult portion of the population.

Beck *et al.* (2001) suggested that the value of nurseries should be measured in the number of successful adult recruits per unit area of a particular juvenile or larval habitat. For the white perch population in the Patuxent river estuary, the higher nursery value of the brackish water habitats was not observed for all year classes-- in drought years, the retentive contingent contributed a larger proportion of recruits to the adult stock (Kraus and Secor, 2005). Over many years, the cumulative contributions of the retentive contingents can be ecologically significant. Additionally, the migratory behavior of juveniles had carryover effects in terms of what type of migratory behaviors adults undertook (Kerr *et al.*, 2009). The persistence of resident contingents despite the potential for reduced growth suggests that residence confers some benefit, possibly due to reduced predation risk or elimination of the energetic cost of migration itself (Kerr *et al.*, 2009). Interestingly, the increased nursery value of freshwater habitat under drought conditions may not be universal, even within the Chesapeake Bay; subsequent work on populations of white perch in other Bay estuaries indicate years of relatively high freshwater flow resulted in greater representation of retentive contingents (Kerr and Secor, 2011). Such temporal and spatial variability in responses to ever-changing environmental conditions further emphasizes the importance of phenotypic plasticity in migration behaviors. White perch juvenile dynamics and subsequent spatial structure within natal estuaries highlight the importance of migration behaviors in enhancing the insurance effect.

Here, we evaluated whether juvenile migratory contingent behaviors exist for striped bass, a co-occurring congeneric species of white perch, which heretofore has been a model species for contingent behaviors. Striped bass as adults are piscivorous predators

and support important fisheries in the Chesapeake Bay and Northeast US Atlantic coastal waters. The early life history of striped bass is similar to that of white perch, with broad spatial overlap of eggs, larvae, and juveniles. The principal differences are that older juveniles ( $\geq 1$  year in age) and adults are more migratory, frequently occurring outside of estuaries in coastal habitats (Setzler-Hamilton and Hall, 1991). Adults migrate to tidal fresh and near-fresh waters to spawn (Mansueti, 1958), with the resulting eggs maintained above the estuarine turbidity maximum (ETM; Secor *et al.*, 1995b).

Hatched larvae tend to be retained above the salt front, aided by the inherent physical processes at work in estuaries and, possibly, by their own behavior (Secor *et al.*, 1995b; North and Houde, 2001). Although North and Houde (2001) found little evidence of vertical migration within the water column in the upper Chesapeake Bay during the early-larval period, they did find evidence for the active tracking of prey, which may aid in larval retention (North and Houde, 2006). Over a 3 year study of larval striped bass movement ecology in the San Francisco estuary, Bennett *et al.* (2002) identified changes in vertical migrations that tracked particular flow conditions; larvae inhabited surface waters during incoming tides in a high flow year, moving to greater depths on outgoing tides, while in a subsequent year under average flow conditions these vertical movements followed a diel pattern of surface occupancy during the day and shift to deeper waters at night. Thus, evidence indicates that striped bass larvae may be retained directly through their spatial behaviors or indirectly by tracking prey and that their retention is likely influenced by flow (North and Houde, 2006; Martino *et al.*, 2007; Shideler, 2011).

Juveniles are eventually found distributed throughout fresh and brackish water in natal estuaries (Setzler-Hamilton *et al.*, 1981; Robichaud-Leblanc *et al.*, 1998). Although

the dynamics that lead to these distributions are not clear, they do not appear to be due to simple down-estuary diffusion as might be expected from density dependent dispersal (which would be expected to follow a distribution of exponential decline; Smogor *et al.*, 1995). Spatial behaviors during the first year of life potentially influence overall population dynamics of striped bass. Despite the importance of embryo and larval density-independent mortality on subsequent year-class strength (Secor and Houde, 1995), Martino (2008) demonstrated that growth during the larval and juvenile periods was a factor in survival over the first winter of life. Following their initial dispersal down-estuary, striped bass young-of-the-year (YOY) juveniles may experience disparate growth and physiological condition, as observed in white perch (Kraus and Secor, 2004a); this may lead to contingent-specific differences in mortality and recruitment. Juvenile abundances are highly variable for Chesapeake Bay striped bass (Secor and Houde, 1995) with strong influence on Chesapeake and Atlantic coast fisheries and their assessment (Fabrizio, 1987; Wirgin *et al.*, 1993). Further, despite the potential for early migration behaviors to influence how juvenile abundance is assessed, few directed studies on YOY striped bass migration exist in the literature. Those studies (Dorazio *et al.*, 1991; Secor *et al.*, 1995b) answered important questions about early mortality rates and general migratory patterns, but relied on artificially raised striped bass and were of insufficient scale to resolve the timing or pathways of larval and early juvenile migrations.

### *Study Objectives*

Juvenile migrations are known to be plastic, and the use of varied habitats during this stage can differ remarkably within the same species (Able, 2005). This diversity may



provide a range of responses to varying nursery conditions. A better understanding of juvenile striped bass spatial dynamics, early movements, and habitat usage can improve important monitoring functions, such as assessments of annual recruitment, by providing a behavioral context for observed distributions of young fish and contribute to stewardship tactics that enhance stability and resilience in recruitment dynamics. The goals of this Chapter were to 1) quantify individual movement trajectories of striped bass YOY along a freshwater-brackish water ecocline, 2) classify general types of migratory behavior (i.e. contingents) based on differences in size, age, and seasonal timing of estuarine movements, and 3) describe interannual differences in the frequency of contingent membership. Using otolith Sr/Ca analysis, we took advantage of the natural salinity and strontium gradient present in a striped bass natal estuary, the Patuxent River (Maryland, USA), to discern movement trajectories. Based on the pattern observed in white perch, we predicted that most striped bass YOY would join specific dispersive or retentive contingents, while a small number of individuals would return to freshwater after an initial dispersal. The retentive and dispersive behaviors are those predicted by Secor (1999) to be general for many fishes (i.e. partial migration; Kerr *et al.*, 2009), while the minority dispersal-return behavior was identified in white perch by Kraus and Secor (2004a). We also predicted that the detected changes in Sr/Ca that indicate movement between habitats of differing salinity would coincide with specific size stanzas; in other words estuarine movements of striped bass YOY are ontogenetic by nature, triggered when particular size thresholds are broached. Additionally, we anticipated that the proportion of individuals in each contingent would be similar across years. Subsequently in Chapter 2 we will use identified contingents to explore the causes and consequences of

migratory behavior in juveniles; we will be particularly interested in identifying inter-contingent differences in pre- and post-dispersal growth, size, and age.

### Methods

#### *Study System: The Patuxent River*

The Patuxent River (MD) is a partially mixed tidal estuary on the western shore of the Chesapeake Bay. The 70 river-kilometer extent of our study area (Fig. 1.1) consists of tidal fresh, oligohaline, and mesohaline habitats. The estuary provides important spawning and nursery habitats for a number of estuarine species, including striped bass. Spawning habitat in the estuary ranks 5<sup>th</sup> in terms of areal extent among Chesapeake Bay striped bass spawning grounds (Uphoff, 2008). The estuary has also been the site of extensive studies on the life history and ecology of striped bass (Mansueti, 1958).

Strontium is a conservative tracer of salinity within the Patuxent River that is taken up by fish otoliths, and has been employed to interpret habitat-use patterns by striped bass and white perch (Kraus and Secor, 2004b). The salinity gradient within the Patuxent River has been relatively stable over the last 75 years (Ritchie and Genys, 1975), continuing to the present (Fig. 1.2). Based on the legacy of research on striped bass ecology and the well-described, annually stable and consistent environmental conditions, the Patuxent River is a model natal estuary for exploring striped bass YOY migratory contingent behavior.

#### *Sample Collection*

We collected striped bass larvae and juveniles from the Patuxent River between April and October of 2009 and 2010. April and May sampling in 2009 entailed stepped-depth bongo net tows to collect striped bass larvae at ~2 km intervals from Jug Bay (river

kilometer (*RKM*) 75, i.e. 75 km distance from the mouth of the estuary) to Eagle Harbor (*RKM* 43). From June through October, parallel beach seines to collect striped bass juveniles during 1-3 d surveys at 12 sites located throughout the estuary (Fig. 1.1). Striped bass YOY were found at sites throughout the estuary, from tidal fresh (Selby Landing, *RKM* 72) to mesohaline segments (Solomons Beach, *RKM* 5) (Table 1.1). A random subsample of individuals representing the range of sampled habitats, sizes (total lengths), and dates were selected for analysis. The otoliths of these individuals (2009, n=71; 2010, n=34) were subsequently used to estimate past patterns of habitat use and age and growth.

#### *Salinity and Sr/Ca*

Any description of juvenile estuarine movements based on otolith chemistry requires a well-founded understanding of the ambient chemistry (here salinity) to which the individual is exposed (Elsdon *et al.*, 2008). To ensure an accurate depiction of the estuary for these years, we modeled salinity based on a dataset provided by the Chesapeake Bay Program (2011); this dataset consists of measurements from the surface to the bottom at 9 measurement locations throughout the estuary (Fig. 1.1). We modeled salinity for each cruise using a form of the logistic differential equation,

$$Sal_{RKM} = \frac{Sal_{max}}{1 + \exp^{(\beta \cdot (RKM - \delta))}}$$

where  $Sal_{RKM}$  is the mean daily salinity at river kilometer *RKM* *a*,  $Sal_{max}$  is the maximum mean daily surface salinity observed during the cruise,  $\beta$  is the estimated rate of salinity decline with increasing *RKM* in the estuary, and  $\delta$  is the estimated *RKM* where salinity is halfway between the maximum and minimum daily mean salinities.  $\beta$  and  $\delta$  were estimated using nonlinear regression (PROC NLIN; all analyses were conducted using

the statistical package SAS version 9.2 (2011)) for each cruise, resulting in a relationship between salinity and *RKM*. This equation models the declining influence of saltwater with increasing distance of intrusion into an estuary. For the days between cruises, salinity at river kilometer was estimated through linear interpolation. These interpolated daily mean surface salinity levels were then used to construct weekly mean surface salinity for use in interpreting striped bass YOY salinity records translated from Sr/Ca profiles (see Otolith Analysis).

The relationship between salinity and Sr uptake in striped bass YOY otoliths has been determined experimentally, tested in the field, and parameterized as a logistic function of the environmental Sr/Ca ratio (Secor *et al.*, 1995a),

$$Sal_{Sr/Ca} = 40.302 \cdot \left( 1 + 56.337 \cdot \exp^{\frac{-1523310}{Sr/Ca}} \right)$$

where  $Sal_{Sr/Ca}$  is predicted salinity based on *Sr/Ca* (the ratio of molar weights of Sr to Ca measured in the sagittal otolith). This relationship was assumed to apply to striped bass YOY otoliths during the 2009- 2010 study period as it has been applied generally to striped bass in past studies (Secor *et al.*, 2001).

#### *Otolith Analysis*

Otoliths were prepared for microchemical analysis following previous procedures (Secor *et al.*, 1995a; Kraus and Secor, 2004b). Briefly, sagittal otoliths were embedded in epoxy and sectioned transversely using a slow-speed wafering saw. Sections were attached to glass slides with a thermoplastic adhesive and ground using aluminum oxide compound on a jeweler's wheel until the primordium was exposed and daily increments were clearly visible under magnification. Final manual processing using a very fine grit aluminum oxide powder ensured a flat, level surface through the primordium. Prepared

otolith sections underwent microchemical analysis at the University of Maryland's Center for Microanalysis (College Park, MD). Sections were carbon-coated and molar weights of carbon, calcium, and strontium were measured by X-ray wavelength dispersive spectroscopy using a JEOL © JXA-840a microprobe. Microprobe analysis comprised a series of small volume (diameter= 5 µm, depth=1 µm) measurements from the first identifiable increment (adjacent to the primordium) to the edge of the otolith with measurements made at 10-18 µm intervals (Fig. 1.3). The resulting sets of Sr/Ca measurements were referred to as profiles.

Daily increments were enumerated from the primordium to the otolith edge (Fig. 1.4). Microstructural increments have been verified to form at a daily rate in striped bass YOY sagittal otoliths (Secor and Dean, 1989) but the timing of the first increment formation is temperature dependent (Houde and Morin, 1990). We used the original counts as estimated ages, subtracting them from the date of collection to estimate hatch dates. We adjusted ages by applying Houde and Morin's striped bass increment formation temperature correction,

$$age_{TC} = count + 11.56 - (0.45 \cdot T)$$

where  $age_{TC}$  is the temperature-corrected age,  $count$  is our original count, and  $T$  is the weekly mean surface (mean depth=1.3 m) temperature in Patuxent River spawning habitat (as measured at Jug Bay; MDDNR, 2011) on the estimated hatch date.

Temperature-corrected ages were used in all analyses. We determined the age and date for each otolith microprobe Sr/Ca measurement for the aged individuals. Since daily increment formation in striped bass otoliths is limited to the larval and early juvenile periods (Jones and Brothers, 1987; Secor and Dean, 1989), we did not include individuals

whose original (i.e. not temperature corrected) counts were >85 increments. We based this estimation threshold on the results of a separate aging effort involving juveniles collected in 2007 and 2009 (n=300 from each year); otoliths of individuals >85 increments produced imprecise age estimates when interpreted independently by two investigators due to narrow and indistinct increments (Fig. 1.5). Individuals that were not aged were included in length-based analyses (larger sample size) but excluded from age- or date-based analyses of Sr/Ca (smaller sample sizes).

Individual striped bass YOY total lengths (TL) for each microprobe measurement within a profile were estimated through back-calculation. The total otolith radius (um) and radius at each measurement point were measured from the primordium to the ventral edge along the ventral transverse axis (Fig. 1.6) using the image processing program ImageJ (Rasband, 1997). Total length at each microprobe point was back-calculated using Campana's (1990) biological intercept method,

$$TL_a = TL_c + \frac{(OR_a - OR_c) \cdot (TL_c - TL_i)}{OR_c - OR_i}$$

where  $TL_a$  and  $OR_a$  are the total length (mm) and otolith radius at age or measurement point  $a$ ,  $TL_c$  and  $OR_c$  are the total length and otolith radius at the time of capture, and  $TL_i$  and  $OR_i$  are the total length and otolith radius at the onset of proportionality (biological intercepts).  $TL_i$  and  $OR_i$  were determined using larvae collected in the Patuxent River estuary via bongo net sampling in April and May of 2009. Sagittal otoliths (n=46) of these larvae were mounted, their increments enumerated, and radii measured (Fig. 1.7). If the rostrum was apparent, then the longer of the 2 radii perpendicular to the rostrum was measured; if the rostrum was not apparent and the otolith was circular, the longest measured radius was used in the analysis. Temperature-corrected ages ranged from 8 to

31 days after hatch (dah). Because the relationship between otolith radius and total length was found to be linear ( $F=391.34$ ,  $p<0.0001$ ,  $R^2=0.90$ ), we assumed proportionate fish growth began at 8 dah. At 8 dah, larval total length was predicted at 6.08 mm (based on regression of size at age ( $F=202.71$ ,  $p<0.0001$ ,  $R^2=0.82$ ) and otolith radius was predicted at 23.94  $\mu\text{m}$  ( $F=263.91$ ,  $p<0.0001$ ,  $R^2=0.86$ ). These values were used as the biological intercepts in back-calculations of total length from otolith size.

Sr/Ca values were then compiled into longitudinal profiles for each individual (Fig. 1.3) for further analysis. As described above, microprobe measurements were referenced against age, date, or back-calculated total length. Although otolith elemental concentrations are dependent on environmental concentrations, they lag behind environmental exposures. In experiments, molar weights of Sr and Ca measured in otolith material represented exposures that occurred over the previous week (Secor *et al.*, 1995a; Elsdon and Gillanders, 2005); to account for this we used 7-day moving-mean (previous 7 days) Sr/Ca when constructing weekly mean age and date profiles. Mean Sr/Ca values corresponding to 5 mm size intervals were used to construct the total length profiles.

Separate analyses were performed on length- and age-based profiles for differing larval and juvenile phases: the early resident larval period (total lengths [TL] 0-5 mm; weeks 1-2), a primary sample of smaller juveniles (TL 6-35 mm; weeks 3-9), and a smaller, secondary sample that contained moderately larger juveniles (TL 6-50 mm; weeks 3-11). The primary and secondary sample length ranges were selected to maximize sample size (primary sample) while still including later dispersal events (secondary sample). In addition a later juvenile period was analyzed separately (TL 76-

110 mm). Each sub-sample comprised differing sample sizes based upon maximum sizes and ages of fish encountered during summer and fall collections (see Table 1.1).

### *Statistical Analyses*

Previous studies of estuarine fish have used mean Sr/Ca values (Secor *et al.*, 2001; Kerr *et al.*, 2009) or location of collection (Kraus and Secor, 2004a) to assign individuals to migratory or resident contingents. Within the Patuxent River, Kraus and Secor (2004a) and Kerr *et al.* (2009) used a salinity threshold of 3 to separate fresh and brackish water habitats; this threshold was consistently located between sample sites Eagle Harbor (RKM 43; Fig. 1.1) and Grassy Knoll (RKM 51) and corresponds to Sr/Ca value of  $1 \text{ mmol} \cdot \text{mol}^{-1}$ . In early attempts to follow this precedence, unexpected diversity in profile patterns (see Results) confounded simple contingent classification. Therefore we adopted a multiple step statistical process to classify migration patterns of striped bass YOY. Classifications were then compared between 2009 and 2010.

We applied both principal component (PCA) and hierarchical cluster analyses (CA) to identify contingents and derive classification statistics, following an approach developed by Miller *et al.* (2006) to predict weather patterns using autocorrelated sea level pressure data. Length and age profiles were used in separate classification procedures. We converted Sr/Ca profiles to multivariate formats by considering each length- or age- bin as a separate variable; this separated the variance in Sr/Ca values into size- or time-specific segments, allowing the clustering procedure to define differences in the timing of changes in Sr/Ca, which were then used to classify separate clusters. PCA was used to examine redundancies in Sr/Ca means among length and age intervals. Between 1 and 3 principal components (PCs) were selected based on the proportion of



variance explained and a visual review of scree plots. Generally, we used a threshold of 80% of variance. The presence of only a single size bin for early larval profile analysis precluded the need for PCA; here Sr/Ca values were used directly in the CA. For all other analyses, PC scores were used as the variables in the CAs. We tried six separate clustering methods: average linkage, centroid linkage, median linkage, complete linkage, single linkage, and Ward's method. Ultimately, the clusters resulting from average linkage were used because of this method's inclusion of all observations during each agglomeration step and conservation of original distributions of Euclidean distances between observations (McGarigal and Cushman, 2000). The number of clusters derived from each analysis was determined using the cubic clustering criterion (CCC) and pseudo  $F$  statistic. The statistic  $R^2$  was also used as a diagnostic but not reported in results. Negative CCC values indicated that similar clusters would have resulted from a uniformly distributed data set, implying no underlying group structure (Sarle, 1983). In hierarchical CA, peaks in the pseudo- $F$  indicate maximized separation between clusters in multidimensional Euclidean space (Calinski and Harabasz, 1974).  $R^2$  is a general measure of the between-subject variation explained by the clusters (McGarigal and Cushman, 2000);  $R^2$  values of 0.67 or more were used to identify the appropriate number of clusters. Agreement among CCC and pseudo  $F$  peaks was used in judging the classification of contingents.

To corroborate contingents identified through CA, we used an alternative approach that more explicitly considered the autocorrelated nature of the Sr/Ca profiles: repeated measures mixed models (PROC MIXED). Importantly, this statistical approach allowed us to test at which sizes and ages significant dispersals occurred. Covariance

structure for each analysis was determined by minimizing Akaike's information criteria (AIC) and corrected AIC (AICc). Where contingent classifications were identified as significant, least square means comparisons were used to determine which size, age, or date intervals were significantly different. These comparisons were constrained to contingents with membership of at least five individuals. To control for experiment-wise error, we applied the conservative Bonferroni adjustment. Descriptive statistics and univariate analyses were employed to examine the data distributions among length, age, and date bins.

Comparisons of contingent membership between years and seasons were tested using Fisher's exact tests, applicable to small sample sizes when  $\chi^2$  tests are not valid.

## Results

### *Modeled Salinity within the Estuary*

Modeled estuary-wide surface salinity in 2009 was marked by salinity intrusion up-river from April to early June, followed by a period of estuary-wide low-salinity in late June and then an increase to higher salinity in July that persisted through early October (Fig. 1.8a). Modeled salinity in 2010 was more typical of Patuxent River trends of the past 25 years (Fig. 1.2), with estuary-wide salinity monotonically increasing during spring and early summer months (Fig. 1.8b). In both years, peak mid-estuary (i.e. *RKM* 35-55) salinity occurred in early July as opposed to late September or early October, which has been the norm since 1985. Although, as in 2009, the down-river extent of freshwater habitat (i.e. the location of the prescribed fresh-brackish water habitat threshold salinity of 3) fluctuated between *RKM* 41 and 53 in 2009 and *RKM* 42 and 54 in 2010.

### *Patterns of Occurrence within the Estuary*

Life history profiles for 2009-2010 indicated broad use of the estuary from 0 to >20 salinity (Fig. 1.9). In describing dispersal patterns, we followed the precedent of Kraus and Secor (2004a) who used a fresh-brackish water threshold of  $1.0 \text{ mmol}\cdot\text{mol}^{-1}$  or salinity  $\sim 3$ . For both years, Sr/Ca profiles indicated that most individuals (89% in 2009; 88% in 2010) originated in freshwater and persisted there or in oligohaline waters ( $\leq 1.4 \text{ mmol/mol}$  or salinity  $< \sim 5$ ) during their first few weeks of life until they attained  $\sim 10$  mm total length (Fig. 1.9). Following this early period, most individuals dispersed to higher salinity habitats, while a minority of individuals remained in freshwater habitats.

### *Dispersal Phases – Length-Based Analyses*

Little to no net dispersal was detected during the early larval resident period, from hatch to 5 mm TL (Fig. 1.10). However, we unexpectedly found a wide range of Sr/Ca values in both 2009 ( $0\text{-}3.10 \text{ mmol}\cdot\text{mol}^{-1}$  or salinity  $0.7\text{-}26.9$ ; Fig. 1.11a) and 2010 ( $0\text{-}2.84 \text{ mmol}\cdot\text{mol}^{-1}$  or salinity  $0.7\text{-}23.2$ ; Fig. 1.11b), indicating a very large range of hatch salinities. Mean Sr/Ca values in the 0-5 mm length bin corresponded to habitat salinities of 2.73 in 2009 ( $0.93 \text{ mmol}\cdot\text{mol}^{-1}$ ) and 2.27 ( $0.80 \text{ mmol}\cdot\text{mol}^{-1}$ ) in 2010. Sr/Ca values of 82% of striped bass yolk-sac larvae (TL 0-5 mm) in both years corresponded to salinities of 5 or less; 66% and 74% of yolk-sac larvae in 2009 and 2010 corresponded to salinities  $\leq 3$ . Heavily skewed distributions of initial Sr/Ca values in both 2009 (skewness=1.18) and 2010 (skewness=1.39) indicated that hatch and early residence in freshwater or oligohaline habitats occurred for most individuals. The mean change in Sr/Ca from 0-5 mm to 6-10 mm was slightly negative in 2009 ( $-0.24 \text{ mmol}\cdot\text{mol}^{-1}$ , corresponding to a decrease in salinity of 0.8) and not significantly different from 0 in 2010 ( $t=-0.11$ ,

$p=0.91$ ); this indicated little to no movement from fresh to brackish water habitats within the estuary during the larval period. There were several larvae that did disperse prior to 10 mm total length, experiencing increases in Sr/Ca; these individuals were identified in later analyses as larval dispersers. Cluster analysis of Sr/Ca values during the early larval resident period in both 2009 and 2010 indicated no underlying structure (no positive cubic clustering criterion (CCC) statistics; Table 1.2).

Initial dispersal from fresh and oligohaline habitats to higher salinities occurred between 6 mm and 35 mm TL (primary sample) for most individuals in 2009 (only 3 individuals dispersed at lengths greater than 35 mm) and all individuals in 2010 (Fig. 1.12). During this phase the first three principal components explained 88% and 92% of the variance in Sr/Ca values in 2009 and 2010, respectively. Classification of dispersal behaviors by cluster analysis of the resulting PC's (Table 1.2) yielded four remarkably similar groups between years (Fig. 1.12). Profiles associated with these clusters exhibited four discrete behaviors: (1) a combined cluster of juveniles that migrated at large sizes ( $>30$  mm) and others that stayed resident (i.e. did not migrate at all), (2) a group that dispersed initially as larvae ( $< 6$  mm), (3) a group that migrated at small juvenile sizes (6-20 mm), and (4) a group that migrated at intermediate sizes (11-30 mm; Fig. 1.12). Members of the resident/large migrant group in both years had either consistently low Sr/Ca or elevated Sr/Ca associated with only the largest size bin (31-35 mm); there were three YOY collected in 2009 that experienced increasing Sr/Ca at lengths  $>35$  mm. Total length bin loadings onto PC's were similar in 2009 and 2010 (Fig. 1.13). In both years, residents/large migrants showed low or negative PC 1 and PC 3 scores reflecting low Sr/Ca at larger length bins. Larval migrants were discrete based

on PC1 scores, corresponding to their consistently high Sr/Ca levels. Intermediate and small migrants were less easily distinguished due to their overlapping sizes at dispersal. However, lower Sr/Ca over total lengths 21-30 mm accounted for their separation in PC 1 and 3 scores. These differences in PC scores allowed for the categorization of individuals into contingents using cluster analysis (examples of dendrograms are given; Fig. 1.14).

The four classified contingents for the primary sample (6-35 mm TL) were corroborated with the mixed model analysis, which showed significant effects due to contingent membership in both years. Best fitting covariance structures varied between years (2009: unstructured; 2010: 1<sup>st</sup> order autoregressive function), but both years showed significant effects of contingent membership on the series of Sr/Ca values across length bins (2009:  $F=11.84$ ,  $p<0.0001$ ; 2010:  $F=11.84$ ,  $p<0.0001$ ). No significant changes in Sr/Ca were identified in the resident/large migrant or larval contingents in either year (Table 1.3). Small migrants experienced significant increases in Sr/Ca between lengths 11-25 mm in both 2009 and 2010. In 2009 intermediate migrants experienced significant increases in Sr/Ca at larger sizes, between lengths 16-30 mm, while in 2010 significant increases were limited to lengths 21-30 mm.

The sample that included sizes larger than 35 mm, although smaller, exhibited additional movement patterns. Therefore we considered a larger interval, 6-50 mm TL, for those fish that were sampled at larger sizes. For this analysis, three PCs explained most of the variance in 2009 (86%) and 2010 (91%). The clusters resulting from classification of dispersal behaviors (Table 1.2) were similar between years apart from the small migrant group, which was present in 2009 but not in 2010 (Fig. 1.15). Profiles

associated with these clusters exhibited six discrete behaviors (1) a resident group with a single, very large migrant (45 mm), (2) a larval migrant group that dispersed at very small sizes (<6 mm), (3) a group that migrated at small juvenile sizes (6-15 mm) with a single individual that migrated prior to 6 mm, (4) a group of juveniles that migrated at intermediate sizes (11-30 mm), (5) a group of large migrants (25-40 mm), and (6) a returning migrant group that experienced migration (11-25 mm) followed by a return to freshwater habitats (31-40 mm). Contingents identified in 2010 were similar to those in 2009, except the intermediate contingent showed a larger range of sizes at dispersal (6-25 mm) and no small migrants were identified. Length bin loadings on PCs were similar in 2009 and 2010 with some small differences in the strength of loadings in the smallest length bin for PC 1 (Fig. 1.16). Residents/very large migrants again had negative PC 1 scores, reflecting consistently low Sr/Ca. Larval migrants were separated from all other individuals by PC2 scores, which were highly positive and corresponded to their consistently high Sr/Ca. Small migrants were less easily distinguished from the intermediate migrant group, with higher PC 1 scores and marginally higher PC 2 scores than the intermediate group. The newly identified large migrant contingent was distinguishable from intermediate migrants by higher PC 3 scores, reflecting low Sr/Ca for TL bin 21-25 mm. The negative PC 3 scores of returning migrants reflected high Sr/Ca across the TL bins 21-35 mm.

The classified contingents for the larger larval-YOY size interval (6-50 mm TL) were corroborated by mixed model analysis for both years (2009:  $F=11.61$ ,  $p<0.0001$ ; 2010:  $F=11.03$ ,  $p<0.0001$ ; both years fitted with a 1<sup>st</sup> order autoregressive function). Residents/very large migrants displayed no significant changes in Sr/Ca across size bins

in either year (Table 1.4). Small membership in the larval migrant group between years precluded size bin comparisons, although little overall change in Sr/Ca was observed between size bins in either year. Small migrants were unique to 2009 and although their early dispersal is apparent (Figure 1.15), no length bin comparisons were significant (significance based on Bonferroni-adjusted means comparison). In 2009 intermediate migrants experienced increases in Sr/Ca between lengths 11-30 mm, while in 2010 this increase was limited to lengths 16-25 mm (Table 1.4); although a difference was apparent in Sr/Ca at 21-25 mm and 26-30 mm it was not significant (Fig 1.15b). In both years, the large migrant group experienced increasing Sr/Ca across sizes 26-35 mm; in 2009 this increase was significant, but in 2010 the small size of this contingent (n=3) prevented means comparisons. Returning migrants in 2009 experienced a significant decrease in Sr/Ca across lengths 31-40 mm; no period of increase in Sr/Ca was found to be significant, although changes in values from 16-25mm approached  $\alpha=0.05$ . In 2010, the lone returning migrant exhibited a Sr/Ca increase ( $1.18 \text{ mmol}\cdot\text{mol}^{-1}$ ) and subsequent decrease ( $-0.85 \text{ mmol}\cdot\text{mol}^{-1}$ ), similar to what was observed for this classified group in 2009.

As opposed to YOY sampled in summer months (above results), YOY sampled in October 2009 all dispersed at a small size (11-30 mm TL), regardless of the location of their eventual collection (Fig. 1.17). Thus there was no evidence of resident behaviors in this subsample as had been observed for juveniles sampled during earlier summer months, despite the fact that many (n=17) of these larger juveniles were sampled in freshwater (a single individuals collected in October failed to disperse but was excluded from this analysis due to size). For this October sample, three PCs explained 88% of the

variance. No distinct clusters were detected (Table 1.2) despite an apparent split in profiles at lengths >100 mm TL, where eight juveniles showed a rapid decline in Sr/Ca, while the remainder showed little overall change. This split was apparent in the bimodal distribution of Sr/Ca values for length bins 101-105 mm and 106-110 mm (Fig. 1.18).

#### *Dispersal Phases – Age-Based Analyses*

The earliest two weeks, corresponding to the larval period showed no apparent structure in dispersal patterns (Fig. 1.19; Table 1.5), similar to the length-based analysis. The distributions of Sr/Ca for both weeks were unimodal (Fig. 1.20), with positive skew (2009: week 1 skewness = 0.92, week 2 skewness = 0.85; 2010: week 1 skewness = 1.29, week 2 skewness = 2.36). The large majority of Sr/Ca values corresponded to salinity < 3 (2009: 70%; 2010: 77%). Mean change in Sr/Ca from weeks 1 to 3 was slightly negative in 2009 (-0.24mmol/mol) and not significantly different from 0 in 2010 ( $t=-0.36$ ,  $p=0.7$ ), indicating no net dispersal during the early larval resident phase.

Initial dispersal of individuals from freshwater occurred over weeks 3 through 9 (Fig. 1.21); these ages correspond roughly to total lengths 6-35 mm. Sr/Ca profiles by week were reduced to 3 PCs, which explained 92% and 93% of the variance in 2009 and 2010, respectively. The cluster analysis identified six contingents in 2009 and four contingents in 2010; however, three of the 2009 contingents were larval migrants. Considering the three larval migrants as a single group, the contingents identified in both years were (1) a resident group, which included a single 2009 migrant that did not breach the  $1 \text{ mmol} \cdot \text{mol}^{-1}$  threshold until week 10, (2) larval migrants that dispersed at very early ages (before reaching 3 weeks of age), (3) a young migrant group (dispersing between weeks 3 and 5), and (4) an intermediate migrant group (dispersing between weeks 5



through 8; Fig. 1.21). Similar to the length-based dispersal analysis, PC loadings by group were quite similar between years (Fig. 1.22). In both years residents/old migrants had lower (negative) PC 2 scores than all other groups apart from the larval migrants, but also had negative PC 1 scores, reflecting low Sr/Ca throughout weeks 3 through 9. High Sr/Ca in week 3 resulted in a positive PC 3 score for a single member of the 2010 resident/old migrant contingent. Larval migrants were distinguished by high PC 1 scores associated with high Sr/Ca across weeks of age. In both years young migrants were distinguished from intermediate migrants by slightly higher PC 1 scores and lower PC 3 scores reflecting the difference in the timing of dispersal. Young migrants had higher Sr/Ca over weeks 5 and 6, which were positively loaded on PC 1 and negatively loaded on PC 3.

For both years, mixed model analysis of age bins confirmed a contingent effect on Sr/Ca profile series (2009:  $F=17.86$ ,  $p<0.0001$ ; heterogeneous Toeplitz function; 2010:  $F=17.46$ ,  $p<0.0001$ ; 1<sup>st</sup> order autoregressive function). No significant changes in Sr/Ca were identified in the resident/old migrant contingents in 2009 (Table 1.6); although means comparisons were not possible for the resident/old migrant contingent in 2010, no increases in Sr/Ca indicating dispersal were observed. Due to the limited membership of the larval migrant groups, means comparisons were not possible. Young migrants experienced significant increases from week 5 to week 7 (again, based on Bonferroni adjusted means). In 2010, young migrants dispersed at younger ages, with significant differences between weeks 4 through 6. In 2009, intermediate migrants experienced significant increases in Sr/Ca over weeks 6 through 8, but in 2010, intermediate migrants

experienced a longer period of dispersal, with significantly increasing Sr/Ca from week 5 through week 9 (Table 1.6).

#### *Dispersal Phases – Date-Based Analyses*

In 2009, increasing Sr/Ca values indicative of dispersal occurred during a nine week period, but 67% of the profiles breached the  $1 \text{ mmol} \cdot \text{mol}^{-1}$  fresh-brackish threshold during the two week period, May 29 and June 11 (Fig. 1.23a,b). In 2010, the period over which most dispersals occurred during these same two weeks, but these comprised only 19% of all dispersals; overall dispersal across the fresh-brackish threshold were substantially more dispersed across dates than across lengths or ages. When classified by contingents (age-based analysis), date-based dispersals were substantially more widely distributed in 2010 than 2009 (Fig. 1.23c,d). In 2010, the intermediate and young migrant contingents were spread over seven (May 8 to June 25) and six (May 1 to June 11) calendar weeks, respectively, as compared to five (May 22 to June 25) and three (May 22 to June 11) calendar weeks in 2009. The application of length-based contingent membership on date-based dispersals revealed a similarly more concentrated period of down-estuary dispersal in 2009 than in 2010 (Fig. 1.23d,e).

#### *Contingent Membership Frequency*

The proportion of samples represented by contingents as defined by length (6-50 mm TL) differed significantly between July and October, 2009 (Fisher's exact test,  $p=0.03$ ). Fewer large migrants ( $n=3$ , 11% of sample) and residents ( $n=1$ , 4%) occurred in October in comparison to July ( $n=8$ , 21% and  $n=6$ , 16%, respectively), and no returning migrants (those that experienced Sr/Ca decreases between 31 and 40mm) were identified in October. Seasonal changes in contingent membership in 2010 were tested across a

small interval of dates, July 2 and July 28, and showed no significant differences (size stanzas 6-35mm; Fisher's exact test,  $p=0.20$ ), despite the lack of larval migrants in the later collection.

Between years, significant differences in contingent membership occurred over the size range 6-35mm (Fisher's exact test,  $p=0.01$ ). 58% of individuals collected in 2009 (excluding the October sampling) were classified as intermediate migrants in contrast to 29% in 2010, respectively (Table 1.7). In 2010, small migrants made up a much larger proportion of the sample ( $n=16$ , 47% of sample) than in 2009 ( $n=16$ , 23% of sample). However, inter-annual differences in contingent representation were not detected for either the secondary sample of larger sizes (6-50 mm TL; Fisher's exact test,  $p=0.38$ ) or in the age-based analysis (range weeks 3-9; Fisher's exact test,  $p=0.96$ ).

### Discussion

Movement histories of juvenile striped bass, as measured by otolith Sr/Ca profile analysis, were diverse but underlain by modal patterns of dispersal and residency in natal habitats within the Patuxent River estuary (Fig. 1.9). Common to most movement profiles was an early larval-YOY period of residence in fresh and near-fresh waters followed by the dispersal of most individuals to brackish habitats, which included a large extent of the available estuary. Within individuals, these dispersal events occurred over narrow size and age ranges (Fig. 1.12; 1.15; 1.21), which allowed us to classify juveniles into specific contingents based on overall patterns and timing of migration. That similar classes of resident and migratory contingents occurred in both 2009 and 2010 suggests persistent structuring of the population in natal habitats.

### *Profile Analysis Assumptions*

Although the identification of contingent behaviors in juvenile striped bass implicates diverse early migration patterns and related consequences to population dynamics, certain assumptions inherent in these analyses merit initial consideration. Here, we followed Elsdon *et al.*'s (2008) guidelines for using otolith chemical analysis and profile analysis to define life-history variation and movements through different environments. The assumptions in these methods include: (1) the spatial and temporal variation of chemical markers in the environment is documented; (2) the uptake, rate of accretion, and subsequent stability of calcified structures and chemical markers in the organism of concern are established; and (3) the sampling of individuals is random and representative of all patterns of the chemical marker without influencing frequencies of those patterns in the population. First, an appropriate chemical marker that differs predictably across the environment must be identified. Sr has long been a popular tracer due to its predictable relationship with salinity in most, but not all, estuaries (Ingram and Sloan, 1992; Kraus and Secor, 2004b). The Patuxent River has low Sr/Ca in freshwaters that increase with salinity and has been used previously as a model system for otolith profile analysis of early estuarine movements (Kraus and Secor, 2004a).

Since the Patuxent River is an estuary, vertical stratification of the water column could have influenced our interpretations of migration based on Sr/Ca values. Here any vertical variation in salinity would have confounded interpretations of horizontal movements down- or up-estuary. Salinity measures taken during summertime sampling cruises in 2009 and 2010 showed that bottom salinities varied  $<0.5$  when surface salinities were 0 (i.e. designated as freshwater; Chesapeake Bay Program, 2011). Past

research demonstrated that a sill in the seabed at *RKM 46* curtails up-estuary exchange of water at depth, resulting in a non-stratified, mixed water column mixed above this sill (Hagy *et al.*, 2000). This is particularly important when considering some of the minority behaviors we identified, especially those of returning migrants. At brackish water sites, less than 30% of salinity at depth measurements differed by more than salinity 2; and for all measures <6 m (distribution of juvenile striped bass) salinity differences between deep and surface waters <2 (Chesapeake Bay Program, 2011). Although the Patuxent River is seasonally stratified below *RKM 46* (Hagy *et al.*, 2000), this occurs at depths >6 m. Thus, salinity changes in depth are non-substantial in comparisons with those that separate up- and down-estuary movements.

A valid functional relationship between ambient exposure and uptake of Sr/Ca into the otolith over the developmental stages of concern must exist. Such relationships have been established experimentally for striped bass (Secor *et al.*, 1995a) and the congeneric white perch YOY (Kraus and Secor, 2004b). The nonlinear relationships showed that Sr/Ca is most sensitive to changes in salinity between freshwater and salinity ~10. The influence of temperature, which is known to affect otolith Sr/Ca (Campana, 1999), was significant in these experiments but accounted for very little of the variance in Sr observed in striped bass YOY otoliths (Secor *et al.*, 1995a). The previously established relationship by Secor *et al.* has been generally applied to other systems (Secor *et al.*, 2001; Secor and Piccoli, 2007; Kerr *et al.*, 2009). Still, the relationship does introduce process error, which was accommodated here by describing somewhat coarse patterns of dispersal – those between freshwater and brackish water. Efforts to reduce

observational error in otolith elemental analysis were made through consistent application of established procedures.

Assumptions pertaining to otolith growth and daily increment formation have also been met through previous directed research (Secor and Dean, 1989; 1992). However, potential errors introduced related to ageing interpretations and measurement of otoliths must be considered. Blind, independent counts of otolith increments were held to a strict 10% deviation between results following an initial, pre-ageing calibration count of a training otoliths set; despite these precautions, no known- age fish were available from either year. Additionally, our limit of 85 increments exceeded validated daily increment formation for juvenile striped bass (Jones and Brothers, 1987; Secor and Dean, 1989). A limited number of larval striped bass were available for use in determining biological intercepts, with the youngest individuals available being caught at 8 dah. A lack of small, just hatched larvae may have resulted in error in assigning the biological intercept, although our estimates derived from 2009 larvae were similar to published species-specific intercepts (Secor and Dean, 1992). To match resolution against these sources of error, back-calculated total lengths and estimates of Sr and Ca, were integrated over 5 mm stanzas, representing approximate 5-10 d intervals.

Ideally, the YOY population would have been quantitatively sampled in both years to evaluate the relative proportion of contingents. Given the patchy distribution of YOY striped bass and the nature of seine-based sampling this was not possible. Further, it is important to recognize that we are examining the movement ecology of survivors, such that representation at any point in their growth season will be influenced by differences in contingent-specific survival. For instance, the observation that larval

dispersers were rare among our YOY samples might have been caused by high mortality rates for this group. Further, sampling intensity in time varied substantially between 2009 (sampling occurred over 12 weeks) and 2010 (comprehensive sampling was limited to 2 weeks). In 2009, sampling between June and July occurred over 6 weeks but only over a single week in October (Table 1.1). Low sampling intensity and resource limitations (vessel and labor costs) led to smaller sample sizes than were ideal for analysis and interpretation. Still, seining sites were representative of all salinity habitats available in the estuary (Fig. 1.1) with a similar number of sites sampled during each cruise. The consistency of contingent classes between years suggests that their incidence was correctly classified, if not their relative contributions.

Finally, our decision to use mean Sr/Ca values averaged over length and age stanzas may have introduced some bias into the results of these analyses. Our assumptions when constructing size- and age-based profiles was that specific stanzas represented biologically meaningful stages of life history. However, we recognize that we may have artificially increased the probability of clustering discrete stanzas rather than observing a continuously graded dispersal response to size or age. This does not necessarily invalidate the finding of smaller versus larger dispersers, but rather limits our ability, based on the tool at hand (otolith profile analysis), to resolve precise lengths and ages when dispersals occurred.

#### *Juvenile Contingent Behaviors*

The premise that striped bass YOY dispersal patterns would emulate those of juvenile white perch contingents was based on the previously noted similarities in early life history between these congeneric species. Using the same environmental threshold

between fresh and brackish water that characterized white perch YOY dispersal patterns, expected classes of resident, migratory, and returning migration patterns were observed in both years' samples of striped bass juveniles. Despite the similar nature of early migration histories of these two species, there were some noteworthy differences. In comparison to dispersing white perch, which migrate over a narrow week-long ( $SD = 1$  week) period at c. 45 dah (Kraus and Secor, 2004a), striped bass were younger at dispersal (between 5 and 6 weeks after hatch, or 35-42 dah) and moved into brackish waters over a wider range of ages (2009,  $SD = 1.5$  weeks; 2010,  $SD = 1.75$  weeks). This distribution of ages indicates that factors other than ontogeny are likely influencing dispersal. That 67% of 2009 dispersal events occurred over a two week period in late May and early June (Fig. 1.23) indicates environmental factors and events may also play a role (see Chapter 2).

The proportion of contingents differed between sampling periods in 2009, suggesting that differential mortality may have occurred specific to early migration patterns. For instance, the resident contingent represented 11% and 4% of the July and October 2009 samples. Indeed although a moderate size sample was collected at freshwater sites in October ( $N=27$ ), all but one of these exhibited a behavior that indicated they returned to freshwater from brackish water habitats. This large reduction in the frequency suggests contingent-specific mortality. If sampling was unbiased, these seasonal changes in contingent structure also suggest that in 2009 freshwater habitats were vacated by active migration or mortality, and then recolonized by migrants. Unfortunately, we did not examine YOY striped bass sampled in October in 2010 to



determine whether or not freshwater residents vacated that region prior to fall as they did in 2009.

An unexpected pattern of dispersal was larvae that exhibited high Sr/Ca levels characteristic of occurrence in brackish waters by 6 mm total length or 3 weeks in age. Striped bass larvae have been identified in brackish waters in past studies, even making up more than half of sampled feeding-stage individuals in the upper main stem of the Chesapeake Bay in 2008 (Shideler, 2011), but were assumed to face high mortality. Still, in most studies of Chesapeake Bay estuaries, few larvae have been found below the ETM and/or assumed to face high mortality rates (Secor *et al.*, 1994; Secor *et al.*, 1995b; North and Houde, 2001; Martino *et al.*, 2007). One such study undertaken in the Patuxent River resulted in no recaptures of marked larvae below the salt front despite release in this area (Secor *et al.*, 1995b). Evidence of very low survival has been supported by the relatively poorer feeding conditions for larvae that exist below the salt front and the associated ETM, (Roman *et al.*, 2001; Campfield and Houde, 2011). This is compounded by the physical characteristics of the salt front and ETM, where the turbidity peak offers refuge and currents aid in retention (Odum, 1988; North and Houde, 2001; 2003; 2006). If larvae stray too far into brackish habitats, the threat of starvation may be compounded by increased osmotic costs associated with salinities above 9 (Winger and Lasier, 1994). Thus, higher mortality resulting from poorer conditions for growth and higher predation has been assumed to preclude contributions from early inhabitants of brackish habitats. However, we identified larval dispersers in both years among collected juveniles, accounting for 4% and 3% of the represented patterns in 2009 and 2010, with representatives as late as October in 2009. Considering the small sizes (larvae of this size

do not have functioning swim bladders) and early ages at which these individuals moved down-estuary, larval migration may have occurred through passive advection. As a result of increased mortality compared to undispersed individuals, these larvae could represent a small number of survivors from a larger group that moved past the ETM.

The low rates of occurrence of larval dispersal in both 2009 and 2010 raise the possibility that either observation or process error explained this phenomenon. The increased Sr/Ca values at small sizes and early ages we interpreted as down-estuary movement may be the result of a unique functional relationship between Sr/Ca and salinity, specific to the larval period. Experimental evidence for this relationship is thus far limited to the juvenile period.

#### *Dispersal Thresholds*

Dispersal of striped bass YOY based solely on ontogeny was not supported by size- and age-based analyses. We expected a very narrow range of lengths at dispersal (e.g. that associated with larval-juvenile transformation; Kraus and Secor 2004a), reflecting the crossing of an important size threshold that would trigger migratory behavior; we also expected a somewhat larger range of ages at dispersal, indicating differences in growth prior to migration. As previously indicated, the dispersion of ages at which migration occurred was wider than those observed in white perch (as indicated by reported SD) dispersal sizes were similarly widely distributed. Still, it is likely significant that the large majority of striped bass only migrated to brackish habitats once they completed metamorphosis to the juvenile stage (~17mm TL; Setzler-Hamilton *et al.*, 1980) in 2009 (83%) and 2010 (76%). Excepting larval migrants, those that did migrate prior to reaching this threshold did so as larger post-finfold larvae (> 10mm), capable of

sustained swimming speeds similar to adults (Meng, 1993). Improved swimming capacity can translate to increased success in feeding and ability to evade predation in brackish water.

Differences in early growth have been identified as a proximate cause of contingent structuring in white perch YOY (Kerr and Secor, 2009). For instance, low early growth prompts migrant white perch to adopt dispersive behaviors, which offer access to habitats where their higher scope for growth may be fulfilled. Based on growth rates, which are in turn influenced by early environmental conditions, Kerr and Secor speculated that the timing of dispersal may vary annually due to environmental factors. Our results for striped bass migrants suggest that a range of size-specific dispersals may exist that is dependent on early growth rates. Instead of a binary response, contingent behaviors may reflect a range of responses to specific and individual early growth conditions. The importance of early growth to striped bass dispersal is the focus of Chapter 2.

The two years differed in the range of dates over which dispersals occurred. The majority of dispersals in 2009 took place over a 2 week period (67%; Fig. 1.23). These dispersals included members of small, intermediate, large, and even larval migratory contingents. The effects of environmental condition on this en masse migration may have been influenced by certain environmental changes or events, which will be further explored in Chapter 2. In 2010 no such concentration of dispersal events was identified. Taken together, the two years' results suggest that date as a proxy for environmental conditions didn't entirely influence the onset of migratory behavior, but may have been a factor in the timing of dispersal.

### *Interannual Comparison of Contingent Membership*

Similar contingent memberships (Table 1.7) across years supported the consistency in their incidence but we are cautious in advancing that contributions among contingents are invariant. As a principal example, we observed large differences in contingent memberships within 2009 between sampling months where the resident behaviors were common in July but rare in October. More representative sampling and information on contingent-specific survival would be needed to draw inferences on how contingent membership varies year to year. Strong interannual variation was observed for Patuxent River white perch juvenile contingents, which varied according to spring rainfall (Kraus and Secor, 2004a). These differences in contingent memberships had carryover effects to adult migration behaviors and population dynamics (Kerr and Secor, 2011). By examining juvenile portions of adult otoliths and assigning them to juvenile contingent behaviors, Kraus and Secor (2004a) were able to connect the recruitment success of white perch within the Patuxent River with frequencies of surviving residents. They found that residents showed increased representation during years of poor overall juvenile production. The two years, 2009 and 2010, represented intermediate year-class strengths (Weedon and Durell, 2011); a longer time series of contingent contribution rates to juvenile production across years of contrasting year-class strengths would be needed to support how contingent structure contributes to population dynamics of Patuxent River striped bass.

### *Larger Implications and Future Work*

Among anadromous fishes, striped bass are well known for their variable migration behaviors, which have strong influences on their exploitation, contamination,

and resilience to habitat degradation; still we do not understand what leads to these plastic behaviors. Using the congeneric white perch as a model system, we might expect that lifetime migratory contingent behaviors are initiated early in life: that carryover effects occur related to larval and juvenile contingent behaviors. Kerr *et al.* (2009) through simultaneous juvenile and adult otolith profile analysis determined that juvenile behaviors had a strong influence on whether adult white perch undertook resident or migratory behaviors. For instance, adults that showed resident behavior were all resident as YOY juveniles. Further, migratory juvenile white perch grew more rapidly and matured earlier as adults indicating juvenile contingent behaviors influenced population dynamics. In support of lifetime consequences to early migration behaviors, Secor *et al.* (2001) provided some evidence that sub-adult (juveniles > 1 year in age) migration patterns influenced subsequent behaviors.

Further work on the lifelong effects of early migratory behavior is needed to fully understand the implications of contingent membership. In particular, the application of size- and age-based profile analysis based on adult otoliths may reveal how juvenile contingents recruit to the adult population. Further, striped bass are highly migratory, frequently occurring in non-natal estuaries and ocean waters. How long adults persist in each type of habitat and how often they migrate between them is likely to be less easily classified than the simpler behaviors of YOY juvenile contingents (or the largely non-migratory white perch for that matter). Kerr *et al.* (2011) observed that populations of adult white perch differed in the representation of migratory versus resident contingents. Therefore, relating identified contingent frequencies in adult striped bass to particular conditions in specific nurseries will be confounded by the mixing of adults from many

natal estuaries. However, this does not discount the potential importance of early migratory behavior on population dynamics for this species.

In white perch, adult behaviors were strongly influenced by behaviors initiated in the juvenile phase, resulting in differences in fitness that had population-wide effects (Kerr and Secor, 2009). Additionally, weak year-classes were dominated by residents and correlated with specific environmental conditions in natal estuaries (Kraus and Secor, 2004a; Kerr and Secor, 2011). Changes in climate may affect the environmental conditions faced by striped bass YOY, including the location of the ETM, which defines critical larval habitat (Dyer, 1995). Monitoring of contingent behaviors associated with these environmental changes could forecast subsequent population responses. Temporal or spatial changes in the location or strength of the ETM may result in poorer conditions for early growth and survival (Martino and Houde, 2010). Since partial migration in juvenile estuarine fishes has been shown to be influenced by environmental conditions (Kerr and Secor, 2011), contingent frequencies may vary as climate changes. Depending on conditions influencing reproduction and early habitats, migratory behaviors may become more or less prevalent. Whatever the response, a reduction in the diversity of responses to early environmental conditions will negatively impact stability and resilience and may lead to a subsequent reduction in the diversity of behaviors (McCann, 2000).

Juvenile contingent behaviors, here defined by the threshold between fresh and brackish waters, likely track salient features of the striped bass's nursery habitat. Once past this threshold, most migrants remain in brackish habitats throughout the juvenile stage while residents stay in freshwater habitats; therefore contingents should show the

effects of occupancy in specific estuarine habitats, with their vital rates reflecting habitat quality. This hypothesis is explored further in Chapter 2. In the Patuxent River, as in other estuaries, fresh and near-fresh waters are dominated by different prey and potential predators compared to higher salinity mesohaline habitats (Wagner, 1995; Campfield, 2004). Although stable over decades (Fig. 1.2), this boundary, and associated features like the salt front and ETM, vary in location both within (Fig. 1.1; Secor and Houde, 1995) and between years (Martino *et al.*, 2007). Invariably, changes in the location of salinity features can have wide-ranging effects on estuarine populations. Variation in the location of salinity features has been shown to have important consequences on the availability of prey items to larval striped bass (Martino and Houde, 2010). Although beyond the scope of our study, changes in migratory behavior and resulting contingent frequencies due to the location and temporary stability of estuarine salinity features merits further examination, preferably including identification of both physical and forage conditions that may influence contingent representation and success.

### *Summary*

A “brief” review by Able (2005) of mid-Atlantic coastal fishes whose young rely at least in part on estuarine habitat identified 70 such species. Most of these species were not exclusively dependent on estuaries, but striped bass represent an ecologically and commercially important species that can be considered estuarine-dependent. Still, it shows widely ranging migrations into coastal ocean habitats. Here, we have documented juvenile contingent migratory behavior in striped bass, adding another species to the list of estuarine fishes showing complex and variable spatial behaviors in ontogeny. Due to spatially and temporally variable estuarine environments, persistent migratory behaviors

(those undertaken year to year by a population segment), even movements on seemingly small scales measured in <5 km rather than scores of kms, may have important consequences for population dynamics. Further research on these partially and fully estuarine dependent species may identify particular movements as important in maintaining the diversity of responses so important to McCann's (2000) insurance effect.



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Tables

Sample Site	River km	6/1	6/7	6/14	6/21	6/28	7/5	7/12	7/19	7/26	8/2	8/9	8/16	8/23	8/30	9/6	9/13	9/20	9/27	10/4	10/11	
Selby Landing	72			+	+	+	+	+	+			+				+					+	
DNR	61		+	+	+	+	+	+	+													+
Lower Marlboro	54	+		+	+	+	+	+	+													+
Grassy Knoll	51			+	+	+	+	+	+													+
Eagle Harbor	43		+	+	+	+	+	+	+	+		+				+						+
God's Grace	39			+	+	+	+	+	+			+				+						+
Mac's Hollow	31			+	+	+	+	+	+													+
Sheridan Point	30			+	+	+	+	+	+			+										+
Coatigan's Run	27			+	+	+	+	+	+													+
Broome's Island	18			+	+	+	+	+	+													+
Cage Stables	16			+	+	+	+	+	+													+
Solomons Beach	5			+	+	+	+	+	+													+

Table 1.1a. Site names, river kilometers (*RKM*), and weeks of striped bass sampling in the Patuxent River estuary, June-October 2009. Symbols (+) indicate at least one seine haul site during the week. *RKM* is measured as distance from the river mouth/Chesapeake Bay.

Sample Site	River km	5/30	6/6	6/13	6/20	6/27	7/4	7/11	7/18	7/25	8/1	8/8	8/15	8/22	8/29	9/5	9/12	9/19	9/26	10/3	10/10
Selby Landing	72										+										
DNR	61				+						+										
Lower Marlboro	54																				
Grassy Knoll	51				+						+										
Eagle Harbor	43				+						+										
God's Grace	39				+						+										
Mac's Hollow	31				+																
Sheridan Point	30				+						+										
Coatigan's Run	27				+																
Broome's Island	18				+						+										
Cage Stables	16				+						+										
Solomons Beach(+)/CBL(●)	5 / 3			●	+●	●				●	+	●									

Table 1.1b. Site names, river kilometers (*RKM*), and weeks of striped bass sampling in the Patuxent River estuary, June-August 2010. Symbols (+●) indicate at least one seine haul site during the week.

Year	No. of Clusters Identified	Average Linkage		
		CCC	pseudo <i>F</i>	R <sup>2</sup>
Size Classes				
<b>2009</b>				
sizes 0-5mm	0	N/A <sup>‡</sup>	N/A	N/A
sizes 6-35mm	4	2.03	46.2 <sup>#</sup>	0.67
sizes 6-50mm	6	1.75 <sup>*</sup>	40.1 <sup>#</sup>	0.77
sizes 76-110mm	0	N/A <sup>‡</sup>	N/A <sup>‡</sup>	N/A <sup>‡</sup>
<b>2010</b>				
sizes 0-5mm	0	N/A <sup>‡</sup>	N/A	N/A
sizes 6-35mm	4	2.14	26.5 <sup>#</sup>	0.73
sizes 6-50mm	5	2.31 <sup>*</sup>	22.7 <sup>#</sup>	0.82

<sup>‡</sup>indicates no positive peak in CCC  
<sup>\*</sup>indicates positive peak in CCC  
<sup>#</sup>indicates coinciding localized peak in pseudo *F*  
N/A indicates no positive non-zero value

Table 1.2. Cluster analysis statistics for Sr/Ca profiles by total length (mm) of juvenile striped bass. Measures of clustering explanatory power (cubic clustering criterion (CCC), pseudo *F*, and R<sup>2</sup>) are reported. Reported numbers of clusters are those identified and used in analyses.

Least Square Means Comparisons of Total Length Bin $\alpha$ and Total Length Bin $\alpha + 1$					
	6-10mm → 11-15mm	11-15mm → 16-20mm	16-20mm → 21-25mm	21-25mm → 26-30mm	26-30mm → 31-35mm
<b>Contingent</b>					
<b>Intermediate Migrant</b>	$t = 3.08$ $p = 0.0030$ adj. $p^{\#} = 0.8279$	ns	$t = -9.02$ $p < 0.0001$ adj. $p < 0.0001$	$t = -9.74$ $p < 0.0001$ adj. $p < 0.0001$	$t = -2.61$ $p = 0.0113$ adj. $p = 1.00$
<b>Small Migrant</b>	ns <sup>†</sup>	$t = -9.81$ $p < 0.0001$ adj. $p < 0.0001$	$t = -6.41$ $p < 0.0001$ adj. $p < 0.0001$	ns	ns
<b>Larval Migrant</b>	n/a <sup>§</sup>	n/a	n/a	n/a	n/a
<b>Resident &amp; Large Migrant</b>	ns	ns	ns	ns	ns

<sup>#</sup> *adj. p* refers to the estimated p-value following the Bonferroni adjustment to alpha  
<sup>†</sup> *ns* indicates non-significant t-test results without Bonferroni adjustment  
<sup>§</sup> *n/a* indicates insufficient contingent size to justify means comparisons

Table 1.3a. Results of least square means comparisons of Sr/Ca between successive periods of growth for the primary sample (6-35 mm TL) of 2009 striped bass juveniles. Significant differences (adjusted p) indicate changes in Sr/Ca that follow changes in habitat salinity. Due to sample size constraints, some contingents were not analyzed.

Least Square Means Comparisons of Total Length Bin $\alpha$ and Total Length Bin $\alpha + 1$					
	6-10mm → 11-15mm	11-15mm → 16-20mm	16-20mm → 21-25mm	21-25mm → 26-30mm	26-30mm → 31-35mm
<b>Contingent</b>					
<b>Intermediate Migrant</b>	ns <sup>‡</sup>	ns	$t = -3.12$ $p = 0.0022$ adj. $p = 0.5938$	$t = -9.24$ $p < 0.0001$ adj. $p < 0.0001$	$t = -2.25$ $p = 0.0256$ adj. $p = 1.00$
<b>Small Migrant</b>	ns	$t = -6.43$ $p < 0.0001$ adj. $p^{\#} < 0.0001$	$t = -7.88$ $p < 0.0001$ adj. $p < 0.0001$	$t = -2.52$ $p = 0.0129$ adj. $p = 1.00$	ns
<b>Larval Migrant</b>	n/a <sup>§</sup>	n/a	n/a	n/a	n/a
<b>Resident &amp; Large Migrant</b>	ns	ns	ns	ns	$t = -3.20$ $p = 0.0017$ adj. $p = 0.4647$

<sup>#</sup> *adj. p* refers to the estimated p-value following the Bonferroni adjustment to alpha

<sup>‡</sup> *ns* indicates non-significant t-test results without Bonferroni adjustment

<sup>§</sup> *n/a* indicates insufficient contingent size to justify means comparisons

Table 1.3b. Results of least square means comparisons of Sr/Ca between successive periods of growth for the primary sample (6-35 mm TL) of 2010 striped bass juveniles. Significant differences (adjusted p) indicate changes in Sr/Ca that follow changes in habitat salinity. Due to sample size constraints, some contingents were not analyzed.

Least Square Means Comparisons of Total Length Bin $\alpha$ and Total Length Bin $\alpha + 1$								
	6-10mm → 11-15mm	11-15mm → 16-20mm	16-20mm → 21-25mm	21-25mm → 26-30mm	26-30mm → 31-35mm	31-35mm → 36-40mm	36-40mm → 41-45mm	31-45mm → 46-50mm
<b>Contingent</b>								
<b>Intermediate Migrant</b>	ns <sup>‡</sup>	$t = -4.79$ $p < 0.001$ adj. $p^{\#} = 0.0032$	$t = -8.74$ $p < 0.0001$ adj. $p < 0.0001$	$t = -6.44$ $p = 0.0001$ adj. $p = 0.1252$	ns	ns	$t = -3.31$ $p = 0.0010$ adj. $p = 1.00$	ns
<b>Small Migrant</b>	ns	$t = -2.95$ $p = 0.0033$ adj. $p = 1.00$	$t = -3.22$ $p = 0.0014$ adj. $p = 1.00$	ns	ns	ns	ns	ns
<b>Large Migrant</b>	ns	ns	ns	$t = -2.45$ $p = 0.0145$ adj. $p = 1.00$	$t = -6.90$ $p < 0.0001$ adj. $p < 0.0001$	$t = -3.79$ $p = 0.0002$ adj. $p = 0.2390$	$t = -2.16$ $p = 0.0316$ adj. $p = 1.00$	ns
<b>Larval Migrant</b>	n/a <sup>§</sup>	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<b>Returning Migrant</b>	ns	ns	$t = -4.10$ $p < 0.0001$ adj. $p = 0.0706$	$t = -3.08$ $p = 0.0022$ adj. $p = 1.00$	ns	$t = 4.74$ $p < 0.0001$ adj. $p = 0.0041$	$t = 3.75$ $p = 0.0002$ adj. $p = 0.2810$	ns
<b>Resident</b>	ns	ns	ns	ns	ns	ns	ns	ns

<sup>#</sup> *adj. p* refers to the estimated p-value following the Bonferroni adjustment to alpha

<sup>‡</sup> *ns* indicates non-significant t-test results without Bonferroni adjustment

<sup>§</sup> *n/a* indicates insufficient contingent size to justify means comparisons

Table 1.4a. Results of least square means comparisons of Sr/Ca between successive periods of growth for the secondary sample (6-50 mm TL) of 2009 striped bass juveniles. Significant differences (adjusted p) indicate changes in Sr/Ca that follow changes in habitat salinity. Due to sample size constraints, some contingents were not analyzed.

Least Square Means Comparisons of Total Length Bin $\alpha$ and Total Length Bin $\alpha+1$								
	6-10mm → 11-15mm	11-15mm → 16-20mm	16-20mm → 21-25mm	21-25mm → 26-30mm	26-30mm → 31-35mm	31-35mm → 36-40mm	36-40mm → 41-45mm	41-45mm → 46-50mm
<b>Contingent</b>								
<b>Intermediate Migrant</b>	ns <sup>‡</sup>	$t = -2.80$ $p = 0.0057$ adj. $p^{\#} = 1.00$	$t = -6.06$ $p < 0.0001$ adj. $p < 0.0001$	$t = -3.93$ $p = 0.0001$ adj. $p = 0.1252$	$t = -2.48$ $p = 0.0143$ adj. $p = 1.00$	ns	ns	ns
<b>Large Migrant</b>	n/a <sup>§</sup>	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<b>Larval Migrant</b>	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<b>Returning Migrant</b>	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<b>Resident</b>	ns	ns	ns	ns	ns	ns	ns	ns

<sup>#</sup> *adj. p* refers to the estimated p-value following the Bonferroni adjustment to alpha

<sup>‡</sup> *ns* indicates non-significant t-test results without Bonferroni adjustment

<sup>§</sup> *n/a* indicates insufficient contingent size to justify means comparisons

Table 1.4b. Results of least square means comparisons of Sr/Ca between successive periods of growth for the secondary sample (6-50 mm TL) of 2010 striped bass juveniles. Significant differences (adjusted p) indicate changes in Sr/Ca that follow changes in habitat salinity. Due to sample size constraints, some contingents were not analyzed.



Year	No. of Clusters Identified	Average Linkage		
		CCC	pseudo <i>F</i>	R <sup>2</sup>
Size Classes				
<b>2009</b>				
weeks 1-2	0	N/A <sup>†</sup>	N/A	N/A
weeks 3-9	6	2.59	32.4 <sup>#</sup>	0.81
<b>2010</b>				
weeks 1-2	0	N/A <sup>†</sup>	N/A	N/A
weeks 3-9	4	2.95	27.5 <sup>#</sup>	0.75

<sup>†</sup>indicates no positive peak in CCC

\* indicates positive peak in CCC

<sup>#</sup> indicates coinciding localized peak in pseudo *F*

N/A indicates no positive non-zero value

Table 1.5. Cluster analysis statistics for Sr/Ca profiles by juvenile striped bass by age (week). Measures of clustering explanatory power (cubic clustering criterion (CCC), pseudo *F*, and R<sup>2</sup>) are reported. Reported numbers of clusters are those identified and used in analyses.

Least Square Means Comparisons of Week  $\alpha$  and Week  $\alpha+1$

	Week 3 → Week 4	Week 4 → Week 5	Week 5 → Week 6	Week 6 → Week 7	Week 7 → Week 8	Week 8 → Week 9
<b>Contingent</b>						
<b>Intermediate Migrant</b>	$t = 3.53$ $p = 0.0005$ adj. $p^{\#} = 0.4293$	ns	$t = -2.45$ $p = 0.0149$ adj. $p = 1.00$	$t = -9.12$ $p < 0.0001$ adj. $p < 0.0001$	$t = -8.27$ $p < 0.0001$ adj. $p < 0.0001$	$t = -2.33$ $p = 0.0209$ adj. $p = 1.00$
<b>Young Migrant</b>	$t = 2.02$ $p = 0.0444$ adj. $p = 1.00$	$t = -3.85$ $p = 0.0002$ adj. $p = 0.1315$	$t = -10.43$ $p < 0.0001$ adj. $p < 0.0001$	$t = -4.37$ $p < 0.0001$ adj. $p = 0.0164$	ns	ns
<b>Larval Migrant</b>	n/a <sup>§</sup>	n/a	n/a	n/a	n/a	n/a
<b>Resident &amp; Old Migrant</b>	ns <sup>†</sup>	ns	ns	ns	ns	ns

<sup>#</sup> *adj. p* refers to the estimated p-value following the Bonferroni adjustment to alpha

<sup>†</sup> *ns* indicates non-significant t-test results without Bonferroni adjustment

<sup>§</sup> *n/a* indicates insufficient contingent size to justify means comparisons

Table 1.6a. Results of least square means comparisons of Sr/Ca between successive weeks of age for the primary sample (3-9 weeks after hatch) of 2009 striped bass juveniles. Significant differences (adjusted p) indicate changes in Sr/Ca that follow changes in habitat salinity. Due to sample size constraints, some contingents were not analyzed.

Least Square Means Comparisons of Week $\alpha$ and Week $\alpha+1$						
	Week 3 → Week 4	Week 4 → Week 5	Week 5 → Week 6	Week 6 → Week 7	Week 7 → Week 8	Week 8 → Week 9
<b>Contingent</b>						
<b>Intermediate Migrant</b>	ns <sup>†</sup>	ns	$t = -4.37$ $p < 0.0001$ adj. $p = 0.0085$	$t = -8.96$ $p < 0.0001$ adj. $p < 0.0001$	$t = -5.77$ $p < 0.0001$ adj. $p < 0.0001$	$t = -4.59$ $p < 0.0001$ adj. $p = 0.0034$
<b>Young Migrant</b>	$t = -2.73$ $p = 0.0070$ adj. $p^{\#} = 1.00$	$t = -5.26$ $p < 0.0001$ adj. $p = 0.0002$	$t = -5.10$ $p < 0.0001$ adj. $p = 0.0004$	ns	ns	ns
<b>Larval Migrant</b>	n/a <sup>§</sup>	n/a	n/a	n/a	n/a	n/a
<b>Resident &amp; Old Migrant</b>	n/a	n/a	n/a	n/a	n/a	n/a

<sup>#</sup> *adj. p* refers to the estimated p-value following the Bonferroni adjustment to alpha  
<sup>†</sup> *ns* indicates non-significant t-test results without Bonferroni adjustment

Table 1.6b. Results of least square means comparisons of Sr/Ca between successive weeks of age for the primary sample (3-9 weeks after hatch) of 2010 striped bass juveniles. Significant differences (adjusted p) indicate changes in Sr/Ca that follow changes in habitat salinity. Due to sample size constraints, some contingents were no analyzed.

Method	2009		2010	
	No.	%	No.	%
<b>Contingent</b>				
<b>Size (10-35 mm)</b>				
Larval Dispersers †	3	4.2%	1	2.9%
Small Migrants †	16	22.5%	16	47.1%
Intermediate Migrants †	41	57.8%	10	29.4%
Residents / Large Migrants †	11	15.5%	7	20.6%
<b>Size (10-50 mm)</b>				
Larval Dispersers	2	3.1%	1	4.0%
Small Migrants	7	10.8%	0	0.0%
Intermediate Migrants	32	49.2%	15	60.0%
Large Migrants	11	16.9%	3	12.0%
Returning Migrants	6	9.2%	1	4.0%
Residents / Very Large Migrants	7	10.8%	5	20.0%
<b>Age (weeks 3-9)</b>				
Larval Dispersers	3	7.0%	1	3.2%
Young Migrants	9	20.9%	6	19.4%
Intermediate Migrants	25	58.1%	20	64.5%
Residents / Old Migrants	6	14.0%	4	12.9%

† indicates significant difference between 2009 and 2010

Table 1.7. Juvenile striped bass contingent membership frequencies by year and method (size and age). Size-based contingents in 2009 exclude October collections to ensure similar sampling periods across years. Significantly different contingent frequencies between years (as determined by  $\chi^2$ -analog Fisher's Exact Test) are noted.

*Figures*

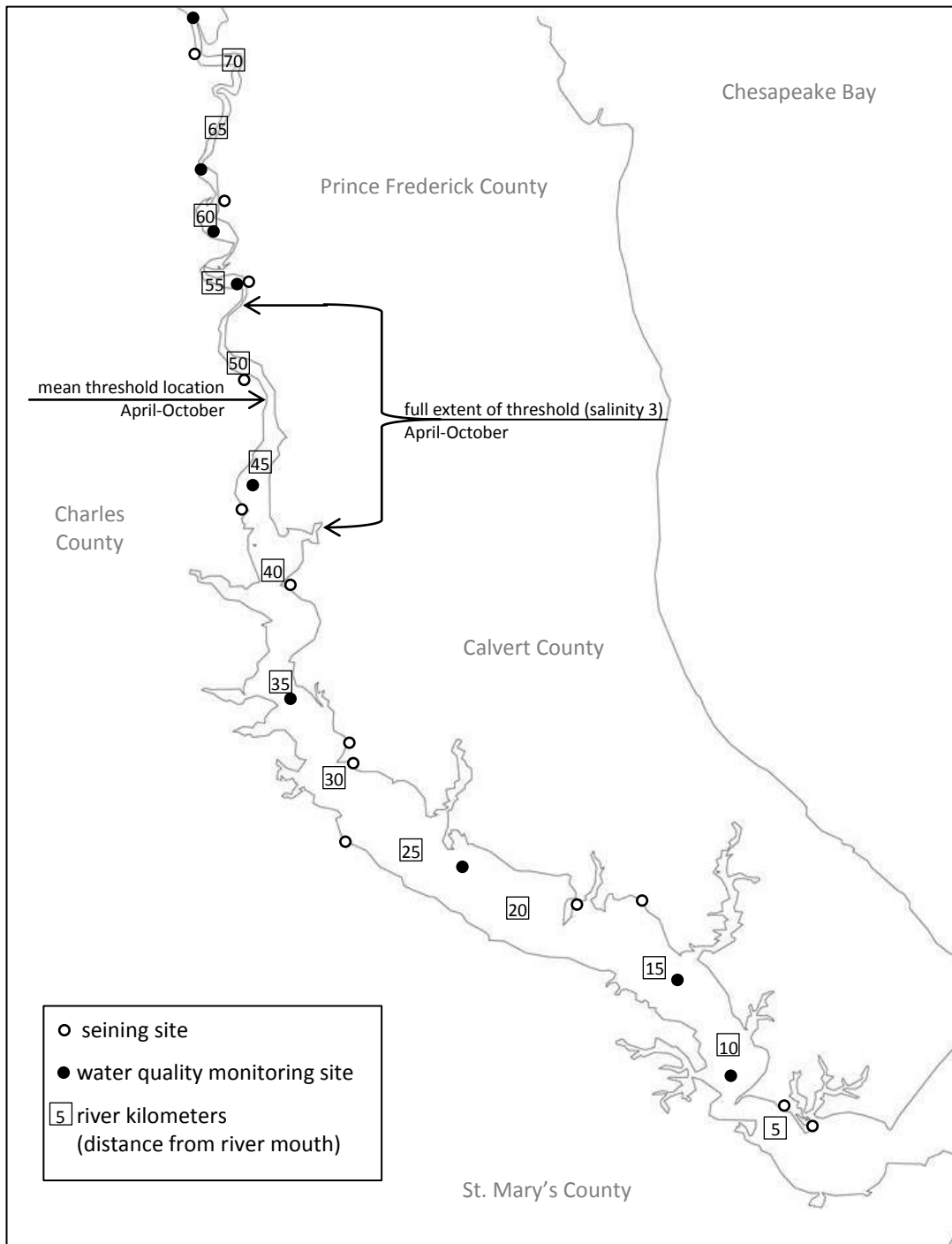


Figure 1.1. Map of the study area, the Patuxent River tidal estuary, Chesapeake Bay. Sites where striped bass were collected via seine are indicated (○), as well as the locations of long-term water quality monitoring (●). *RKM* are listed for reference.

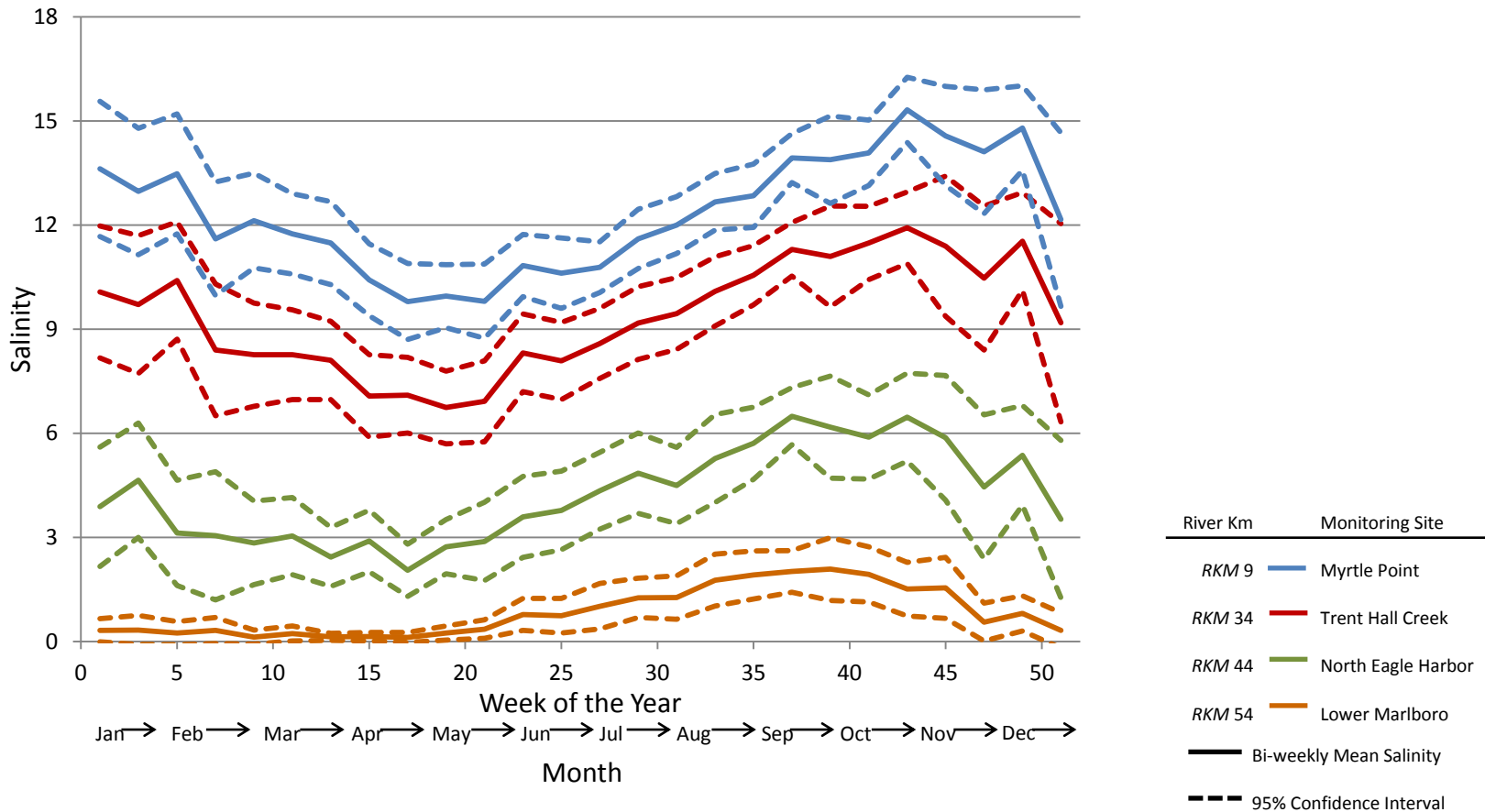


Figure 1.2. Semi-monthly mean salinity and 95% confidence intervals at four sites arrayed throughout the fresh (river kilometer (*RKM*) > 45) and brackish (*RKM* < 45) reaches of the Patuxent River estuary. Salinity means and CI's were determined using 25 years of salinity measurements from 1985-2010. Data from the Chesapeake Bay water quality monitoring program (Chesapeake Bay Program, 2011).

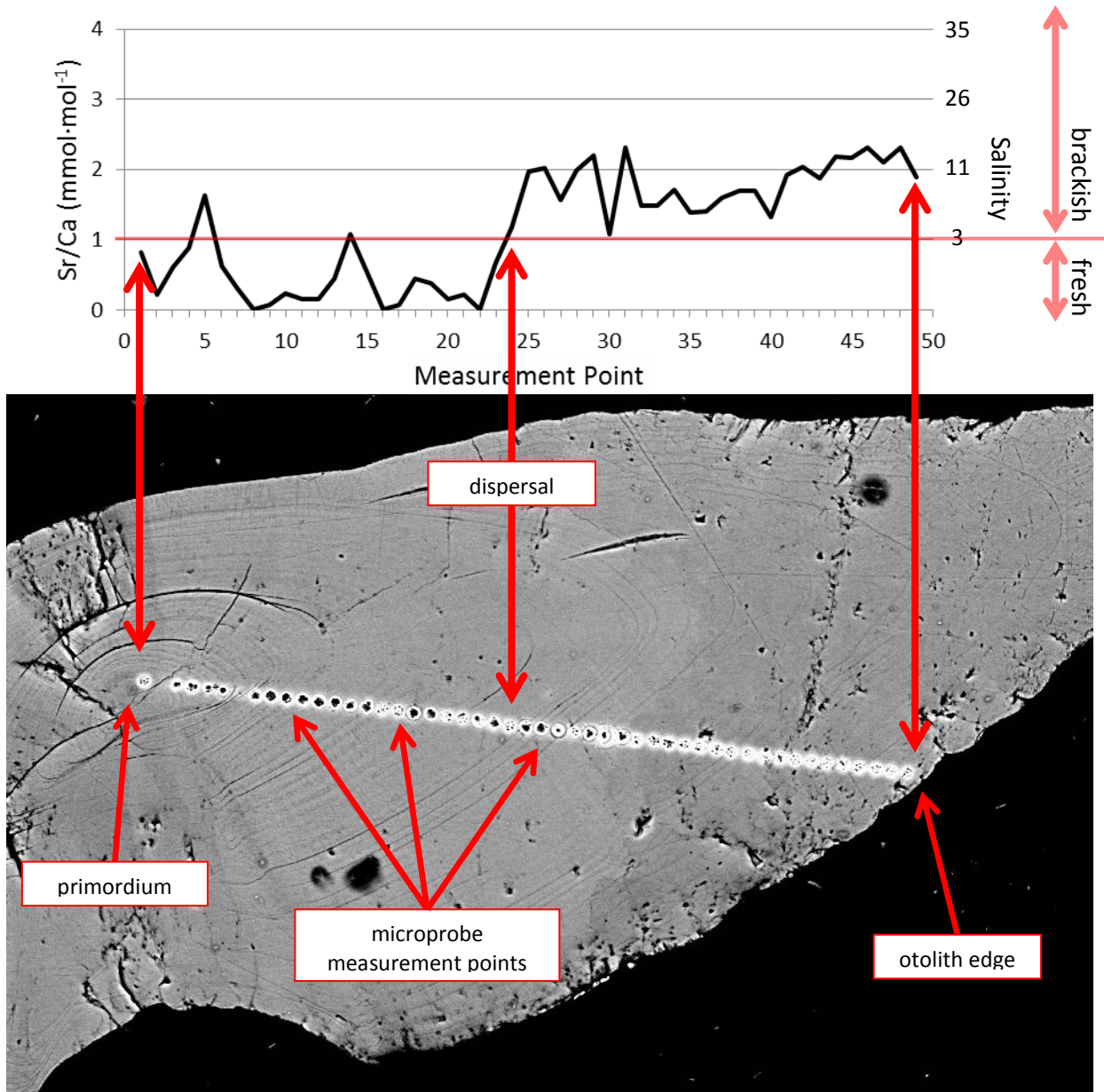


Figure 1.3. Electron back-scatter image of a transverse section of a juvenile striped bass otolith showing the orientation of microprobe measurement path (black and white circles) and resulting Sr/Ca profile (line plot above). The location of a Sr/Ca increase above the fresh/brackish water threshold that would indicate dispersal is identified.

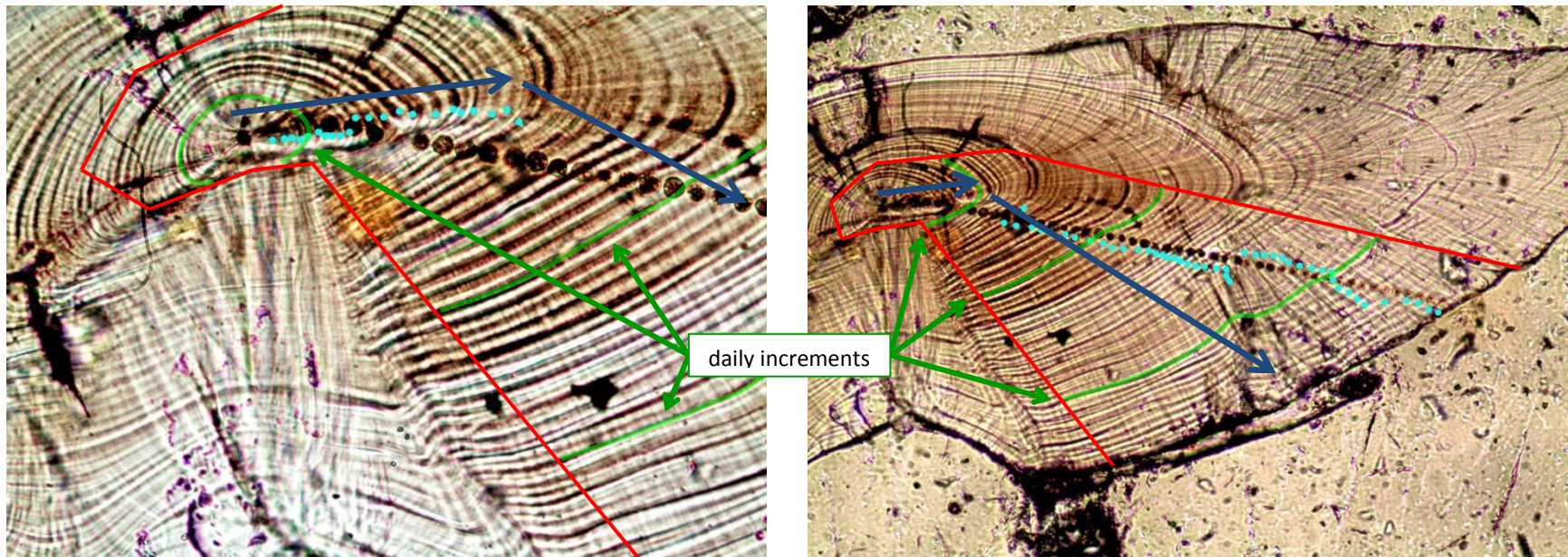


Figure 1.4. Image (transmitted light microscope) of otolith microstructure within transverse section from a juvenile striped bass. Region where daily increments were enumerated is outlined in red (—). Example daily increments are highlighted through counting region in green (—). Full count of daily increments are marked in light blue (•); direction of count from primordium to edge demonstrated with blue arrow (→). Note presence of microprobe samples where Sr/Ca was measured.



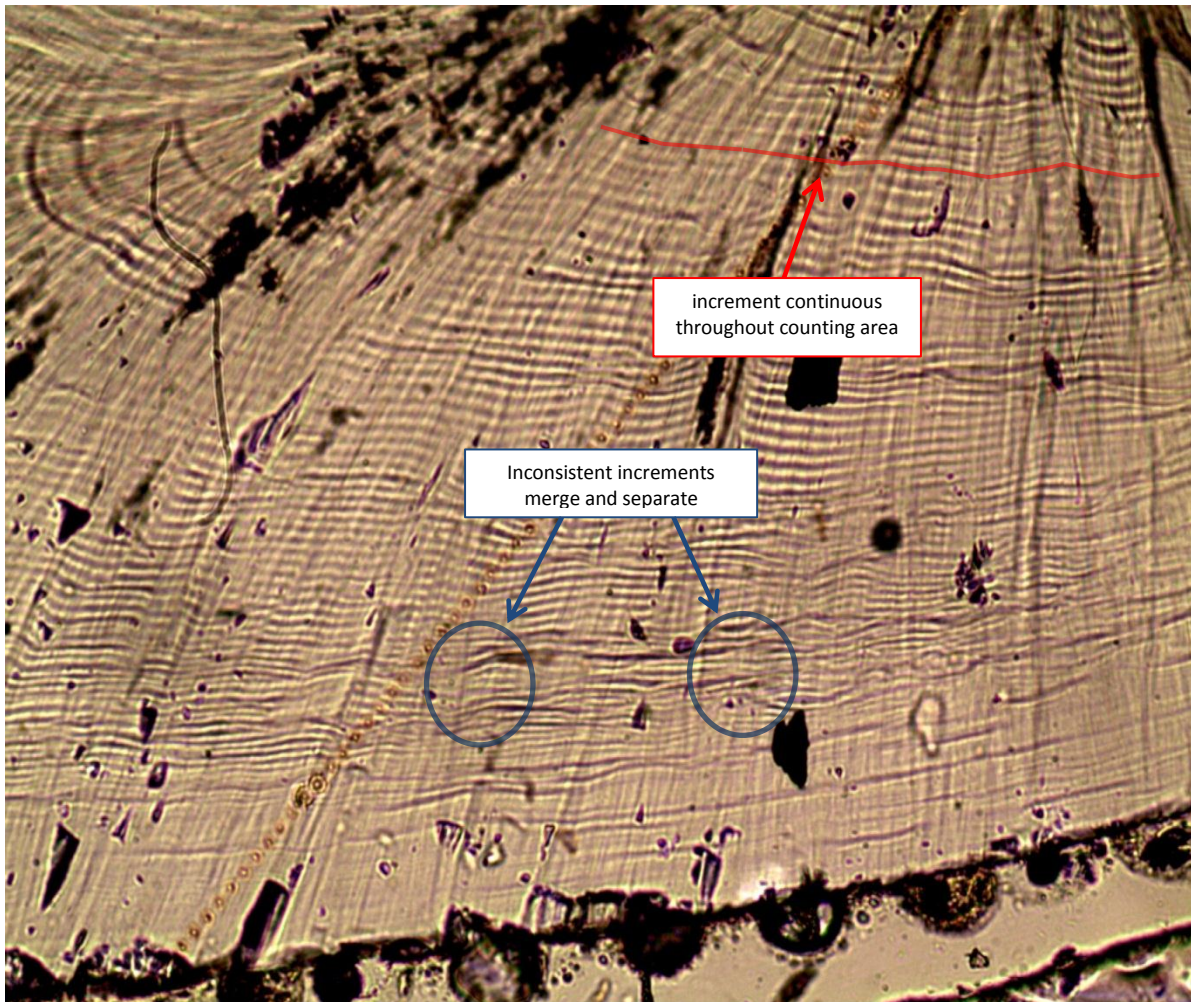


Figure 1.5. Image (transmitted light microscope) of a transverse section from a striped bass juvenile otolith including interpretable and non-interpretable microstructure. Example of an interpretable continuous increment is highlighted in red (—). Example of merging and separating increments that could not be easily interpreted are circled in blue (○). Note presence of microprobe samples where Sr/Ca was measured.

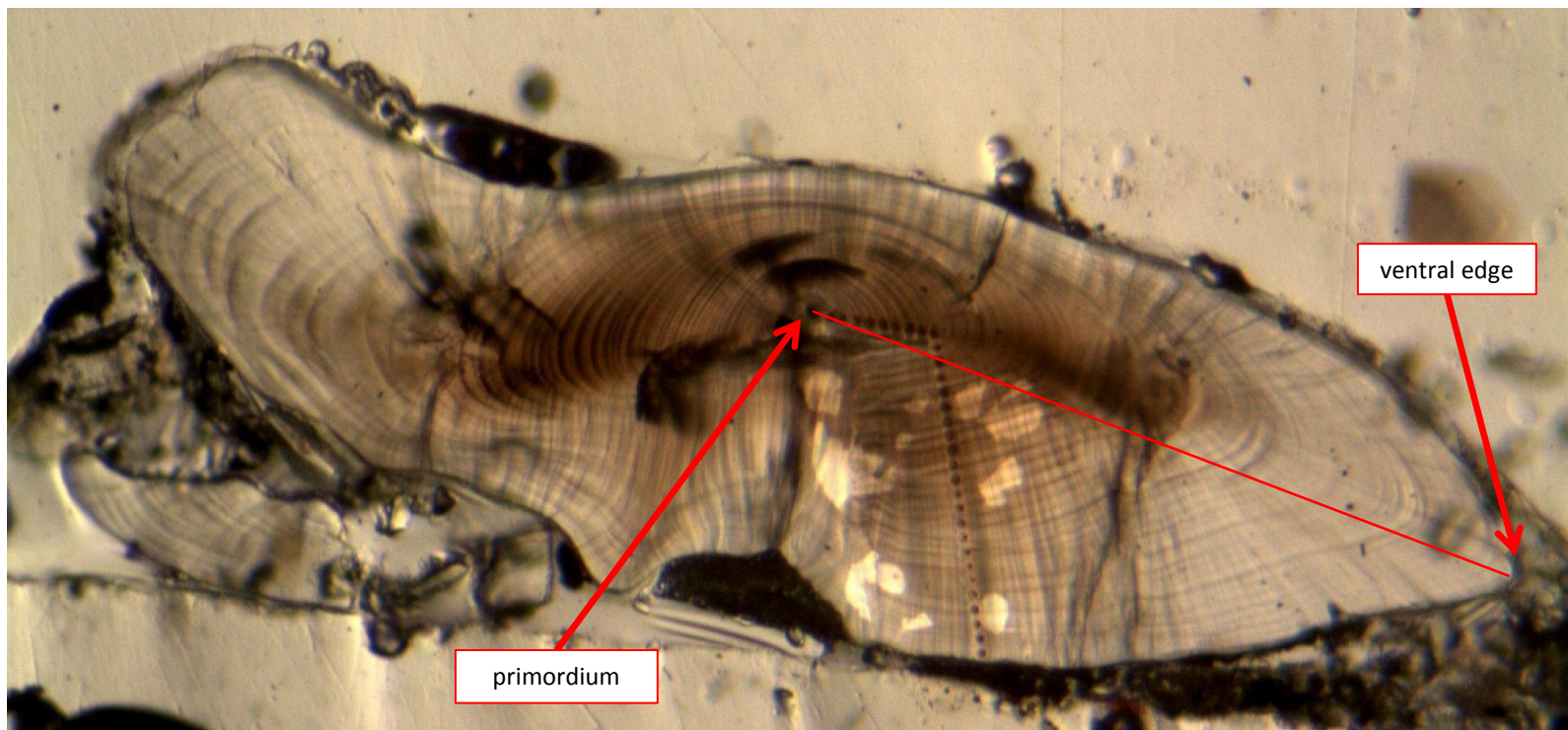


Figure 1.6. Image (transmitted light microscope) of transverse section of a striped bass juvenile otolith. Measured otolith radius, from the primordium to the ventral edge along the ventral transverse axis, is highlighted in red (—); all measures of otolith radius were made along this axis. Note presence of microprobe points where Sr/Ca was measured.

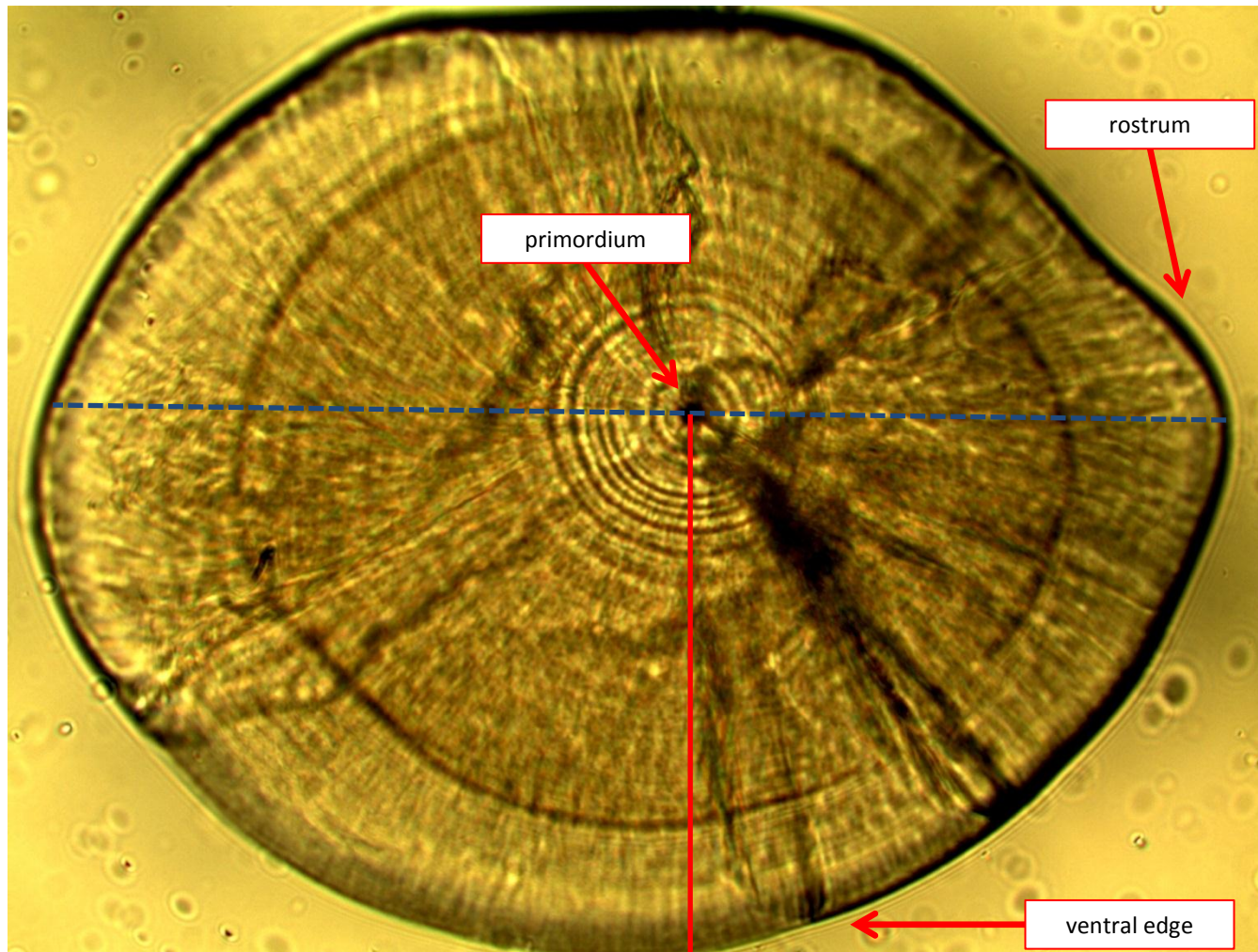


Figure 1.7. Image (transmitted light microscope) of an unsectioned sagittal otolith from a larval striped bass (TL=10.5 mm) with recently distinguishable rostrum. Broken blue line (— —) indicates primordium-rostrum axis. Red line (—) indicates measured otolith radius; all measures of otolith radius were made along this axis.

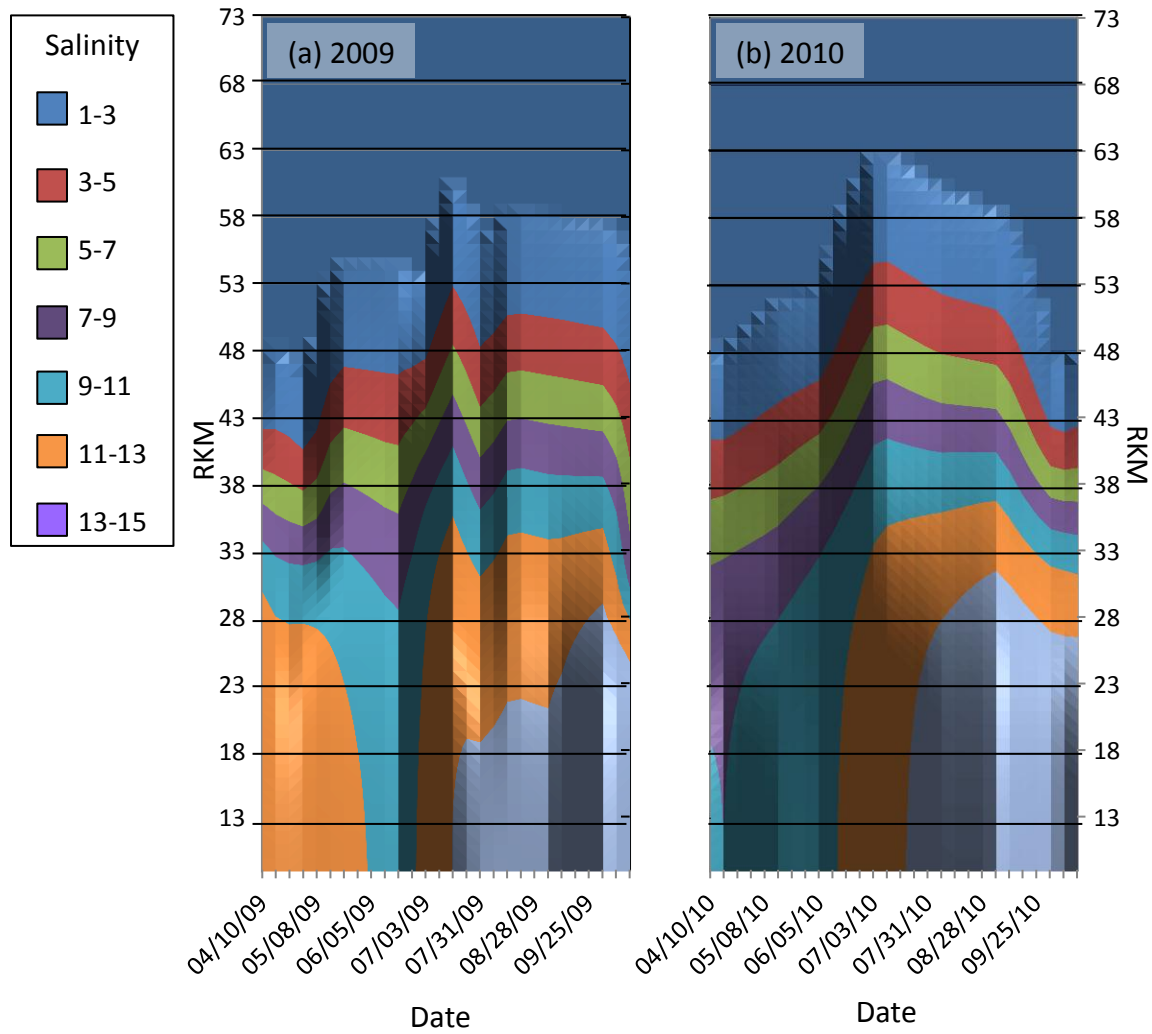


Figure 1.8. Contour plots of the modeled relationship between surface (depth  $\leq 1.5\text{m}$ ) salinity and river kilometer (*RKM*) in the Patuxent River estuary during the period April through mid-October for 2009 and 2010. Weekly salinity values are displayed.

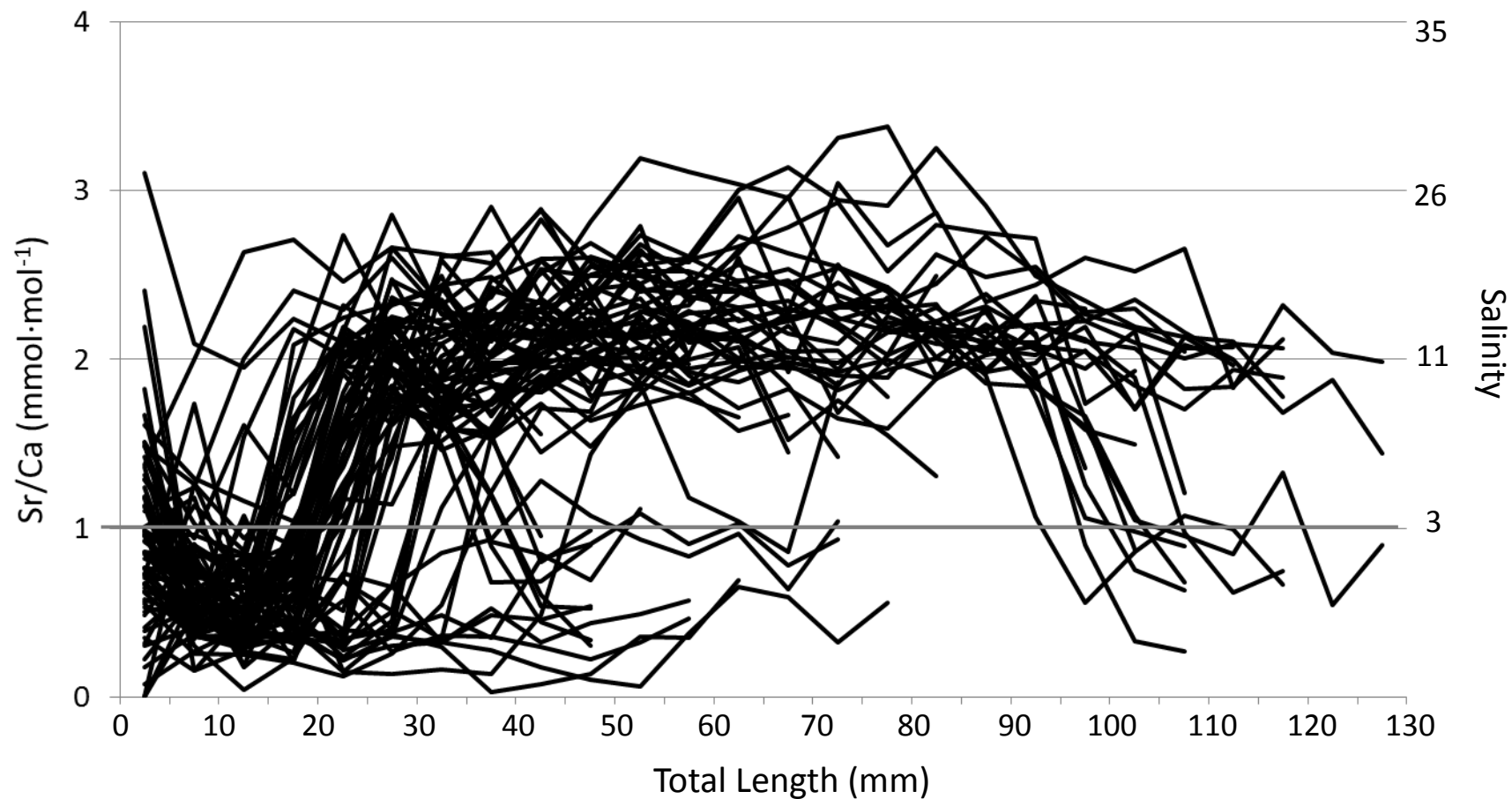


Figure 1.9a. 2009 Sr/Ca profiles by back-calculated total length bins (5 mm) of juvenile striped bass, representing lifetime habitat salinity from hatch until collection. The Sr/Ca ( $1 \text{ mmol}\cdot\text{mol}^{-1}$ ) and salinity value (3) of the transition between fresh and brackish water is marked ( $\text{—}$ ).

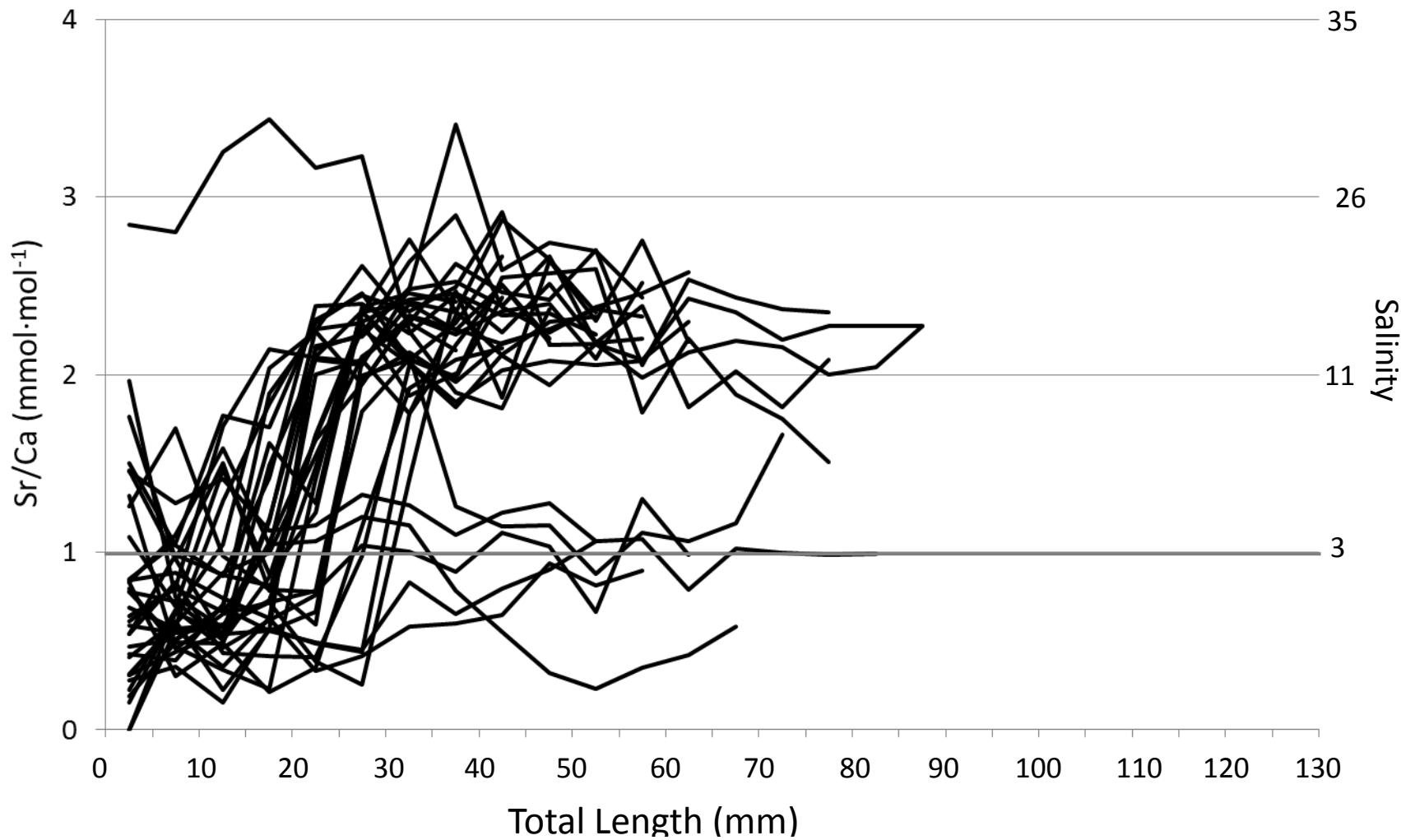


Figure 1.9b. 2010 Sr/Ca profiles by back-calculated total length bins (5 mm) of juvenile striped bass, representing lifetime habitat salinity from hatch until collection. The Sr/Ca ( $1 \text{ mmol}\cdot\text{mol}^{-1}$ ) and salinity value (3) of the transition between fresh and brackish water is marked ( $\text{—}$ ).

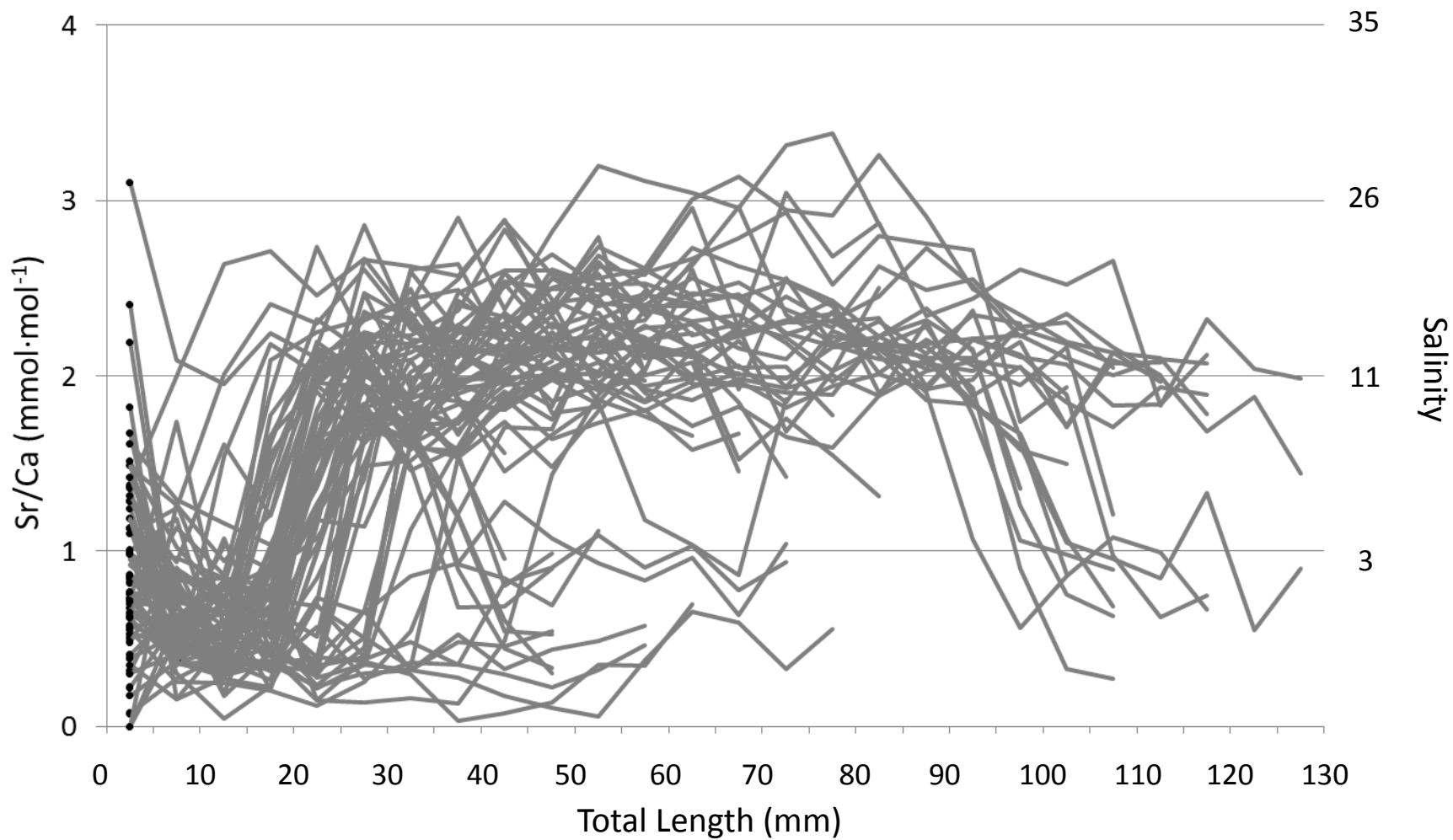


Figure 1.10a. 2009 Sr/Ca profiles by back-calculated total length bins for juvenile striped bass. Sr/Ca during the initial larval period (0-5 mm) is indicated in black (•). Sr/Ca depicted in gray was not included in this analysis.

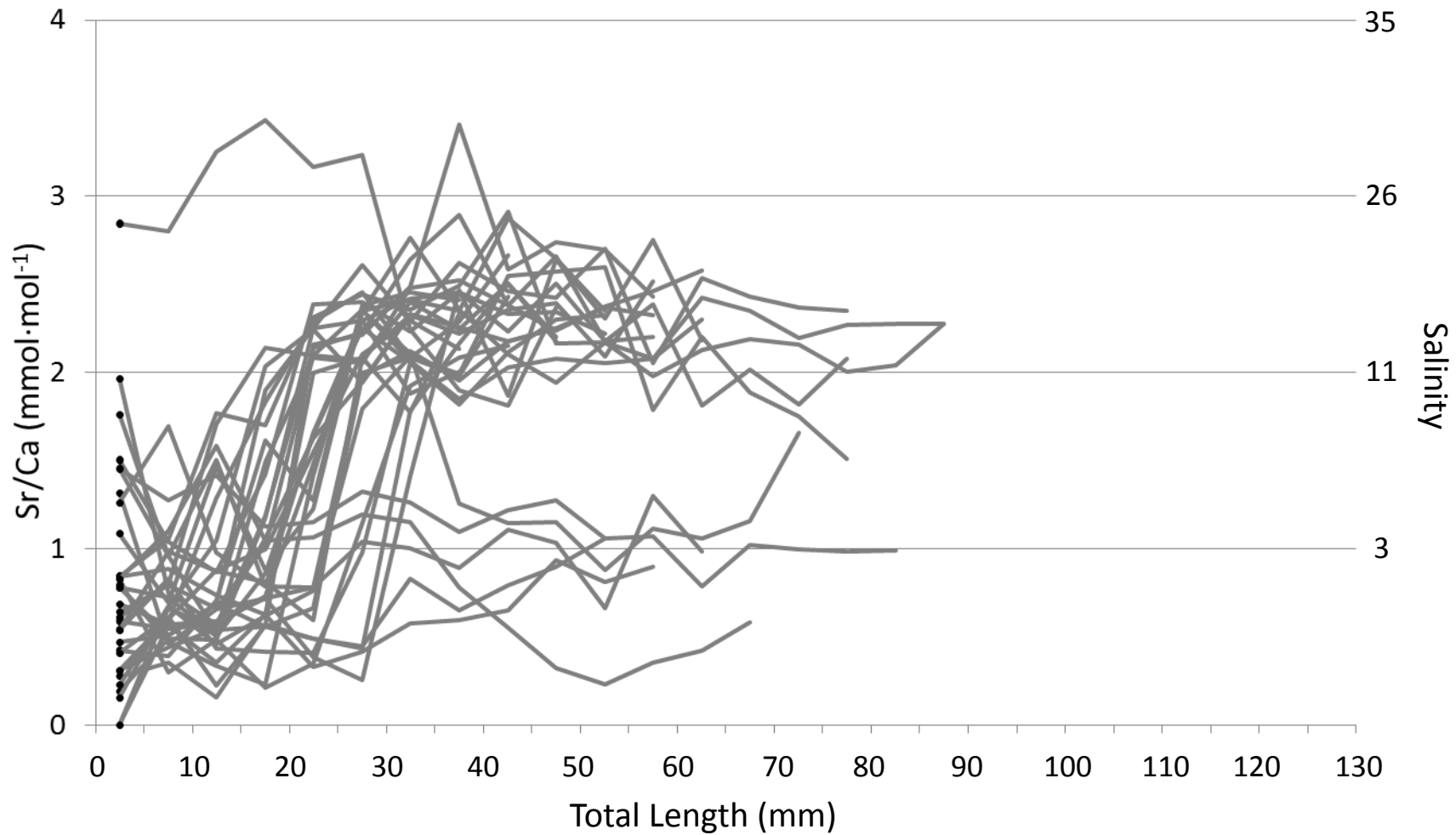


Figure 1.10b. 2010 Sr/Ca profiles by back-calculated total length bins for juvenile striped bass. Sr/Ca during the initial larval period (0-5 mm) is indicated in black (•). Sr/Ca depicted in gray was not included in this analysis.



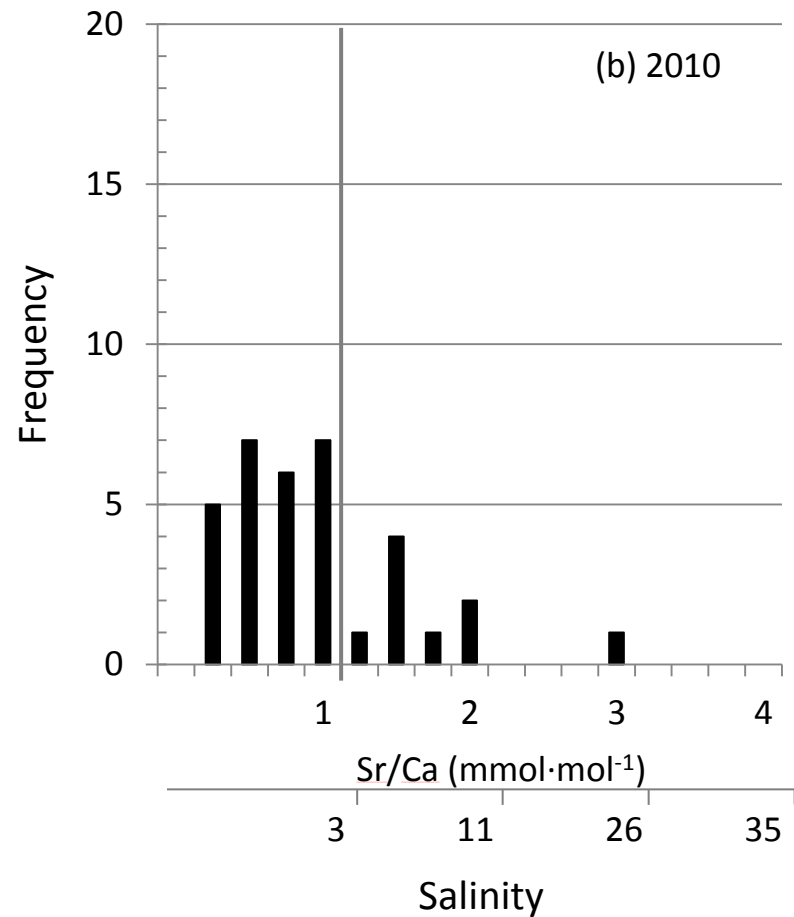
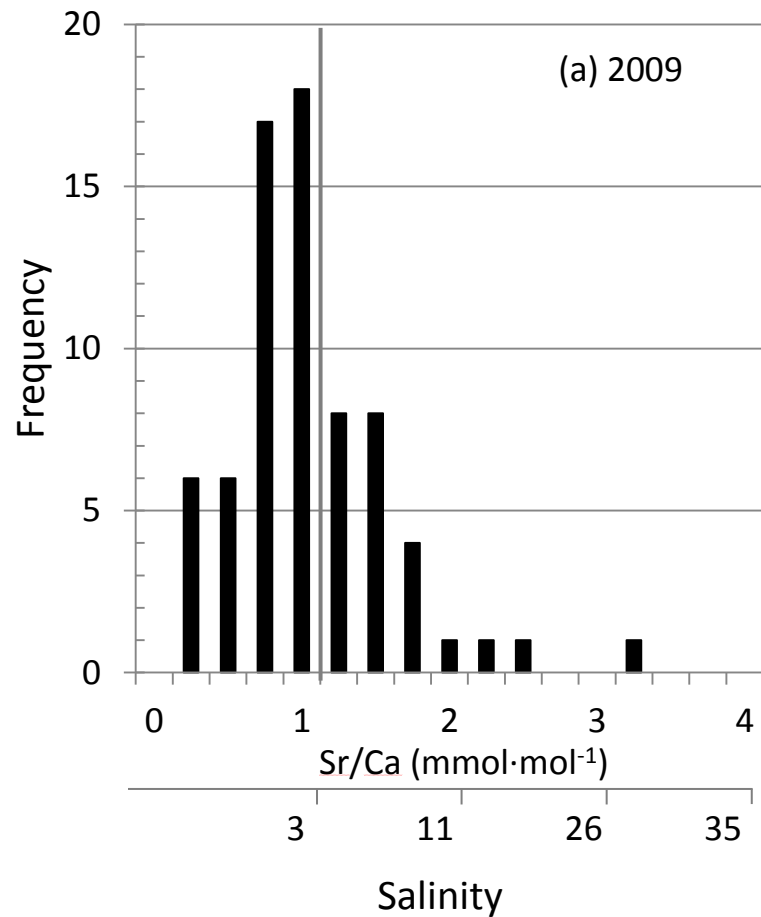


Figure 1.11. Histogram of initial (total lengths 0-5 mm) otolith Sr/Ca of juvenile striped bass and corresponding salinity for 2009 (a) and 2010 (b). The vertical gray line (—) indicates the fresh-brackish water threshold at 1.0 mmol·mol<sup>-1</sup> (salinity of 3).

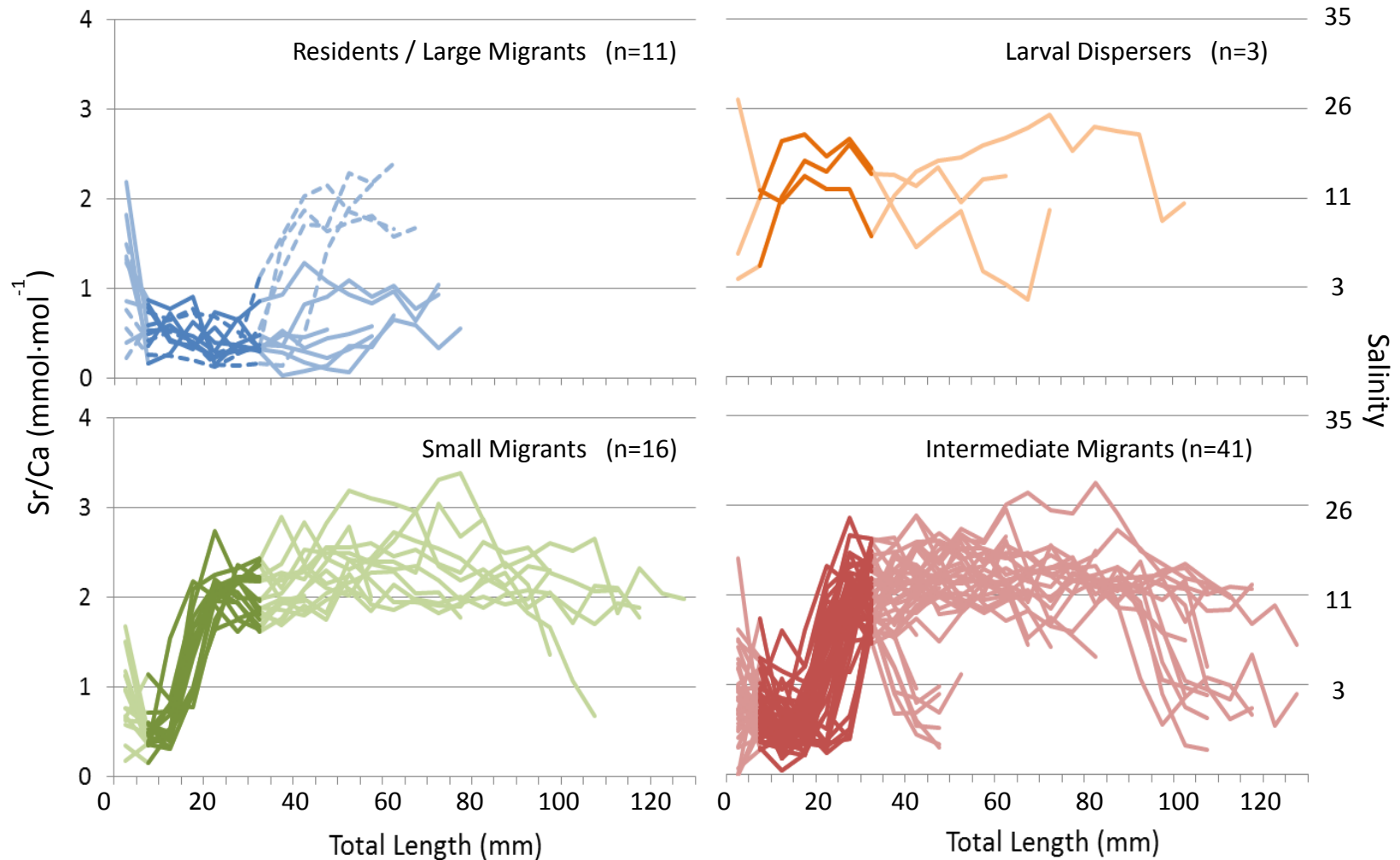


Figure 1.12a. 2009 Sr/Ca profiles by length separated by juvenile striped bass contingent, total lengths 6-35 mm (primary analysis sample; n=71). Darkly colored sections of the profiles indicate sizes included in the analysis. The dashed blue lines (— —) in the Residents & Large Migrants profile plot identify contingent members that do disperse eventually. The sample size of each contingent is given in the upper right corner of each plot. Contingents identified using PCA/CA analysis.

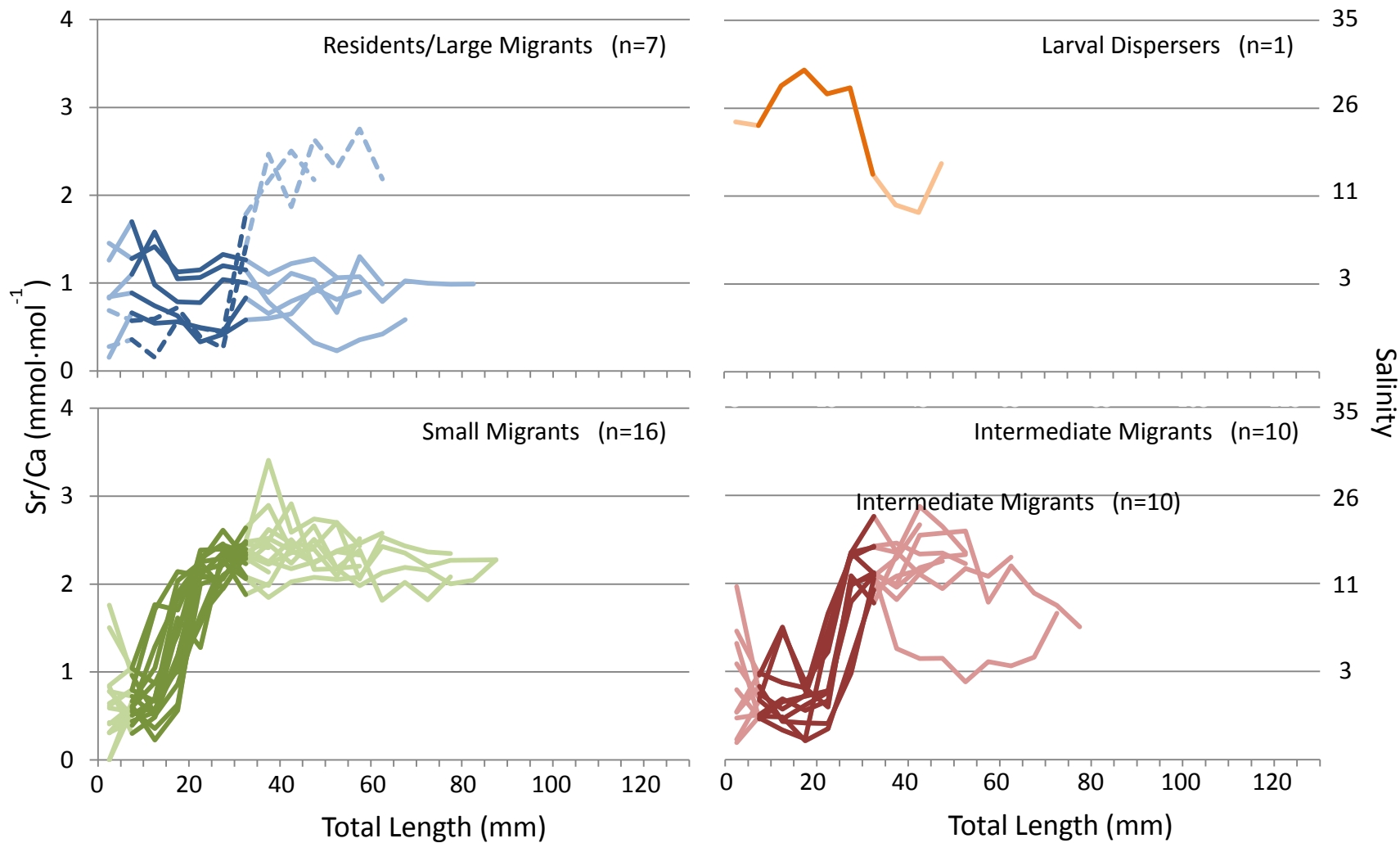


Figure 1.12b. 2010 Sr/Ca profiles by length separated by juvenile striped bass contingent, total lengths 6-35 mm (primary analysis sample; n=34). Darkly colored sections of the profiles indicate sizes included in the analysis. The dashed blue lines (— —) in the Residents & Large Migrants profile plot identify contingent members that do disperse eventually. The sample size of each contingent is given in the upper right corner of each plot. Contingents identified using PCA/CA analysis.

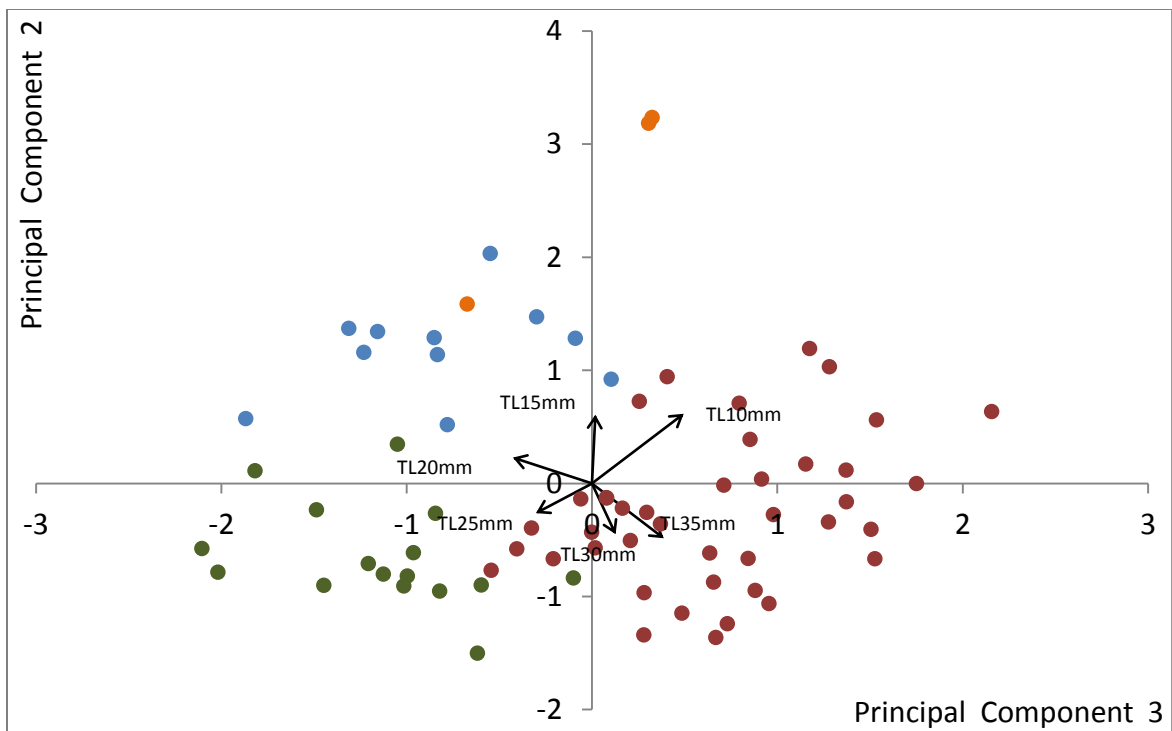
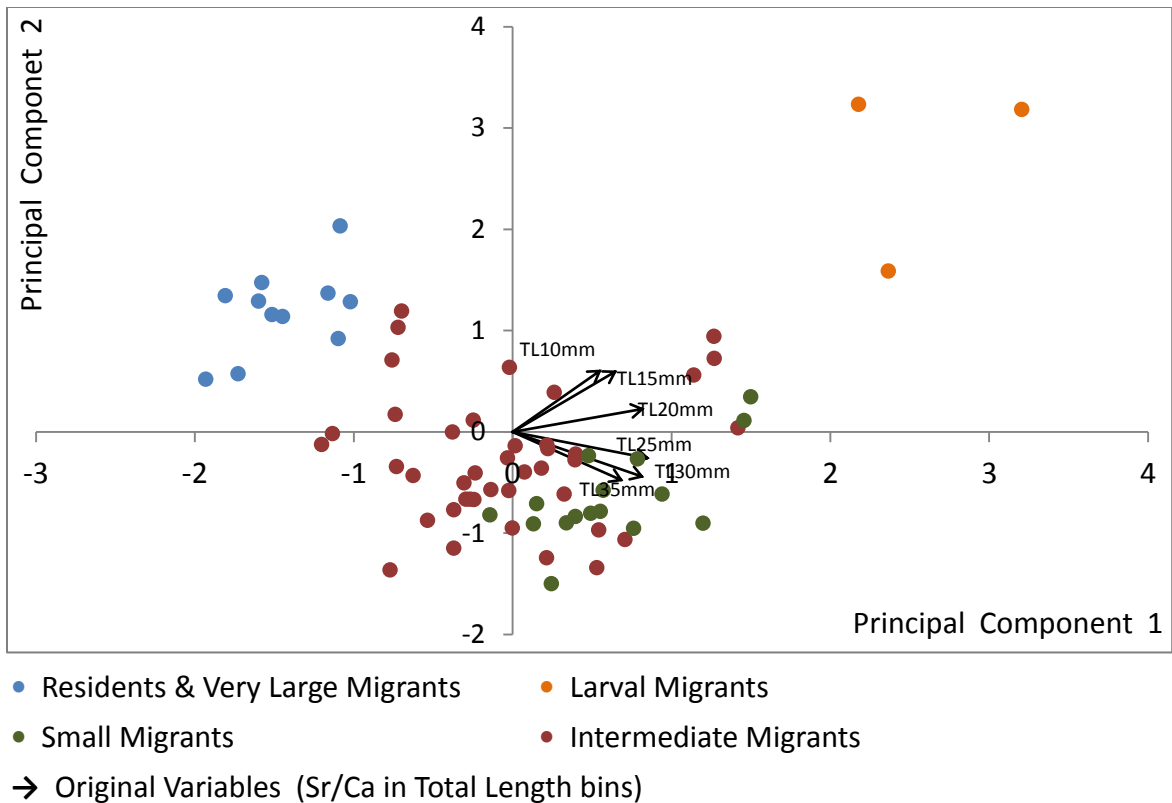
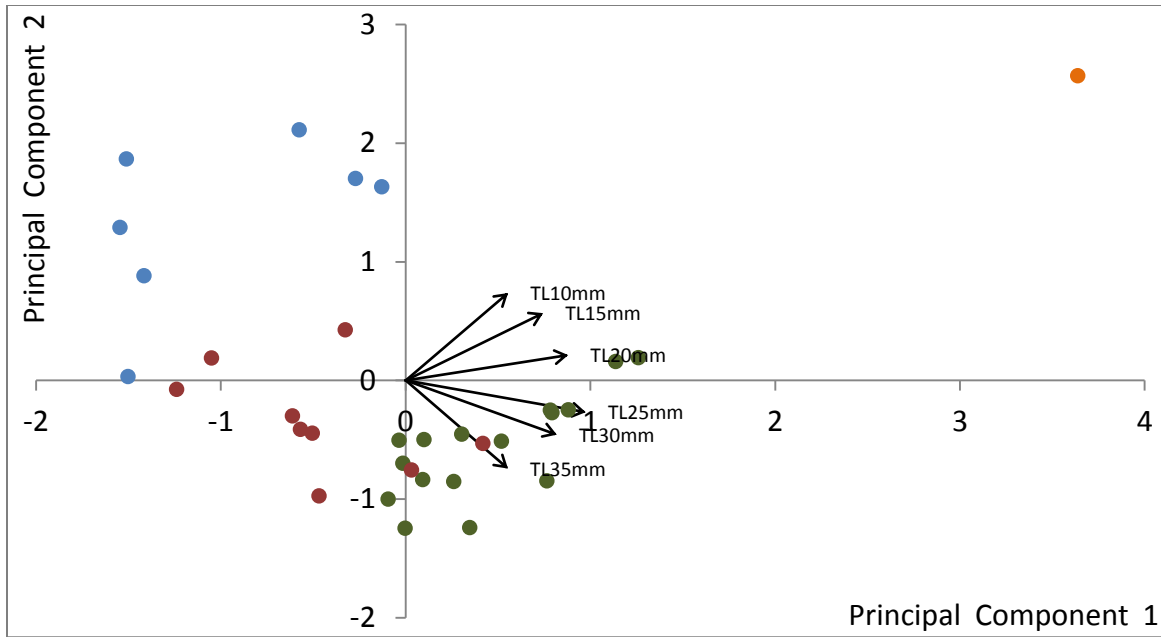


Figure 1.13a. Principal component loading bi-plots of 2009 Sr/Ca by length bins, total lengths 6-35 mm. Individual striped bass YOY contingents color coded as shown elsewhere in profile plots. Arrows (↑) indicate total length bin vectors.



- Residents & Very Large Migrants
- Larval Migrants
- Small Migrants
- Intermediate Migrants
- Original Variables (Sr/Ca in Total Length bins)

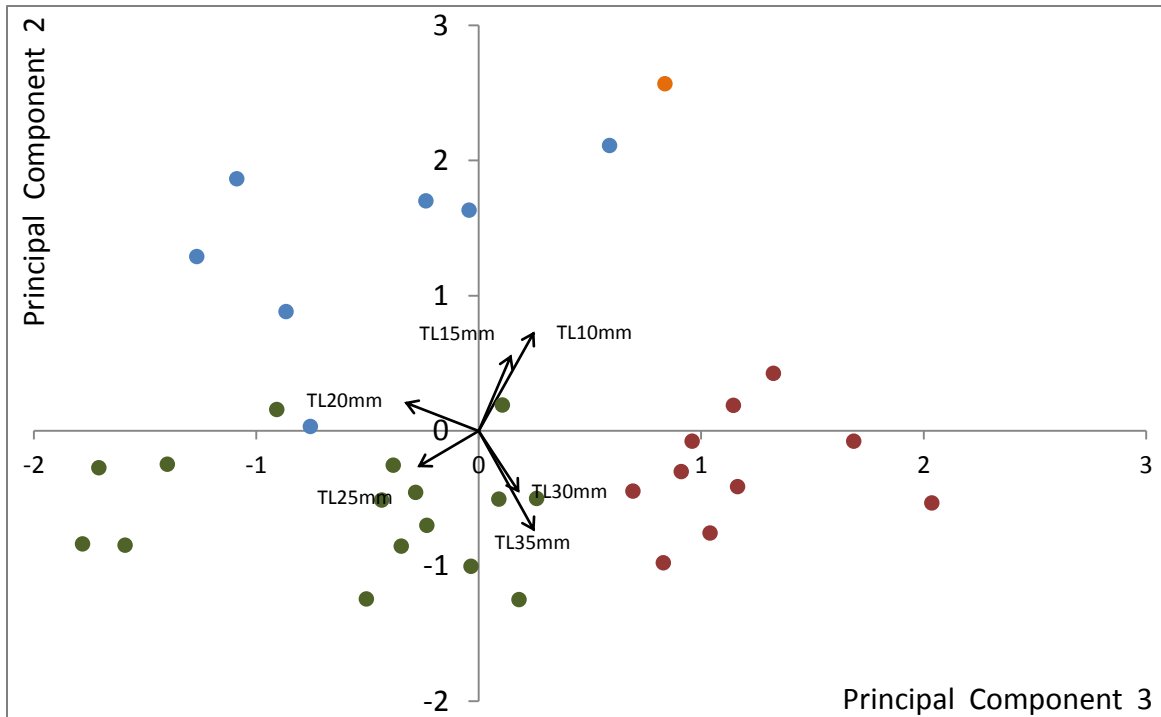


Figure 1.13b. Principal component loading bi-plots of 2010 Sr/Ca by length bins, total lengths 6-35 mm. Individual striped bass YOY contingents color coded as shown elsewhere in profile plots. Arrows (↑) indicate total length bin vectors.

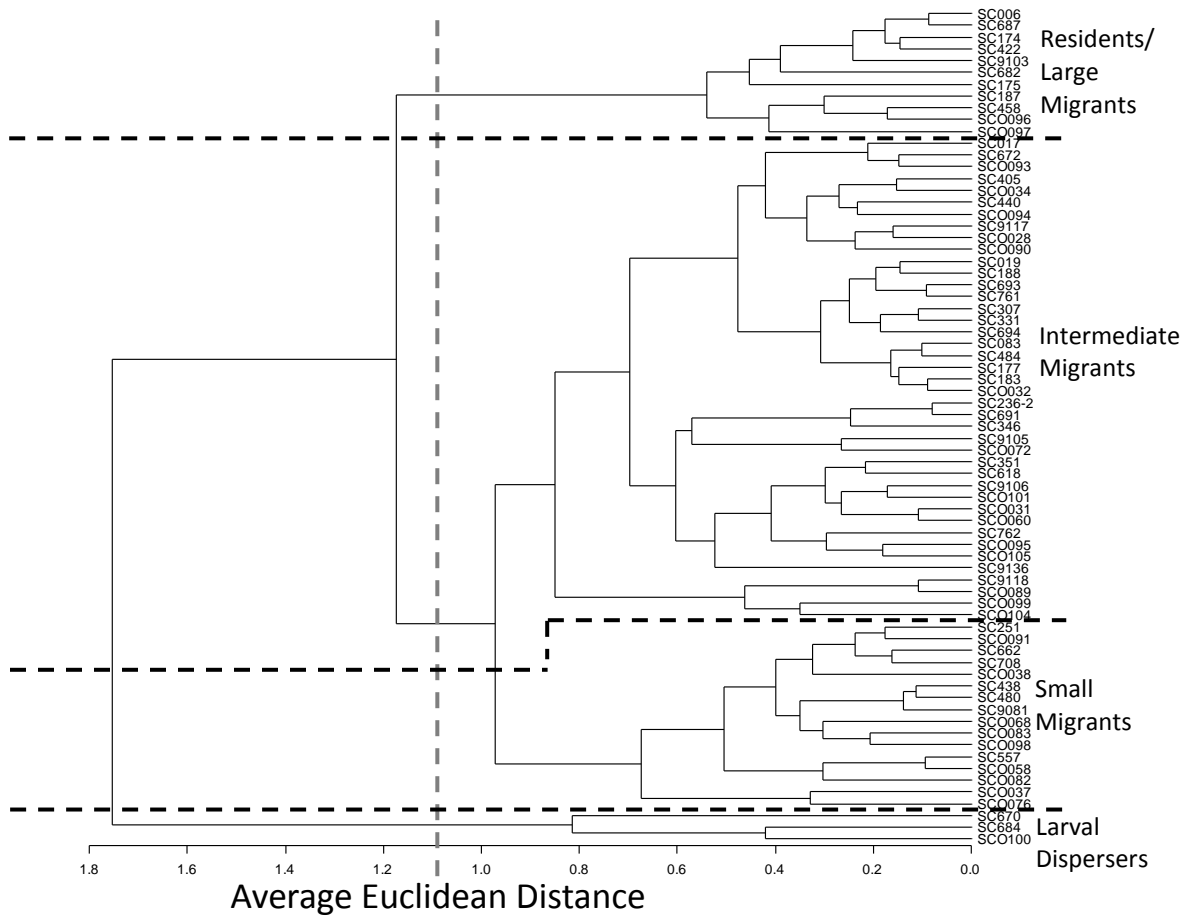


Figure 1.14a. Dendrogram of average-linkage cluster analysis results, 2009 primary sample (TL 6-35mm). Vertical gray broken line (— —) indicates the agglomeration step in the cluster analysis where clustering was considered complete. Horizontal black broken lines (— —) indicate separation between contingents. Contingents are identified.

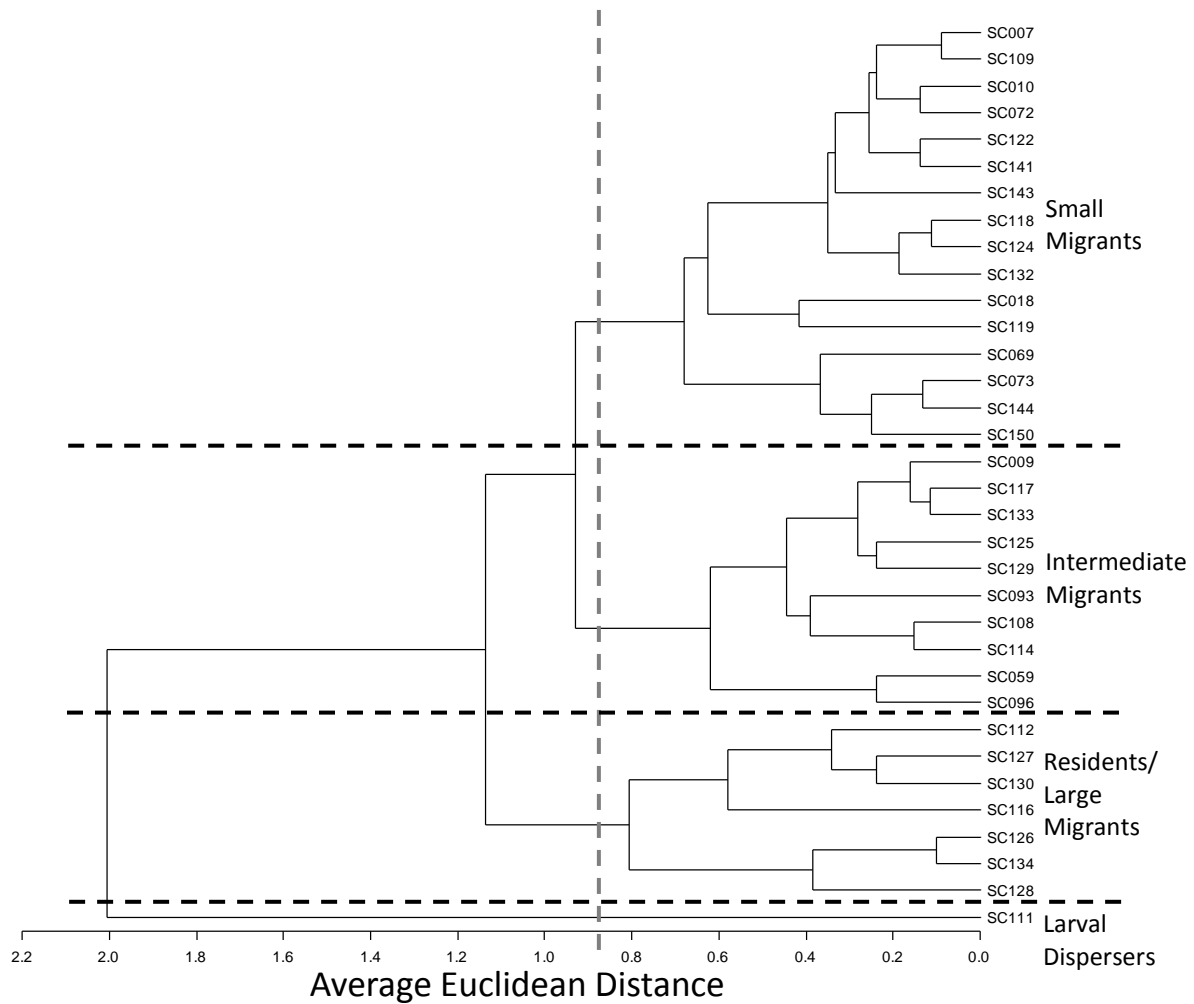


Figure 1.14b. Dendrogram of average-linkage cluster analysis results, 2010 primary sample (TL 6-35mm). Vertical gray broken line (— —) indicates the agglomeration step in the cluster analysis where clustering was considered complete. Horizontal black broken lines (— —) indicate separation between contingents. Contingents are identified.

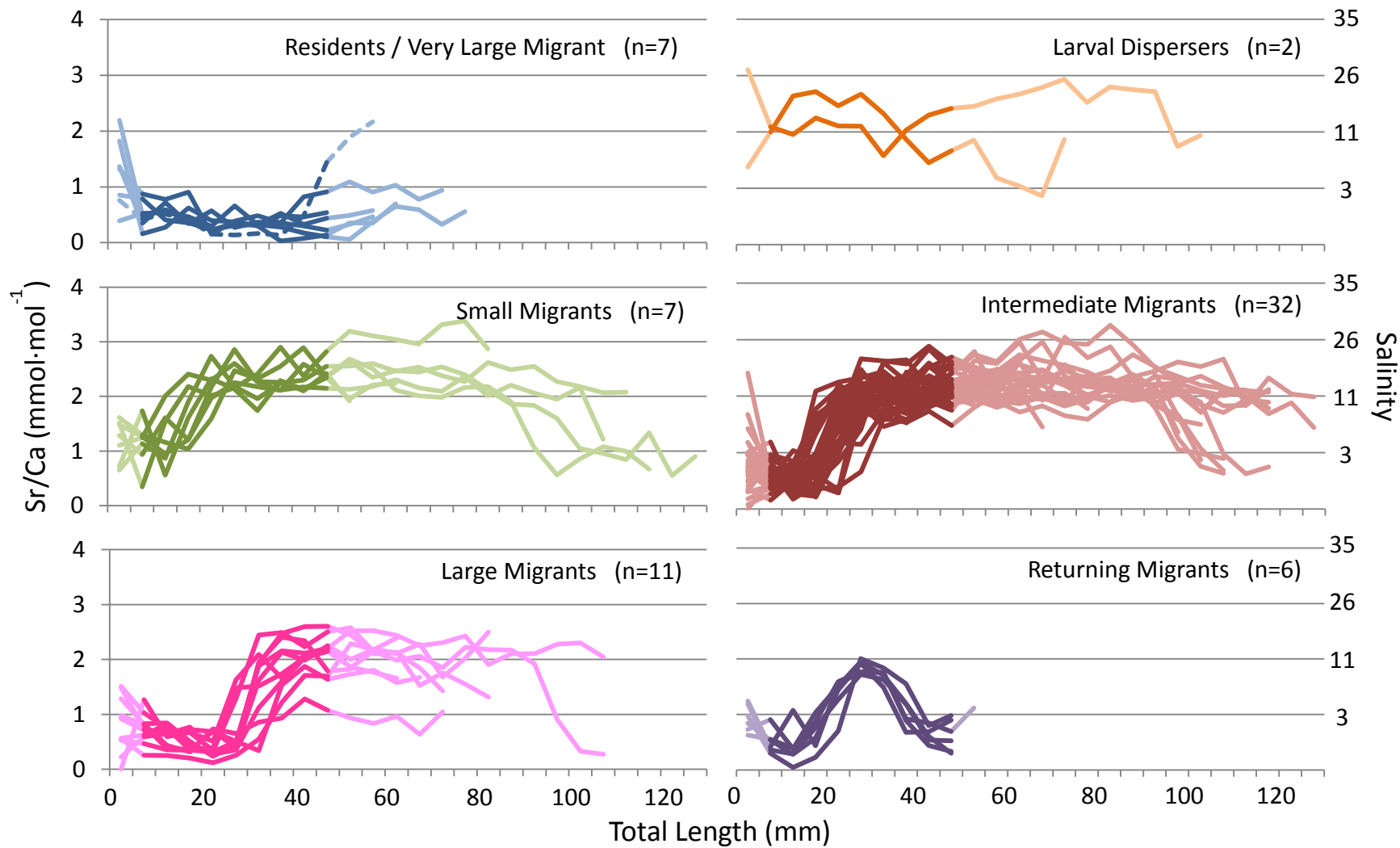


Figure 1.15a. 2009 Sr/Ca profiles by length separated by juvenile striped bass contingent, total lengths 6-50 mm (secondary analysis sample; n=65). Darkly colored sections of the profiles indicate sizes included in the analysis. The dashed blue line (— —) in the Residents & Very Large Migrants profile plot identifies contingent members that do disperse eventually. The sample size of each contingent is given in the upper right corner of each plot. Contingents identified using PCA/CA analysis.



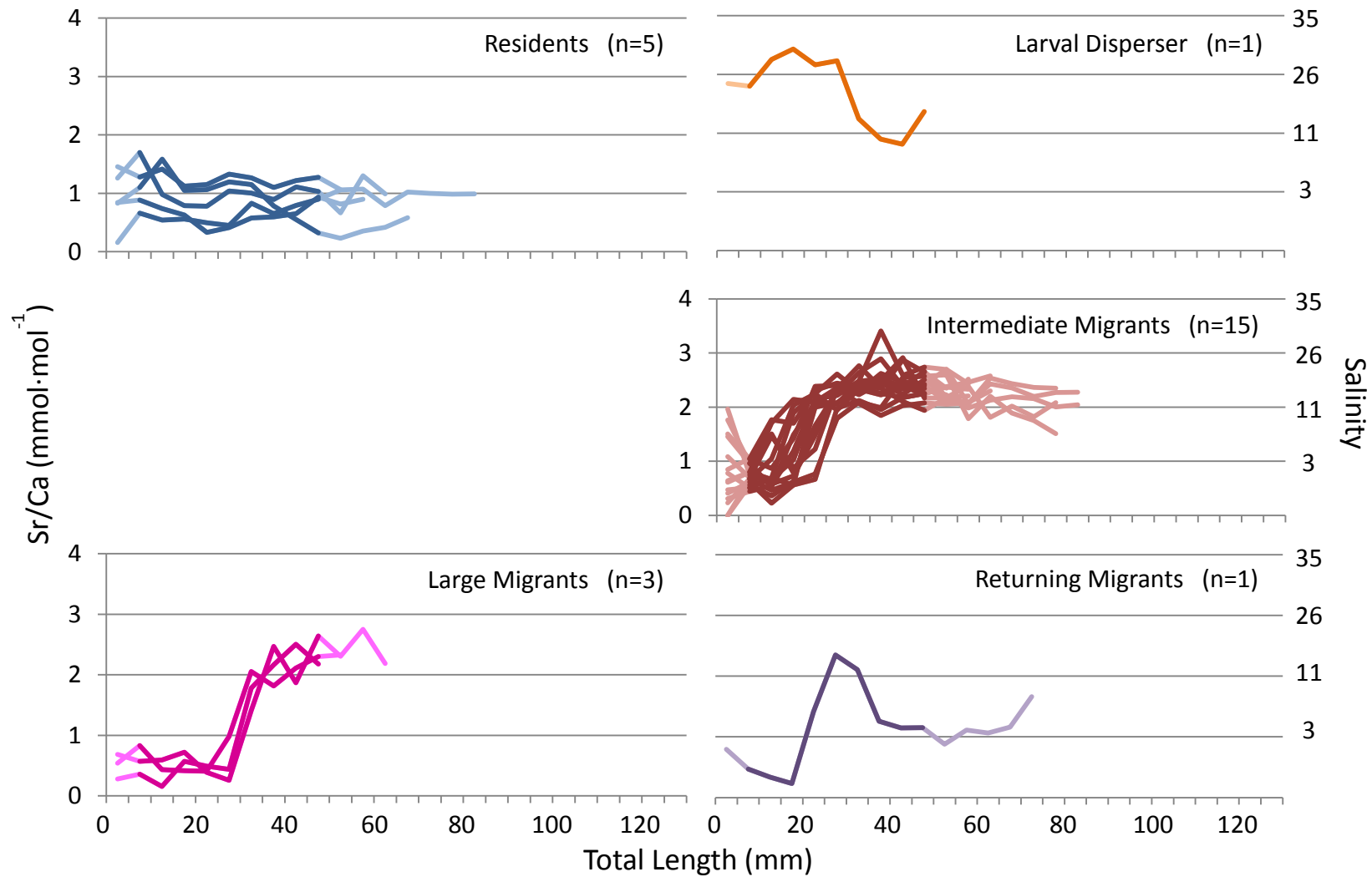
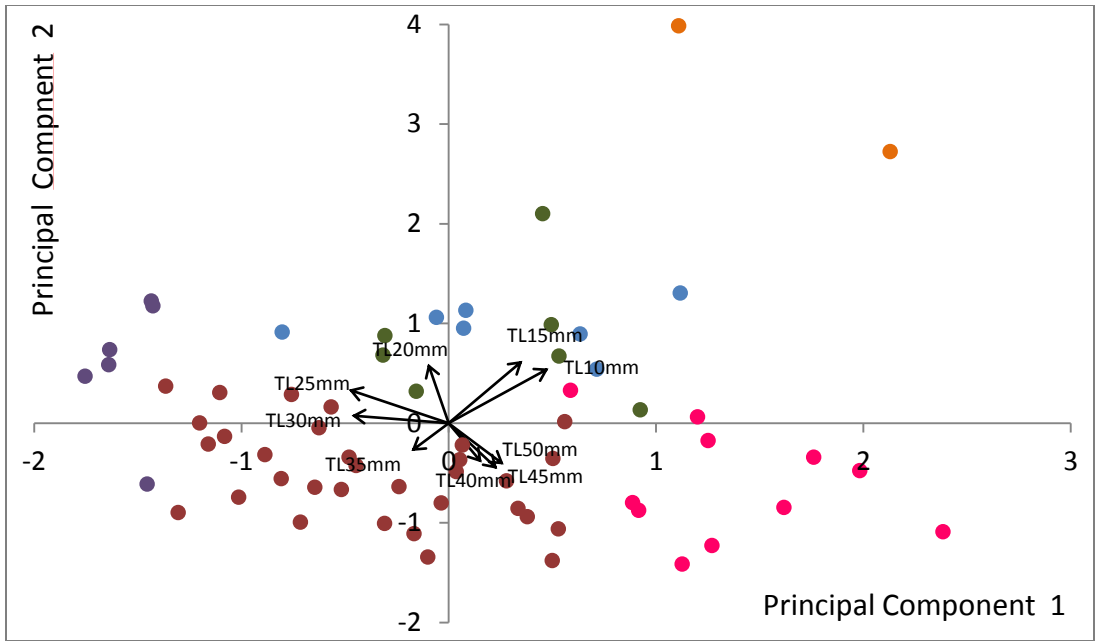


Figure 1.15b. 2010 Sr/Ca profiles by length separated by juvenile striped bass contingent, total lengths 6-50 mm (secondary analysis sample; n=25). Darkly colored sections of the profiles indicate sizes included in the analysis. The sample size of each contingent is given in the upper right corner of each plot. Contingents identified using PCA/CA analysis.



- Residents & Very Large Migrants
- Small Migrants
- Large Migrants
- Original Variables (Sr/Ca in Total Length bins)
- Larval Migrants
- Intermediate Migrants
- Returning Migrants

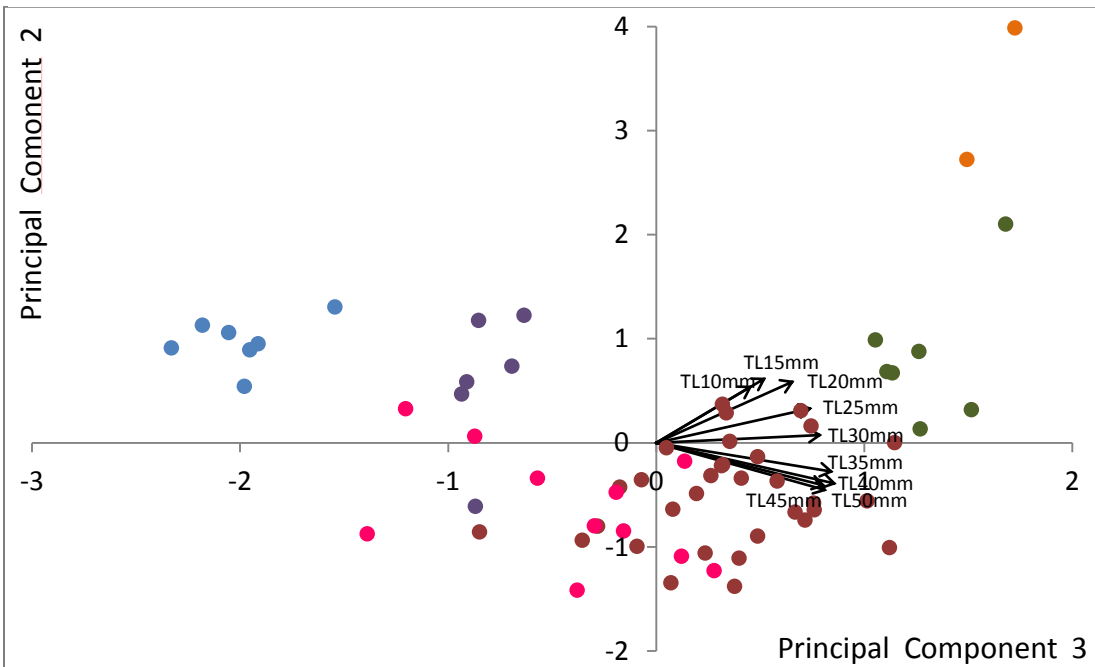
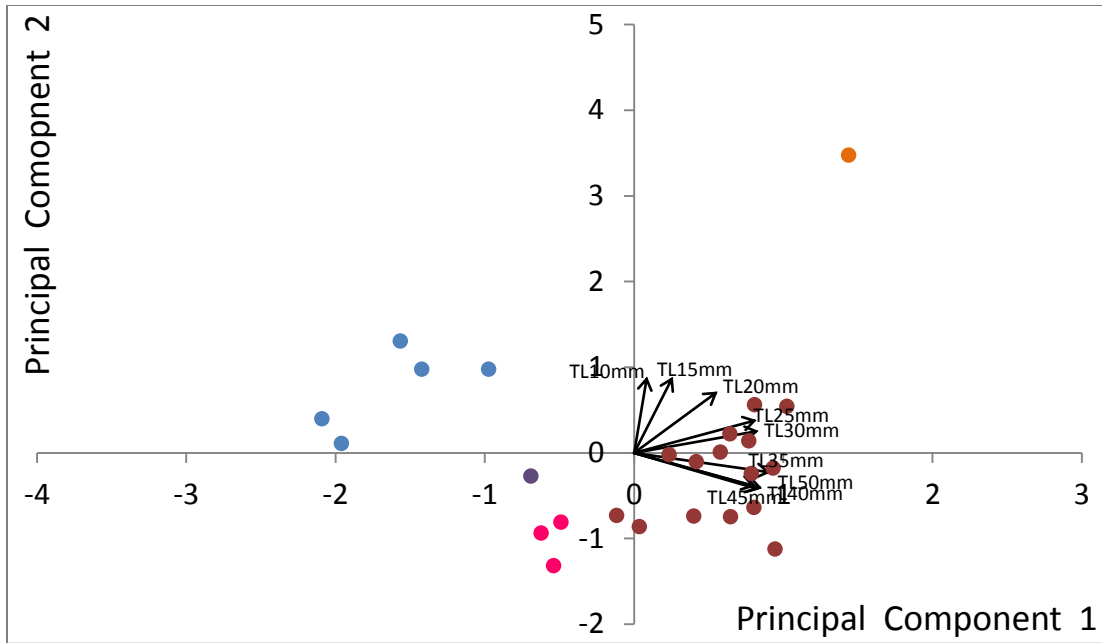


Figure 1.16a. Principal component loading bi-plots of 2009 Sr/Ca by length bins, total lengths 6-50mm. Individual striped bass YOY contingents color coded as shown elsewhere in profile plots. Arrows (↑) indicate total length bin vectors.



- Residents & Very Large Migrants
- Larval Migrants
- Small Migrants
- Intermediate Migrants
- Returning Migrants
- Original Variables (Sr/Ca in Total Length bins)

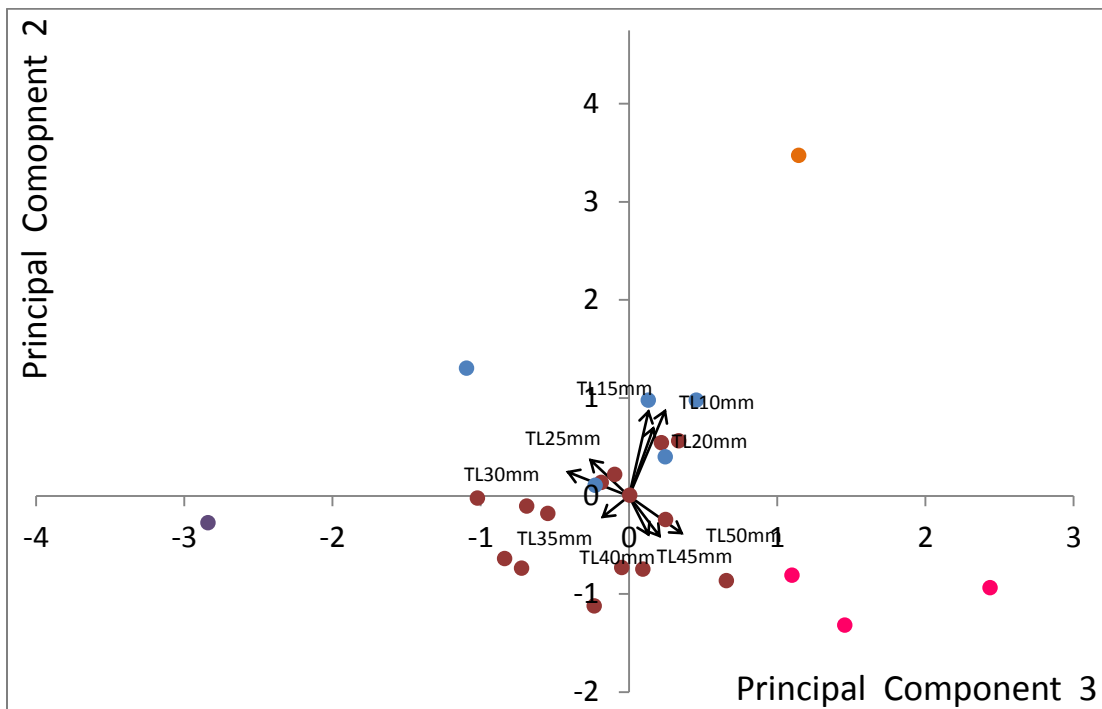


Figure 1.16b. Principal component loading bi-plots of 2010 Sr/Ca by length bins, total lengths 6-50mm. Individual striped bass YOY contingents color coded as shown elsewhere in profile plots. Arrows (↑) indicate total length bin vectors.

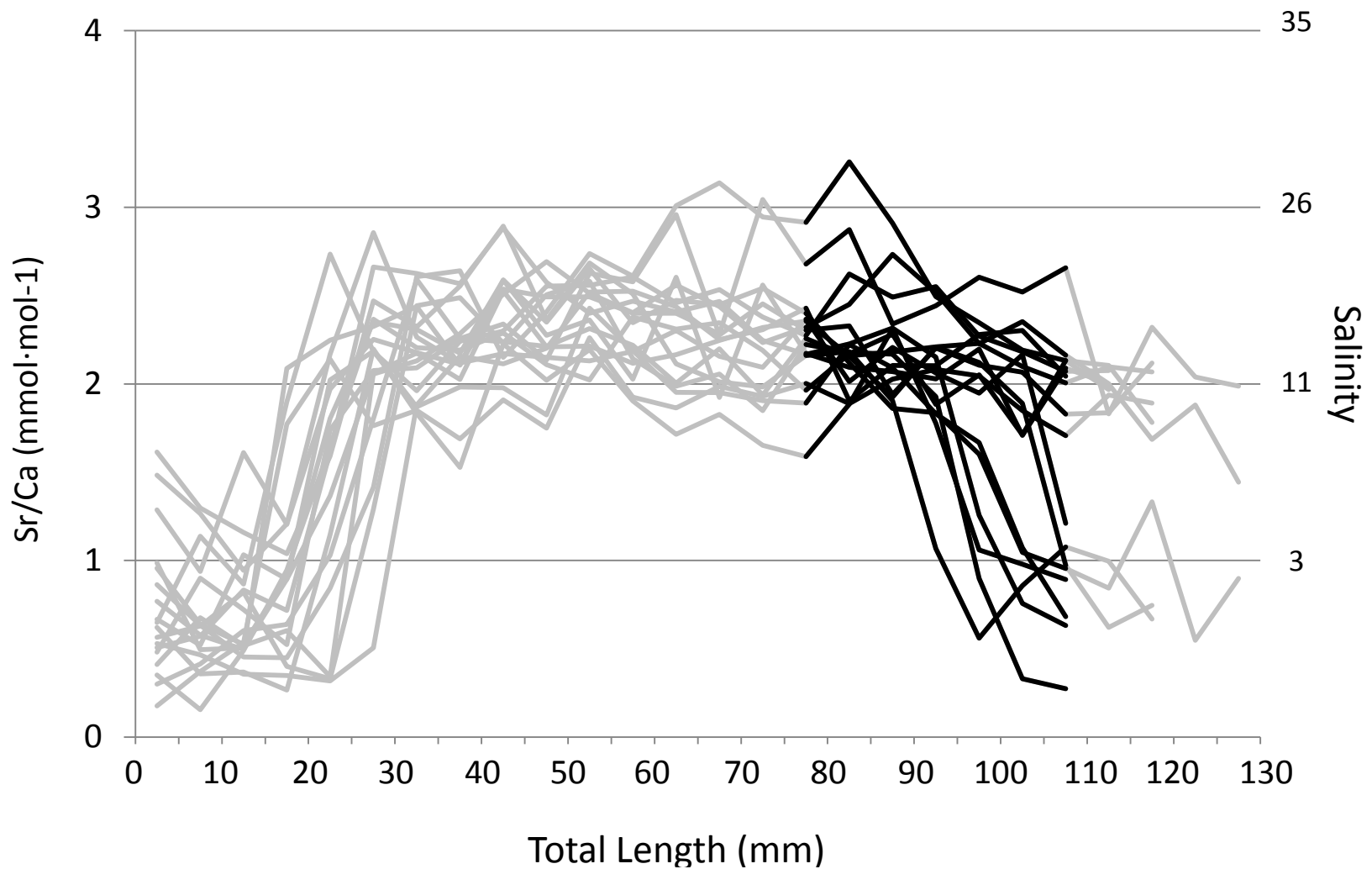


Figure 1.17. Sr/Ca profiles of juvenile striped bass collected in October 2009 (n=18) by back-calculated total length bins. Sr/Ca during late movement (76-110mm) is indicated in black (—). Sr/Ca depicted in gray was not included in this analysis.

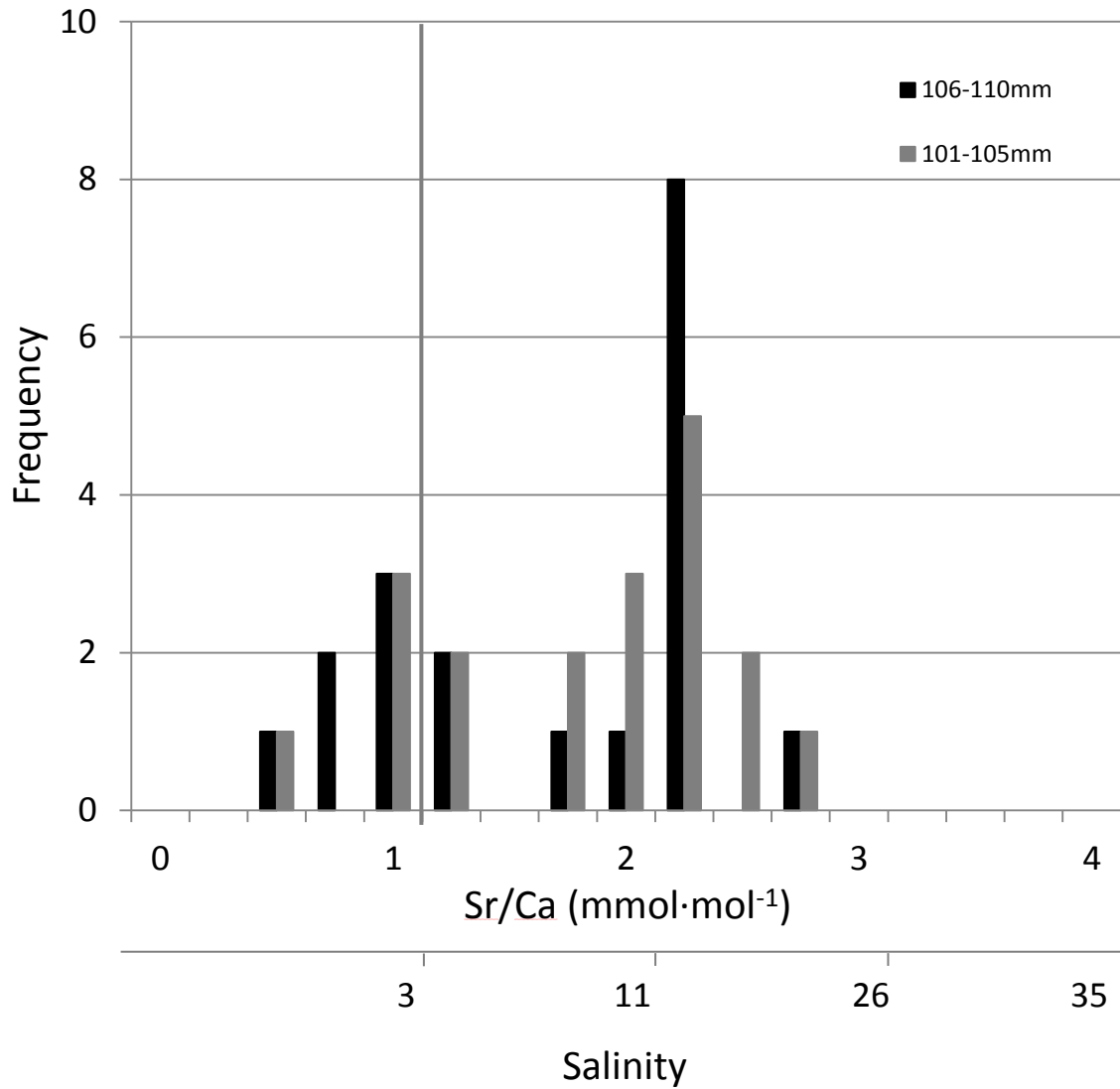


Figure 1.18. Histogram of otolith Sr/Ca over the largest lengths of juvenile striped bass in the late movement period (total lengths 101-110 mm) and corresponding salinity for 2009. The vertical gray line (–) indicates the fresh-brackish water threshold at 1.0 mmol·mol<sup>-1</sup> (salinity of 3).

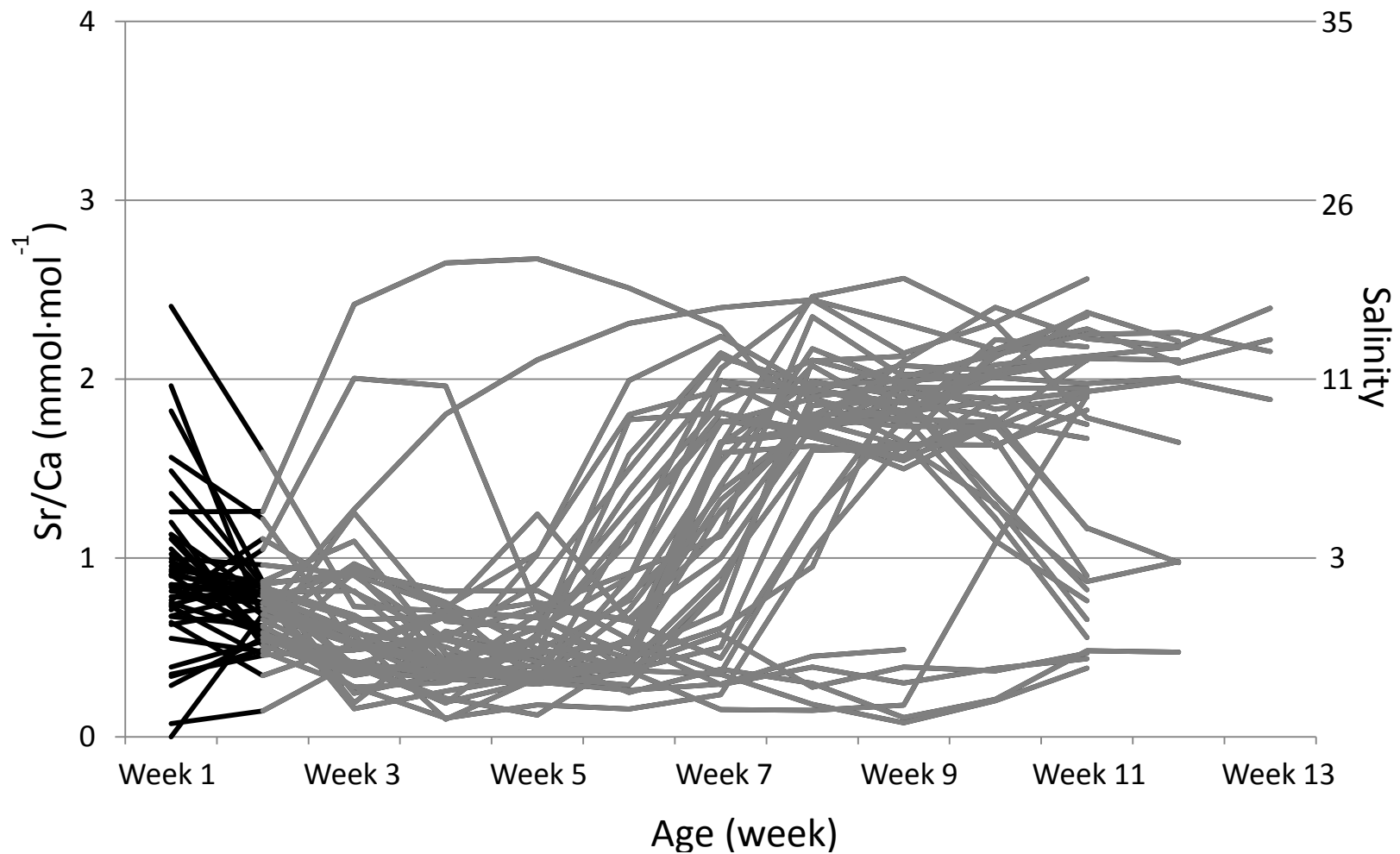


Figure 1.19a. 2009 Sr/Ca profiles by back-calculated total length bins for juvenile striped bass. Sr/Ca during the initial larval period (weeks 1 and 2 post-hatch) is indicated in black (—). Sr/Ca depicted in gray was not included in this analysis.

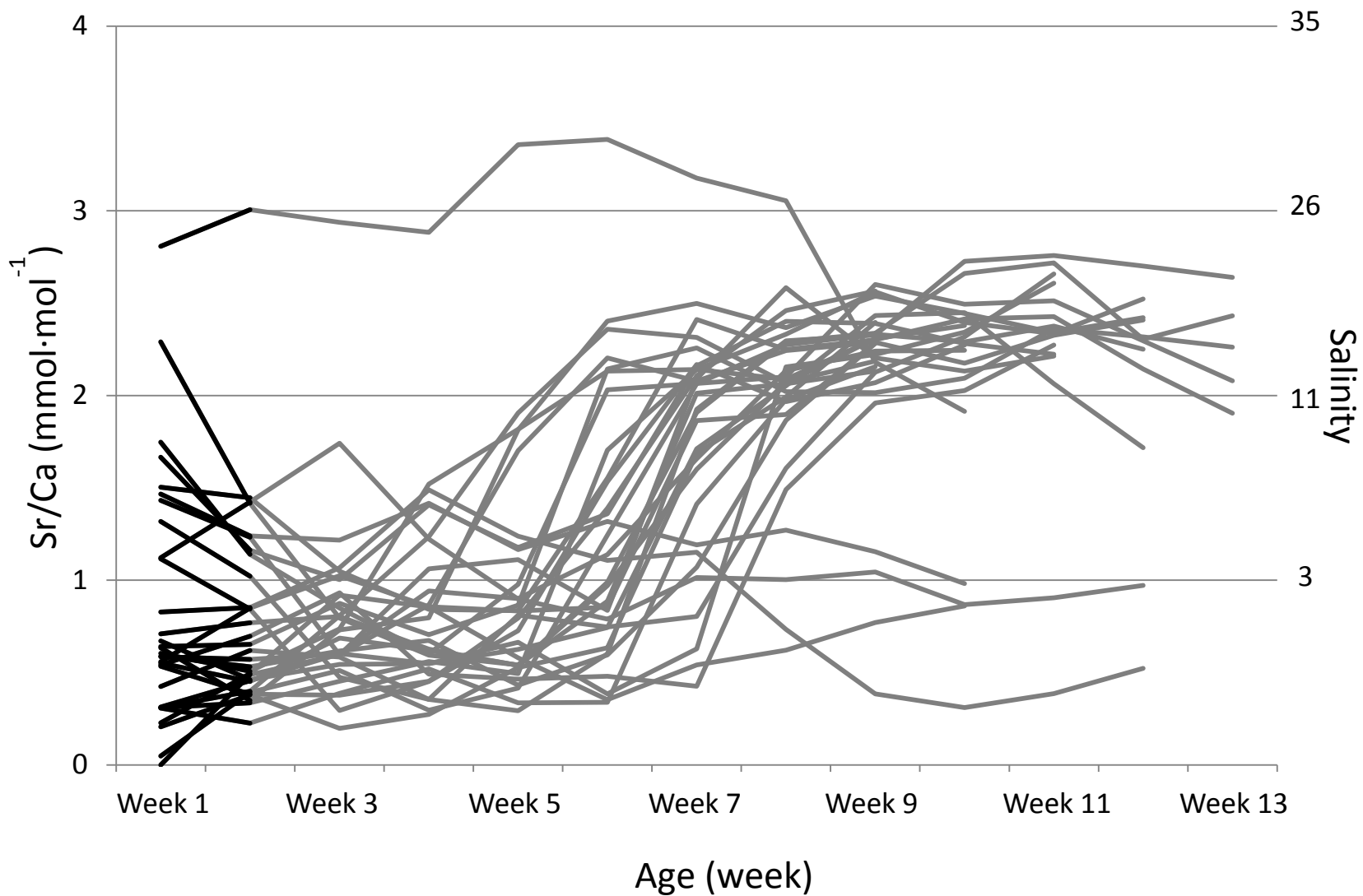


Figure 1.19b. 2010 Sr/Ca profiles by back-calculated total length bins for juvenile striped bass. Sr/Ca during the initial larval period (weeks 1 and 2 post-hatch) is indicated in black (-). Sr/Ca depicted in gray was not included in this analysis.

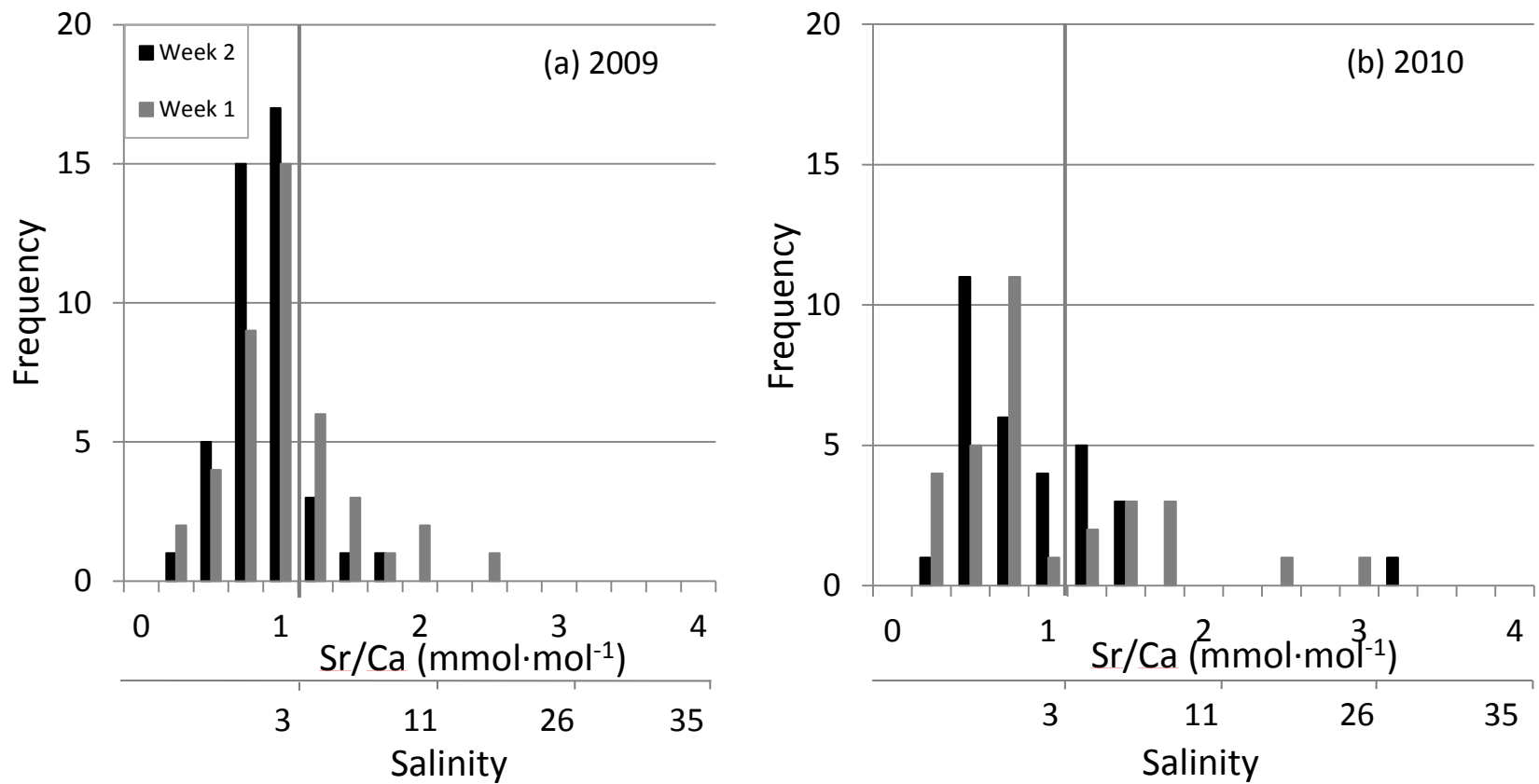


Figure 1.20. Histogram of initial (total lengths 0-5 mm) juvenile striped bass otolith Sr/Ca and corresponding salinity for 2009 (a) and 2010 (b). The vertical gray line (—) indicates the fresh-brackish water threshold at  $1.0 \text{ mmol}\cdot\text{mol}^{-1}$  (salinity of 3).



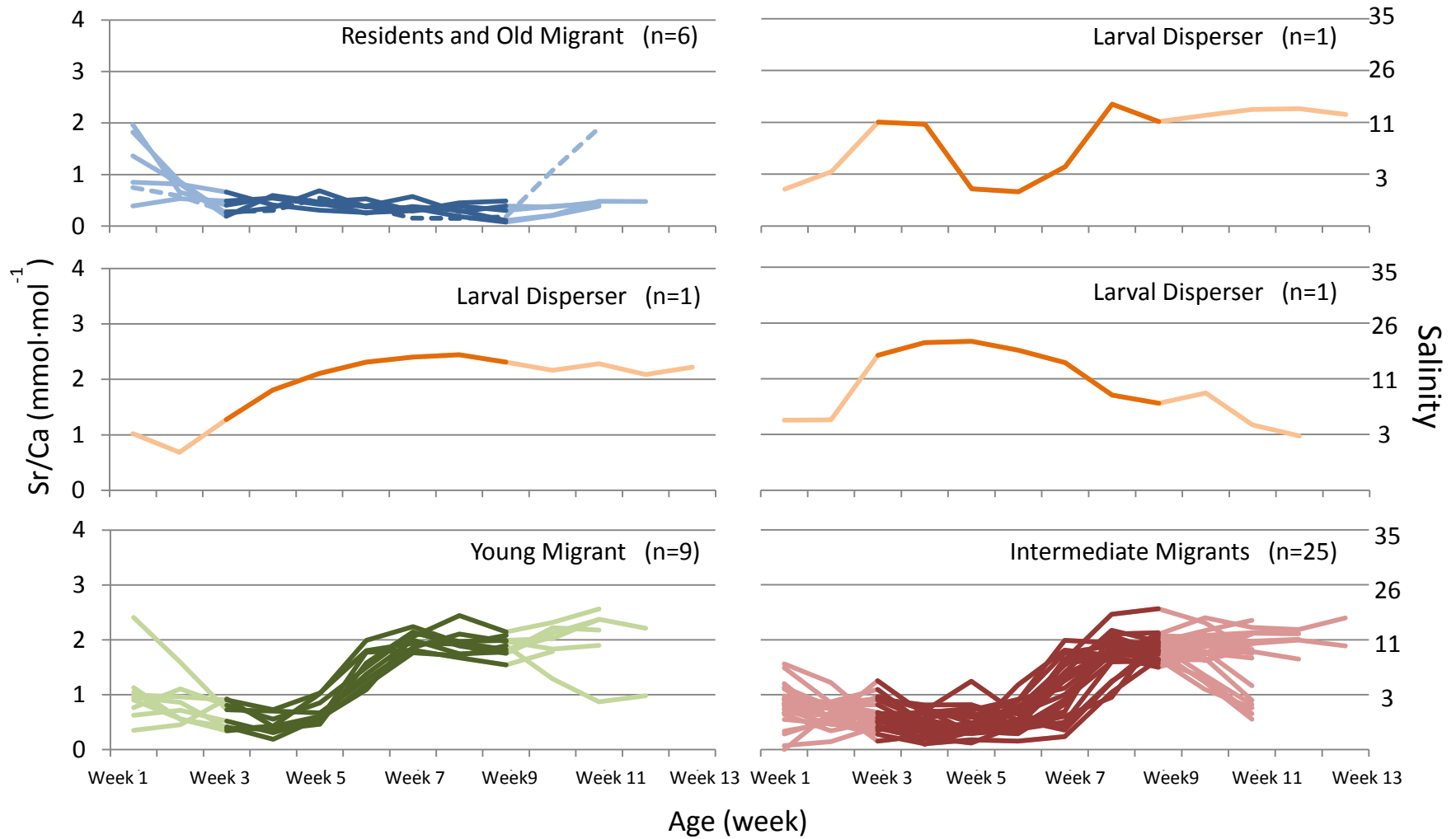


Figure 1.21a. 2009 Sr/Ca profiles by age separated by juvenile striped bass contingent, weeks 3-9 (n=43). Darkly colored sections of the profiles indicate sizes included in the analysis. The dashed blue line (— —) in the Residents & Old Migrants profile plot identifies contingent members that do disperse eventually. The sample size of each contingent is given in the upper right corner of each plot. Contingents identified using PCA/CA analysis.

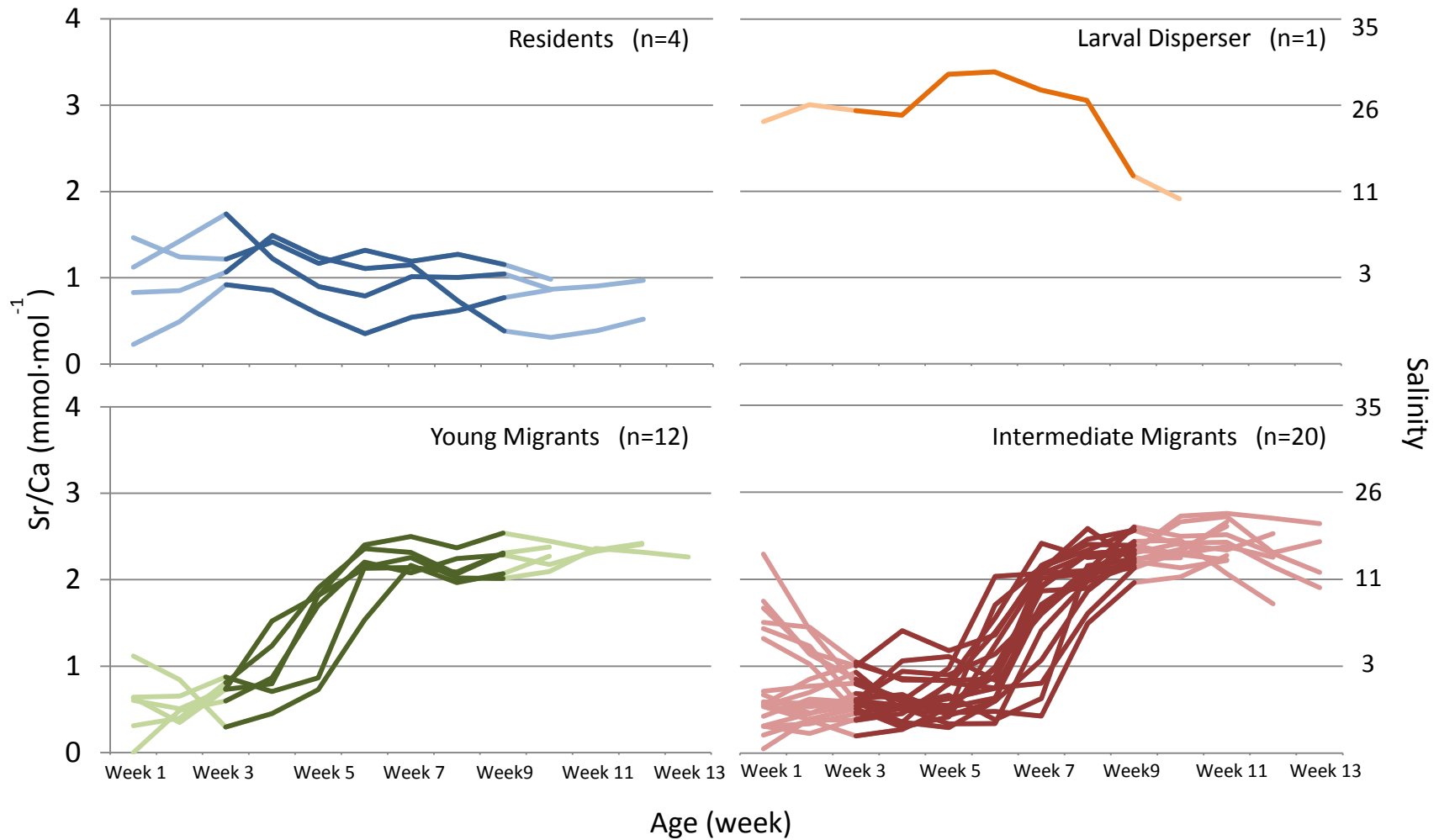


Figure 1.21b. 2010 Sr/Ca profiles by age separated by juvenile striped bass contingent, weeks 3-9 (n=37). Darkly colored sections of the profiles indicate sizes included in the analysis. The sample size of each contingent is given in the upper right corner of each plot. Contingents identified using PCA/CA analysis.

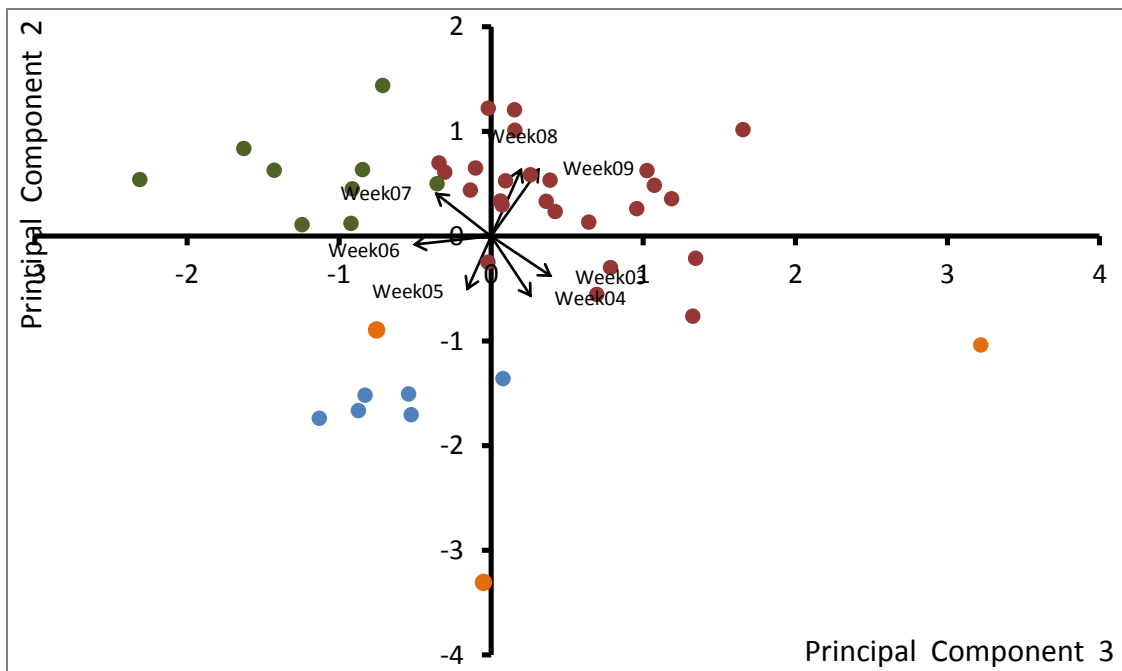
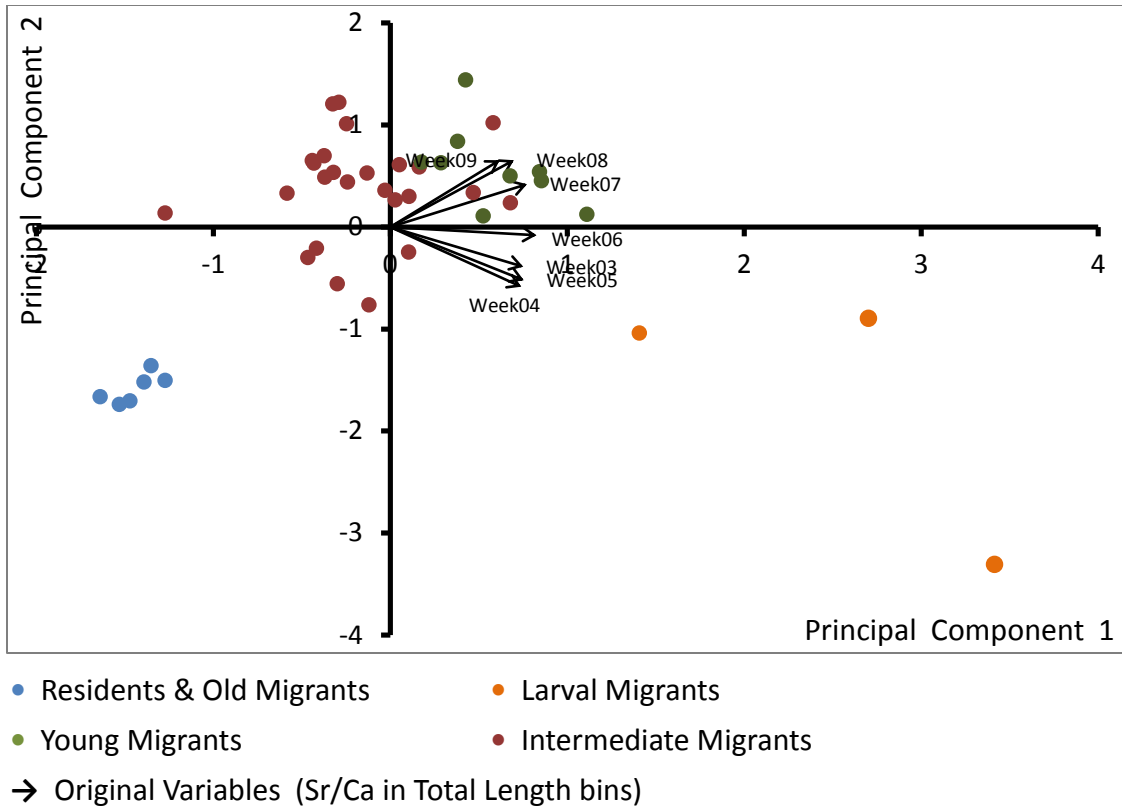


Figure 1.22a. Principal component loading bi-plots of 2009 Sr/Ca by age, weeks 3-9. Individual striped bass YOY contingents color coded as shown elsewhere in profile plots. Arrows (↑) indicate total length bin vectors.

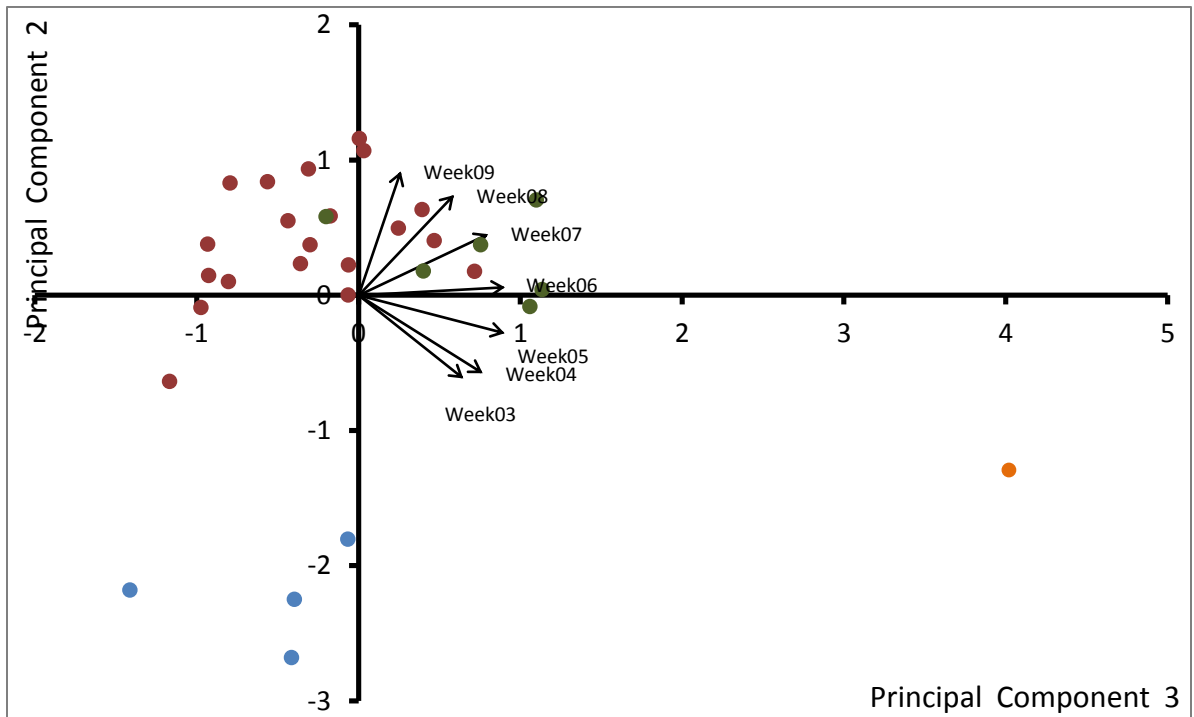
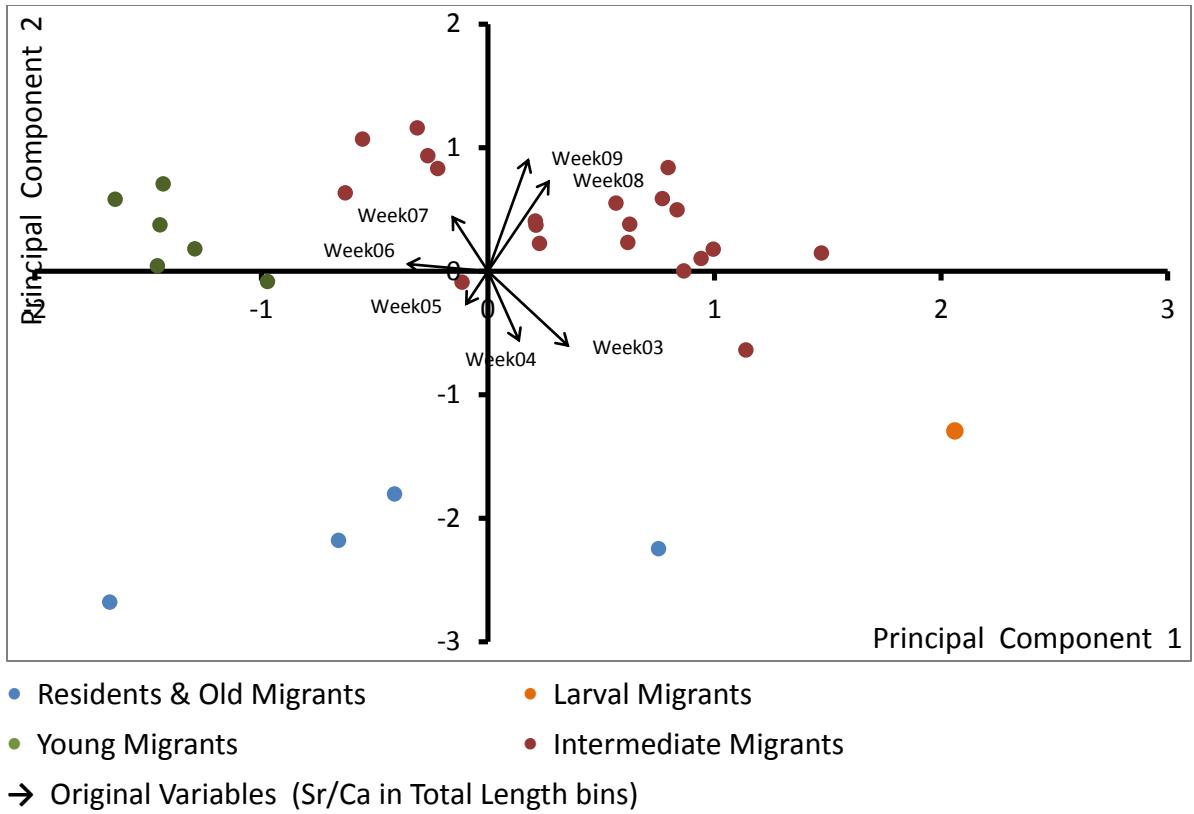


Figure 1.22b. Principal component loading bi-plots of 2010 Sr/Ca by age, weeks 3-9. Individual striped bass YOY contingents color coded as shown elsewhere in profile plots. Arrows (↑) indicate total length bin vectors.

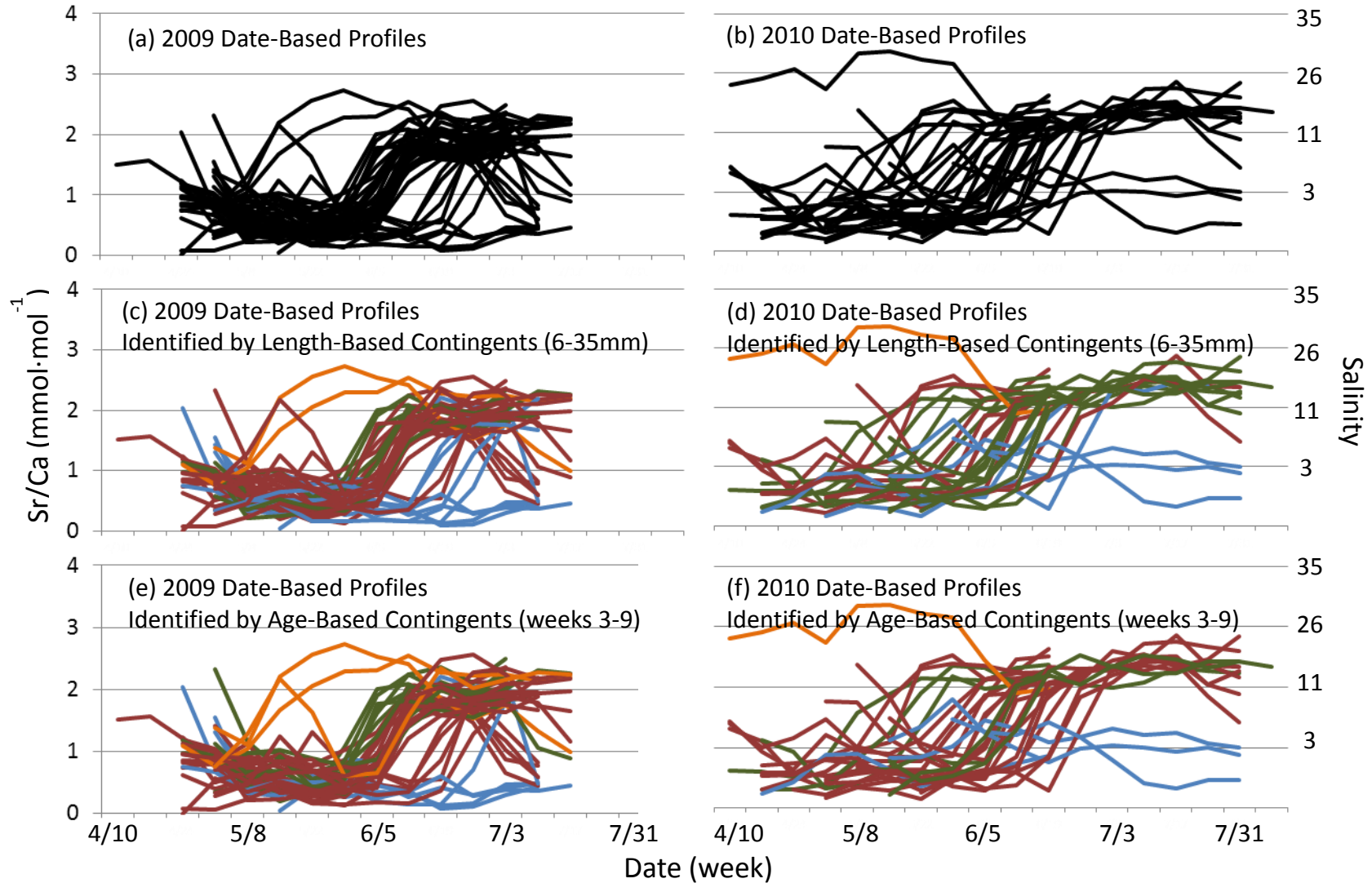


Figure 1.23. 2009 (a,c,e; n=43) and 2010 (b,d,f; n=37) Sr/Ca profiles by date (week). Size- (c,d) and age-based (e,f) contingent memberships are shown on dated profiles for reference. Dates include periods of hatch, early larval residence, and eventual dispersal of all aged juveniles in both years.

## Chapter 2: The proximate causes, apparent consequences, and habitat-independence of partial migration during striped bass ontogeny

### Introduction

#### *Partial Migration*

Migration, the intentional movement of organisms to new locations at some physically removed distance, is a distinct and important behavior for organisms across taxa (Kennedy, 1985). Partial migration occurs where movement decisions are made at the sub-population level, resulting in only some individuals migrating (Lack, 1943). Broad classes of diverse migration behaviors within populations has been generally classified as partial migration (Chapman *et al.*, 2011). Drivers of partial migration include intrapopulation differences in metabolic demands, predator susceptibility, environmental tolerances, available prey suitability, and social competitiveness (i.e. density). As such, partial migration reflects the diversity existing within populations and of their surrounding habitats; but how such diversity affects individual and population fitness remains largely unknown.

Partial migration is likely wide-spread in marine fishes, and often reflected in a diversity of juvenile-stage behaviors (Kerr and Secor, 2011). The development of migrant and resident contingents during the juvenile period is widespread in salmonids and linked to early growth (Jonsson and Jonsson, 1993). The facultative use of estuaries by marine fishes as nurseries and the spatially and temporally variable distribution of young-of-the-year (YOY) among coastal and estuarine habitats suggest that this behavior

may be common for many fishes (Able, 2005). However, based on Kennedy's (1985) succinct definition, in order to be considered migration these movements must be intentional, not passive. Although this definition separates deliberate behavior from passive or random displacements, benefits accrued by individuals and populations may exist regardless of underlying cause. The development of migratory and resident contingents during ontogeny in the estuarine-dependent striped bass *Morone saxatilis* has recently been identified (Chapter 1, this thesis). In order to assess whether or not these observed behaviors represent partial migration, vital rates of striped bass associated with their movements and associated environmental conditions must be considered.

Although a seemingly simple choice- either to migrate or remain resident- the mechanisms that lead to, or influence, a particular "choice" are likely complex and difficult to identify (Chapman *et al.*, 2011). The movement of young fish within and between nursery habitats is likely influenced by the interactions of external forces and inherent qualities. This is known as a "conditional strategy" (Lundberg, 1988), where intrinsic characteristics, such as genetically-determined metabolic rate ranges and maternally-determined hatch dates, interact with extrinsic realities, like seasonal temperature change and forage densities. Separating proximate causes of early movement can be difficult and requires consideration of many factors, both obvious and indirect.

#### *Pre-Dispersal Differences*

Teasing out how the intrinsic attributes of individuals influence movement behavior is difficult but vital to understanding migration (Nathan *et al.*, 2008). Growth and size have been identified as important intrinsic factors influencing migratory

behaviors in young fish. In a land-locked sub-arctic lake, Naslund *et al.* (1993) identified the importance of size in the up-stream migrations of arctic charr *Salvelinus alpinus*, with the largest young fish undertaking migration. The authors suggested that intrinsic factors (chiefly size) were driving migration but found it difficult to separate these from extrinsic influences. Resident white perch *Morone americana* young-of-the-year (YOY) were found to have higher growth rates than their migrant peers prior to dispersal (Kraus and Secor, 2004). Subsequent work by Kerr and Secor (2009) identified increased consumption rates in migrants, which they attributed to compensatory growth. In this case, specific behavioral differences between contingents were identified that coincided with migratory behavior. Forseth *et al.* (1999) discovered that brown trout *Salmo trutta* migration from natal streams to lakes occurred when growth rates exceeded a threshold. Some individuals reached growth and metabolic limits at smaller sizes and earlier ages, prompting them to move to lakes earlier than slower growing peers; thus, growth also has a strong effect on the timing of migration.

Early differences in growth and size are important drivers of differences in migratory behavior and may have important intrinsic components; however, the impact of external conditions plays a large role as well. Nursery conditions in estuaries may vary greatly over days to weeks in temperature, salinity, dissolved oxygen, flow rate, and available forage (Elliott and McLusky, 2002). Indeed, it has been suggested that this environmental variability might select for partial migration (Kerr *et al.*, 2009). Flow rate in particular can have both indirect and direct effects on dispersal. North and Houde (2001) identified high flow with increased retention of larvae and their prey due to hydrographic dynamics and better physical proximity to the preferable habitat of the



estuarine turbidity maximum (ETM), while Davidsen *et al.* (2005) identified high flow rates as favorable to Atlantic salmon *Salmo salar* smolt migration by allowing for directed passive transport and reducing the expenditure of limited energy stores. Other environmental factors may affect local conditions and contribute to highly variable growth and mortality rates during larval periods (Breitburg *et al.*, 1999), ultimately affecting dispersal behavior and the proportion of migrants within populations.

The faster growing resident white perch YOY described above also tend to be hatched at later dates than migrants. Thus, spawning behavior interacted with environmental conditions to introduce varying growth conditions with propensities to produce either resident or migrant juveniles (Kerr *et al.*, 2010). Kerr *et al.* speculated that conditions faced by the later-hatched residents were more conducive to early growth than those faced by earlier-hatched individuals that tended to be migrants. In brown trout, movement behavior was influenced by the availability of high quality prey (Forseth *et al.*, 1999). In these instances, extrinsic circumstances indirectly affected migratory behaviors through their influence on early growth rates. Thus, variable growth conditions were conceived to influence expression of inherent phenotypic plasticity in migratory behavior.

#### *Post-Dispersal Differences*

Regardless of the mechanisms behind partial migration, the experiences of migrants and residents following dispersal often differs. Both white perch and striped bass YOY have been found to have higher physiological condition and experience higher growth following dispersal (Secor *et al.*, 2000; Kerr and Secor, 2009). Differences in the sizes and locations of contingent members can affect feeding ecology in terms of trophic

position and food-web dependencies, and mortality rates may also differ between migrants and residents (Herzka and Holt, 2000; Kraus and Secor, 2004; Litvin and Weinstein, 2004; Chapter 1, this thesis). Changes in the proportion of individuals that migrate and remain resident can have population-wide consequences, exemplified in white perch by Kraus and Secor (2004), who demonstrated that year-class strength was related to the proportion of juveniles that migrated from fresh to brackish water habitats during the first few months post-hatch. Kerr and Secor (2011) later identified differences in this ratio of resident versus migratory contingents between populations of white perch within the Chesapeake Bay.

Just like the intrinsic and extrinsic causes of migration, mechanisms underlying the consequences of migratory behavior are difficult to separate. Although inherent differences between migrants and residents have been identified in the morphological differences in salmonids (Groot *et al.*, 1995), young anadromous fish may also experience better foraging opportunities and higher calorie prey items following migration into brackish water habitats (Boynton *et al.*, 1981; Kerr *et al.*, 2010). Compounding (1) inherent and accrued qualities of migrating individuals and (2) direct environmental influences related to their recently encountered habitats makes the appropriate attribution of migratory consequences difficult. Despite these hurdles, the source of differential growth rates in migrant and resident white perch juveniles was suggested in laboratory experiments, where Kerr and Secor (2009) found that migrant juveniles exhibited an enhanced scope for growth in comparison to resident individuals.

### *Goals and Hypotheses*

In a focused two year field study, we explored possible mechanisms and consequences of partial migration in juvenile striped bass. Our goals were to 1) investigate possible proximate causes of the observed diversity in early estuarine movements and 2) measure apparent consequences in the weeks and months that followed dispersal, and 3) evaluate how principal estuarine habitats (freshwater v. brackish) differed in nursery quality. We anticipated that juvenile partial migration would be triggered by early growth and size differences; specifically, we predicted that resident juveniles, when compared to individuals that would eventually migrate, experienced higher growth rates prior to dispersal. We also thought that the timing of dispersal would follow gradients in early growth, with individuals that dispersed at the smallest sizes experiencing the lowest pre-dispersal growth rates. We held that resident striped bass would have been hatched from later dates than migrants when warmer temperatures favored higher growth rates (Secor and Houde, 1995; Kerr *et al.*, 2010). Following dispersal, we thought that the growth rates and condition of migrants would be higher than those of residents, reflecting the higher quality brackish nursery habitats. These differences in juvenile attributes would result from migrants feeding at higher trophic levels in a largely marine-based food web.

### *Methods*

#### *Study System: The Patuxent River Estuary*

The Patuxent River (MD) is a partially mixed tidal estuary on the western shore of the Chesapeake Bay. The 70 river-kilometer extent of our study area (Fig. 2.1) consists of tidal fresh, oligohaline, and mesohaline habitats (salinity 0-18). The estuary provides

important spawning and nursery habitats for a number of estuarine species, including striped bass (Uphoff, 2008). The estuary has also been the site of extensive studies on the life history and ecology of striped bass (Mansueti, 1958; Dorazio *et al.*, 1991; Secor *et al.*, 1995b). Striped bass spawn above the salt front in freshwater and most newly hatched individuals are retained there until the juvenile period. At this point some individuals remain whereas others depart down-estuary to reside in brackish habitats (Secor *et al.*, 1995b; Robichaud-Leblanc *et al.*, 1998). The transition salinity (3) used to separate resident from migratory contingents is operationally defined by the method deployed (see below), but is geographically stable within and across juvenile production periods (Ritchie and Genys, 1975; Chapter 1, this thesis). A salinity of 3 coincides with important changes in species assemblages and environmental conditions (Wagner, 1995; Campfield, 2004). The early movement behavior of this estuarine species and the strong salinity gradient within this river support striped bass and the Patuxent River as a model species and system for studying the causes and consequences of partial migration.

#### *Contingent Migratory Behavior*

Previous work has established that striped bass YOY occur as migratory and resident contingents during ontogeny (Chapter 1, this thesis). Migratory contingents were structured by the size at which they undertook dispersal, with most individuals leaving freshwater habitats shortly after undergoing metamorphosis to the juvenile stage. As part of this analysis, measurements of otolith strontium and calcium (made along a transect from the primordium to otolith edge) were used to approximate movement histories during ontogeny. Depending on local environmental chemistry, Sr/Ca has been established as an appropriate tracer of estuarine salinity and therefore as a measure of

intra-estuarine movements in many species, including striped bass (Secor *et al.*, 1995a; Secor and Rooker, 2000). Movement profiles of individual striped bass YOY collected during the juvenile period in both 2009 (n=71) and 2010 (n=34) were constructed based on mean Sr/Ca measurements of otolith material corresponding to 5 mm TL growth stanzas; these profiles were then used in subsequent analyses establishing and describing contingent migratory behavior. Over the larval-early YOY period (hatch to 35 mm total length) three separate migratory contingents were identified: larval dispersers (dispersal prior to 5 mm TL), small migrants (mean dispersal 15 mm TL), and intermediate migrants (mean dispersal 20 mm TL). In a secondary analysis that included larger size classes (hatch-50mm), two additional migratory contingents were identified: large migrants (mean dispersal 30 mm TL) and returning migrants (retreated back up-estuary to fresh or near-fresh habitats by 45mm TL). These designations of resident and migratory contingents and dispersal periods are referenced throughout this study.

### *Sample Collection*

We collected striped bass larvae and juveniles from the Patuxent River between April and October of 2009 and 2010. April and May sampling of larvae consisted of stepped-depth bongo net tows to collect striped bass larvae at ~2 km intervals from Jug Bay (river kilometer (*RKM*) 75; i.e., 75 km distance from the mouth of the estuary) to Eagle Harbor (*RKM* 43). Striped bass juveniles were collected between June and October via parallel beach seine; seine surveys occurred over 1 to 3 days and included the sampling of 12 sites located throughout the estuary (Fig 2.1). Striped bass YOY were found at sites throughout the estuary, from tidal fresh (Selby Landing, *RKM* 72) to mesohaline segments (Solomons Beach, *RKM* 5) (Table 1.1). Most samples collected in

both years were preserved in an ice-water slurry, while 5 randomly selected individuals from each site in 2010 were flash-frozen using liquid nitrogen and retained for stable isotope analysis of muscle and liver tissue (n=47).

To evaluate food web dependencies and trophic position using stable isotope analysis, eastern oyster *Crassostrea virginica* was used as a baseline primary consumer species (Fertig *et al.*, 2010; Woodland, 2010). Eastern oyster spat were planted at 9 sites throughout the estuary during late May 2010 (Fig. 2.1). Planted oysters consisted of clutchless spat supplied by the Horn Point Laboratory's Oyster Hatchery program (Cambridge, Maryland). Oysters were placed in 27 mesh cages (3 cages per site, 5-6 oysters per cage), attached to weighted lines, and either secured to existing structures (e.g. dock pilings) or partially submerged with marked floats. Oysters were allowed to equilibrate in the river 118-119 days (May through September 2010) prior to sacrificing. Cages were checked and cleaned on a biweekly basis to ensure their integrity, prevent physical restriction to hinge operation, and clean any fouling. No oysters survived the acclimation period above *RKM* 49. In addition to planted oysters, native Patuxent River adult eastern oysters were collected via dredge from a protected reef located at *RKM* 23 in June.

Stomachs and small sections of epaxial muscle and liver tissue (2010 only) were removed from recently thawed frozen juveniles. Sagittal otoliths were removed, sectioned transversely, set in epoxy, and polished to the primordium for the purposes of assigning contingents (Chapter 1, this thesis), age determination, and back-calculating growth rates. Tissue samples were cleaned of any extraneous tissue, macerated using a scalpel, and rinsed with deionized water. They were then transferred to aluminum drying

trays and dehydrated in a 60°C drying oven for > 48 hours. Dried samples were pulverized in a sterilized and dried mortar using a pestle. Triturated samples were weighed and packaged in tin capsules. All tissue samples underwent stable isotope analysis on a continuous-flow isotope ratio mass spectrometer coupled with an elemental analyzer in the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University. All stable isotope values use the  $\delta$  (“delta”) notation and represent deviations (in molecules per thousand, or “per mil”) in the ratios of isotopes of C ( $^{13}\text{C}:^{12}\text{C}$ ,  $\delta^{13}\text{C}$ ) and N ( $^{15}\text{N}:^{14}\text{N}$ ,  $\delta^{15}\text{N}$ ) from those of international standards Pee Dee Belemnite and ambient air, respectively. Oyster adductor muscle samples were processed and analyzed following the same procedures.

#### *Intrinsic Causes and Influences: Growth*

Ages were determined by counting increments in transverse otolith sections from the primordium to the otolith edge (Fig. 1.4). Microstructural increments have been verified to form at a daily rate in striped bass YOY sagittal otoliths (Secor and Dean, 1989), but the timing of the first increment formation is temperature dependent (Houde and Morin, 1990). We used the original counts as provisional estimates of age; we then subtracted these from dates of collection to estimate provisional hatch dates. We adjusted ages by applying Houde and Morin’s striped bass increment formation temperature correction,

$$age_{TC} = count + 11.56 - (0.45 \cdot T)$$

where  $age_{TC}$  is the temperature-corrected age, *count* is our original count, and  $T$  is the weekly mean surface (mean depth=1.3 m) temperature in Patuxent River spawning habitat (as measured at Jug Bay; MDDNR, 2011) for the estimated hatch date.

Temperature-corrected ages were used in all analyses. Since daily increment formation in striped bass otoliths is limited to the larval and early juvenile periods (Jones and Brothers, 1987; Secor and Dean, 1989), we did not include individuals whose original (i.e., not temperature corrected) counts were >85 increments. We based this threshold on the results of a separate aging effort involving juveniles collected in 2007 and 2009 (n~300 from each year); otoliths of individuals >85 increments produced imprecise age estimates when interpreted independently by two investigators due to narrow and indistinct increments (Fig. 1.5).

Growth rates were estimated utilizing Campana's (1990) biological intercept method; striped bass YOY growth rates were estimated for 5-mm stanzas by substituting length increments (5, 10, 15 mm, etc.) into the rearranged equation,

$$OR_a = OR_i + \frac{(TL_a - TL_c) \cdot (OR_c - OR_i)}{(TL_c - TL_i)}$$

where  $TL_a$  and  $OR_a$  are the total length (mm) and otolith radius at age  $a$ ,  $TL_c$  and  $OR_c$  are the total length and otolith radius at the time of capture, and  $TL_i$  and  $OR_i$  are the total length and otolith radius at the onset of proportionality (biological intercepts – see below).  $TL_a$  for 5 mm, 10 mm, 15 mm, etc. were substituted into the equation to estimate  $OR_a$ , which was then used to visually estimate the age specific to that otolith radius. These ages were then used to estimate 5-mm stanza growth rates. The total otolith radius ( $\mu\text{m}$ ) and radius associated with each size stanza were measured from the primordium to the ventral edge along the ventral transverse axis (Fig. 1.6) using the image processing program ImageJ (Rasband, 1997).

Biological intercepts  $TL_i$  and  $OR_i$  were determined using larvae collected in the Patuxent River estuary via bongo net sampling in April and May of 2009. Sagittal



otoliths (n=46) of these larvae were mounted, their increments enumerated, and radii measured (Fig. 1.7). If the rostrum was apparent, then the longer of the 2 radii perpendicular to the rostrum was measured; if the rostrum was not apparent and the otolith was circular, the longest measured radius was used in the analysis. Temperature-corrected ages ranged from 8 to 31 days after hatch (dah). Because the relationship between otolith radius and total length was found to be linear ( $F=391.34$ ,  $p<0.0001$ ,  $R^2=0.90$ ), we assumed proportionate fish growth began at 8 dah. At 8 dah, larval total length was predicted at 6.08 mm (based on regression of size at age ( $F=202.71$ ,  $p<0.0001$ ,  $R^2=0.82$ ) and otolith radius was predicted at 23.94  $\mu\text{m}$  ( $F=263.91$ ,  $p<0.0001$ ,  $R^2=0.86$ ). The regression of size at age was used to set the theoretical size at age 0 (3.81 mm) for use in estimates of growth immediately following hatch (0-5 mm TL size stanza).

Ages and back-calculated lengths were used in determining growth rates over length stanzas. We used instantaneous growth rates ( $g$ ) to characterize growth during larval and juvenile stages according to the following equation:

$$g = \frac{\ln L_{x+1} - \ln L_x}{t}$$

where  $L_x$  and  $L_{x+1}$  are total lengths separated by 5 mm (apart from initial growth, where total length at age 0 days, 3.81 mm, was used) and  $t$  is the difference between age at total lengths  $L_x$  and  $L_{x+1}$ . Instantaneous growth rates ( $\text{day}^{-1}$ ) were estimated over 5 mm TL intervals from hatch to dispersal and at select sizes following dispersal. These growth estimates were contrasted between contingents via analyses of variance (ANOVA, PROC MIXED; all statistical tests performed in the statistical package SAS version 9.2 (2011) unless otherwise referenced) using least square means comparisons. Comparisons were

made between early, pre-dispersal growth to test for the influence of growth on adoption of contingent behaviors. Increases and decreases in contingent-specific growth over successive length stanzas were similarly identified using least square means comparisons.

*Extrinsic Components: Hatch Date and Environmental Conditions*

Temperature-corrected hatch dates were investigated for their effects on migration both directly and indirectly. Hatch dates in both years were separated into quartiles for testing the effects of early (earliest 25% of dates), average (middle 50%), and late (latest 25%) hatch dates on contingent membership as well as testing for differences in contingent-specific hatch dates between years using  $\chi^2$ -analog Fisher's exact tests (PROC FREQ); small sample sizes limited more resolved comparisons of hatch date influences. The indirect influence of hatch date on migration was evaluated by testing the effects of hatch date quartile on early growth using ANOVA and least square means comparisons (PROC MIXED).

Environmental conditions during dispersal were examined for potential influence on migration. We tested whether flow caused mass displacement of the population. Weekly mean Sr/Ca for each individual was estimated through profile analyses; and the grand sample mean was used as a measure of the center of mass for juveniles each week. Environmental data included episodically and continuously monitored flow rates (USGS, 2011), temperature, dissolved oxygen (DO), and chlorophyll *a* (Chl *a*) concentrations (Chesapeake Bay Program, 2011; MDDNR, 2011). The effect of weekly mean flow rates ( $\text{ft}^3 \cdot \text{s}^{-1}$ ) on the mean sample Sr/Ca was evaluated using autocorrelated regressions (PROC AUTOREG) over the period encompassing dispersal (April 9<sup>th</sup> through August 12<sup>th</sup> in both years). Additionally, we employed a non-parametric Kruskal-Wallis test

(PROC NPAR1WAY) that utilized Wilcoxon rank-sums in order to estimate temporal relatedness between flow rates and weekly mean Sr/Ca levels. Other environmental parameters were visually assessed against estuarine positions of juveniles.

*Consequences of Migration and Differences in Habitat: Growth, Condition, and Feeding Ecology*

Growth, condition, and feeding ecology (trophic position and carbon source) following migration and settlement in either fresh (salinity <3) or brackish habitats (salinity >3) was assessed. Both contingent- and habitat-specific effects were evaluated. Growth consequences over the 5 mm of growth prior to collection (determined through back-calculation, 2009 and 2010) were examined using t-tests (PROC TTEST) under the assumption that this period of life history would best reflect habitat where individuals were sampled.

The condition of juvenile striped bass was examined using both lipid content in sample tissue (2010) and length-adjusted weights (both years). The percentage of lipid found in muscle is highly correlated with the ratio of carbon to nitrogen (C:N) as measured during stable isotope analysis, with this relationship being especially informative in aquatic animals (Post *et al.*, 2007); we used the ratio of C:N as a measure of condition. We compared C:N between contingents and habitats using ANOVA (PROC MIXED) in both years. Due to its highly variable lipid content we did not use C:N measured in liver tissue (Post *et al.*, 2007). We chose an allometric approach as our second method of assessing condition by controlling for length while comparing weights. Based on the distribution of the data, both weight and length underwent a natural log transformation. We then compared weights (ln weight) among contingents, habitats, and

hatch dates quartiles while adjusting for length (ln length) using analysis of co-variance (ANCOVA; PROC MIXED) in both years.

For 2010 samples, we used stable isotope (SI) and diet analysis to investigate the feeding ecology of juveniles following dispersal. Habitat-specific trophic positions (TP), carbon sources (C-sources), and trophic niches were estimated using the results of SI analysis. TP was estimated for both white muscle and liver tissue. The turnover rates of these two types of tissue differ, with turnover of liver tissue occurring ~5 times faster (days to weeks) than white muscle in teleosts (weeks to months) (Buchheister and Latour, 2010). Therefore, the SI signatures of these tissues reflected different time scales in evaluating feeding ecology. We estimated TP using Post et al.'s (2002) equation,

$$TP_{SB} = \frac{(\delta^{15}N_{SB} - \delta^{15}N_{Oy,st})}{\Delta_N} + \lambda$$

where  $TP_{SB}$  is the estimated TP of a striped bass YOY,  $\delta^{15}N_{SB}$  and  $\delta^{15}N_{Oy,st}$  are the isotopic N ratio deviations of a striped bass YOY and the site-specific primary consumer (in this case eastern oyster),  $\Delta_N$  is the per trophic level fractionation of N (generally assumed to be 3.4‰), and  $\lambda$  is the trophic level of the baseline primary consumer ( $\lambda = 2$  for eastern oysters). Tissue- and habitat- specific standard errors of  $TP_{SB}$  were modeled using Vander Zanden and Rasmussen's (2001) Monte Carlo approach. The effects of early migratory behavior on trophic position were tested using ANOVA (PROC MIXED), while the importance of habitat was tested using t-tests (PROC TTEST).

We had planned on using a two-end member mixing model, with initial eastern oyster spat values (prior to deployment) and native Patuxent River adults as the two end members, to determine fully acclimated site-specific baselines. Upon stable isotope analysis, we found that oysters from several of the cages had  $\delta^{15}N$  values outside of

predicted end members of our model; in other words, some of the introduced oysters had become more isotopically enriched than the native adult oysters. The differences in collection time (summer vs. fall) and size and stage (adult vs. spat) between native and introduced oysters indicate that the likeliest explanations for this discrepancy are: 1) the large native Patuxent oysters had grown during a period of relative N depletion within the river and had not experienced sufficient tissue turnover (due to their large size) to reflect recent conditions; and 2) the Patuxent River experiences seasonal variation in  $^{15}\text{N}$  enrichment, with native Patuxent oysters following differing seasonal baselines than the introduced oysters. Although widespread seasonal variation in  $^{13}\text{C}$  enrichment has been identified in estuaries, evidence of similar temporal patterns in  $^{15}\text{N}$  remains mixed (Cifuentes *et al.*, 1988; McClelland *et al.*, 1997; Woodland *et al.*, 2012). For this analysis, we assumed that transplanted oysters had fully equilibrated to local conditions by the early fall as long as they reached a certain relative growth threshold (see below). In order to assess the extent to which introduced oyster spat acclimated to Patuxent River isotopic conditions, we used dimensional measurements (i.e., shell height, width, and depth) made prior to deployment and following collection to estimate growth, employing the conservative oyster dimension-mass models found in literature (see Table 2.1 for a list of models and estimated site-specific growth). We then used Bucheister and Latour's (2010) equation for estimating relative growth required for tissue turnover,

$$G_{\alpha/100} = \exp\left(\frac{\ln\left(1 - \frac{\alpha}{100}\right)}{c}\right)$$

where  $G_{\alpha/100}$  is the relative growth required for  $\alpha/100$  turnover of tissue,  $\alpha/100$  is the selected proportion of tissue turnover. The constant  $c$  is a measure of tissue turnover due

to growth, where  $c = -1$  indicates growth as the sole driver of tissue turnover (i.e., only the addition of new tissue dilutes initial SI signature) and  $c < -1$  indicates some turnover due to metabolism, the proportion of which increases as  $c \ll -1$ . Assuming complete growth-based tissue turnover (i.e.  $c = -1$ ), oysters would have to double in mass ( $G_{\alpha/100} = 100$ ) to ensure 100% tissue turnover ( $\alpha > 99$ ) and complete acclimation. Based on this assumption and estimated growth, all sites with surviving oysters apart from the most upriver site (King's Landing, *RKM* 49) exceeded this growth-based threshold, indicating full-acclimation. Despite less growth at *RKM* 49, very little metabolism-based tissue turnover would be required to assume full acclimation. This threshold turnover constant,  $c = -1.13$  based on the most conservative oyster dimension-mass model, was well within published teleost and invertebrate muscle turnover rates (Fry and Arnold, 1982; Buchheister and Latour, 2010). However, we conservatively rejected the  $\delta^{15}\text{N}$  values at this site. At *RKM* 49 and all other seining sites lacking a local oyster-derived baseline, we substituted the value of the closest accepted site (Fig. 2.1).

We determined habitat-specific C-source using  $\delta^{13}\text{C}$  values of muscle tissue. Since we did not directly measure lipid content or chemically extract fat from sample tissue, we had to account for any depletion effects on  $\delta^{13}\text{C}$  measurements using Post *et al.*'s formula,

$$\Delta\delta^{13}\text{C} = -20.54 + 7.24 \cdot C:N$$

where  $\Delta\delta^{13}\text{C}$  is the adjustment to  $\delta^{13}\text{C}$  due to lipid content and  $C:N$  is the elemental ratio representing tissue lipid content. The  $\delta^{13}\text{C}$  of food web bases (primary producers) were estimated using the equation,

$$\delta^{13}\text{C}_{1^{\circ}} = \delta^{13}\text{C}_{SB} + TP_{SB} \cdot \Delta_C$$

where  $\delta^{13}C_{P^0}$  is the estimated  $\delta^{13}C$  of primary producers,  $\delta^{13}C_{SB}$  is the lipid-adjusted  $\delta^{13}C$  measured for striped bass,  $TP_{SB}$  is the previously estimated trophic position of striped bass juveniles, and  $\Delta_C$  is the per trophic level fractionation of C (assumed to be 0.39‰; Post, 2002). Habitat effects on C source were examined using t-tests (PROC TTEST). We did not use  $\delta^{13}C$  measured in liver tissue due to its highly variable lipid content (Post *et al.*, 2007).

We evaluated differences in feeding ecology characteristics by comparing differences in bivariate SI space between fish collected in fresh and brackish waters. We measured habitat-specific area and dispersion in SI space to characterize differences in the breadth of trophic niche. Differences in niche width were explored using Levene's test for equality of variances of  $\delta^{15}N$  and  $\delta^{13}C$  between habitats (PROC GLM; Bearhop *et al.*, 2004). We constructed convex hulls and estimated their area to describe the SI space occupied by fresh and brackish water fish (i.e., habitat-specific trophic niche); habitat-specific dispersion (i.e., packing within trophic niche) was determined using mean distance to centroid (MCD), mean nearest neighbor distance (MNND), and its standard deviation (SDNND) (Layman *et al.*, 2007; Parnell and Jackson, 2011; R Development Core Team 2011).

Contents of dissected stomachs in 2009 (n=62) and 2010 (n=150) were identified, dried, and weighed. Prey items were categorized into one of 10 diet categories: amphipods, cladocerans, copepods, crabs/shrimp, fish larvae, mysids, polychaetes, unidentified crustaceans, unidentified biomass, and other. We assessed diet choices using percent composition by weight (%W) and by occurrence (%O). We calculated habitat-specific %W and %O for each prey category by year (Hyslop, 1980),

$$\%W = \frac{\sum W_{I,H}}{\sum W_H} \cdot 100\%$$

where  $W_{I,H}$  is the dry weight of prey item  $I$  in all stomachs in habitat  $H$  and  $W_H$  is the dry weight of all prey items in all stomachs in habitat  $H$ ; and,

$$\%O = \frac{\sum N_{I,H}}{\sum N_H} \cdot 100\%$$

where  $N_{I,H}$  is the number all stomachs that contained prey item  $I$  in habitat  $H$  and  $N_H$  is the number of all non-empty stomachs in habitat  $H$ . We tested habitat differences in %W and %O of prey categories in both years using Monte Carlo approximated Fisher's exact tests (PROC FREQ). We judged stomach fullness by using a slightly modified version of the method reported by Hyslop (1980),

$$GF_{SB} = \frac{\sum w_{p,SB}}{(w_{SB} - \sum w_{p,SB})}$$

where  $GF_{SB}$  is the gut fullness of each striped bass YOY  $SB$ ,  $w_{p,SB}$  is the sum of all prey item dry weights in stomach of each striped bass YOY, and  $w_{SB}$  is the dry weight of striped bass YOY  $SB$ . This measure of stomach fullness was compared between habitats using Monte Carlo approximated Fisher's exact tests (PROC FREQ) in both years.

## Results

### *Intrinsic Causes and Influences: Growth*

An overall pattern of declining instantaneous growth was observed from hatch to 35 mm TL (Fig. 2.2; Table 2.2). Early growth for the primary sample (small YOY: hatch to 35 mm TL) influenced contingent membership in both 2009 (n=43,  $F=3.20$ ,  $df=273$ ,  $p=0.02$ ) and 2010 (n=32,  $F=7.07$ ,  $df=196$ ,  $p=0.0002$ ). The resident contingent exhibited higher growth in 2009 than post-larval migrants between 6-10 mm TL; in 2010, initial growth of this contingent was higher than all other contingents just after hatch to 5 mm



TL. Although contingent-specific growth did not differ between years ( $F=1.27$ ,  $df=469$ ,  $p=0.29$ ), growth of the migrant contingents between hatch and 5 mm was higher in 2009 than in 2010; subsequently all contingents experienced decreases in growth between hatch and 10 mm TL in 2009, while migrant contingents in 2010 experienced either little decrease or a small increase in growth over these sizes. The growth rates of residents increased greatly between 16-20 mm TL in 2010; this coincided with a period of either little change or slight rises in growth among migrant contingents. In 2009, only the small migrant contingent experienced enhanced growth over these same sizes.

Among migratory contingents, the relationship between growth rates and dispersal varied. Increase in growth immediately following dispersal was observed for the small migrant contingent (mean dispersal 15 mm TL) in both years, although this change was not significant (Table 2.3). Although intermediate migrants dispersed at slightly larger sizes than small migrants (mean dispersal 20 mm TL), they did not experience post-migration increases in growth. During dispersal both small and intermediate migrant contingents generally saw decreasing growth rates; this was not the case for intermediate migrants in 2010, growth rates for this contingent remained constant through migration. Larval dispersers in 2009 experienced relatively high growth compared to other migrants throughout the early juvenile period, but in 2010 initial growth (i.e. between hatch and 5 mm TL) of this contingent decreased by 33% in 2010 and thereafter remained lower than other contingents.

For the secondary sample that included larger juveniles (50 mm), overall declining growth with size stanza was again observed in both years for 0-35 mm TL stanzas, but thereafter growth rates increased for most contingents (Fig. 2.3). Fewer

statistical differences occurred between contingents (by size stanza) than for the primary sample in 2009 and no significant differences occurred in 2010, perhaps due to a lower sample size (Table 2.4). Including large and returning migrants as part of this secondary analysis resulted in significant effects of migratory behavior on growth in 2009 ( $n=37$ ,  $F=2.64$ ,  $df=307$ ,  $p<0.0001$ ; Table 2.4), but not in 2010 ( $n=23$ ,  $F=1.20$ ,  $df=190$ ,  $p=0.24$ ). Despite limited statistically significant contrasts, common patterns in contingent growth were apparent. In both years, larval dispersers experienced steady increases in late growth. Small and returning migrants in 2009 saw a similar rise in growth following 26 mm TL, but neither of these growth inflections represented significant changes (Table 2.5; in particular returning migrants experienced a 2-fold, significant increase in growth rates over the last c.20 mm period of growth, the largest part of which coincided with return to freshwater habitat (45-50 mm). Growth of large and intermediate migrants remained relatively constant or fluctuated without trend over the largest sizes included in the analysis. Differences between years included the resident contingent, which showed a continued decreasing trend at large sizes ( $>25$  mm) in 2010 but not 2009. The small migrant group was not observed in this secondary sample in 2010; in 2009 size stanzas for this contingent exhibited a cycle of increasing and decreasing growth at stanzas  $> 25$  mm.

#### *Extrinsic Components: Hatch Date and Environmental Conditions*

Hatch dates did not have a significant effect on contingent membership in either year (Fisher's exact test, 2009  $p=0.62$ ; 2010  $p=0.27$ ; Fig. 2.6). Despite this, residents tended to be hatched late in the spawning season, with 38% and 57% of the 2009 and 2010 resident contingent belonging to the latest hatch date quartile. In both years, most

migrants originated from the middle 50% of hatch dates. Small migrants were skewed towards early hatch dates in 2009, when close to half of this contingent belonged to the earliest 25% of hatch dates; but this pattern was not repeated in 2010, when this contingent was more uniformly distributed across hatch date quartiles. The few larval migrants involved in the analysis were hatched during early and late hatch periods.

The timing of hatch had a significant effect on early growth in 2009 ( $F=1.91$ ,  $df=280$ ,  $p=0.03$ ) but not in 2010 ( $F=0.64$ ,  $df=203$ ,  $p=0.53$ ). Juveniles hatched during the latest 25<sup>th</sup> percentile hatch dates grew at significantly greater rates for the stanzas hatch to 5 and 6-10 mm TL (Fig. 2.5a; Table 2.6). Conversely, the early-hatched cohort experienced significantly lower growth than later cohorts at sizes 11-15 mm TL. By 35 mm TL mean growth rates of all cohorts were similar. In 2010, the early-hatched cohort in 2010 also exhibited lower growth during the larval period than other cohorts, but contrasts between stanzas and hatch-date quartiles yielded no significant differences (Fig. 2.5b).

In both years weekly mean population Sr/Ca was related to Patuxent River flow rate (2009, Durbin-Watson  $DW=0.91$ ,  $p<0.0001$ ; 2010,  $DW=1.34$ ,  $p<0.0001$ ). However, the relationship over the weeks of dispersal (April 9<sup>th</sup> through August 12<sup>th</sup>) was actually slightly negative (2009,  $Sr/Ca = -0.0002 \cdot \text{flow rate} + 1.21$ ; 2010,  $Sr/Ca = -0.0027 \cdot \text{flow rate} + 2.11$ ). Despite this negative relationship, a high flow event (mean flow rate  $1455.6 \text{ ft}^3 \cdot \text{s}^{-1}$ ) during the week of June 4 2009 coincided with a major migration event during which > 55% of all individuals included in the analysis dispersed (i.e., surpassed the Sr/Ca threshold value  $1.0 \text{ mmol} \cdot \text{mol}^{-1}$ , analogous to habitat salinity 3; Fig. 2.6). Against the expectation of similar ranks, non-parametric Kruskal-Wallis indicated that weekly

Sr/Ca and flow were ranked dissimilarly in both 2009 ( $\chi^2=169.51$ ,  $df=14$ ,  $p<0.0001$ ) and 2010 ( $\chi^2=121.65$ ,  $df=17$ ,  $p<0.0001$ ). During dispersal no large changes in temperature were observed (Fig. 2.7); however temperature over the first 2 weeks of the time series (April 9 to April 22) was lower in 2009 than in 2010. Shifts in population dispersal were not apparently associated with seasonal changes in dissolved oxygen brackish water habitats (Fig. 2.8; DO: tested by t-test; 2009,  $t=0.98$ ,  $df=10$ ,  $p=0.35$ ; 2010,  $t=0.81$ ,  $df=6$ ,  $p=0.45$ ). Periodically measured chlorophyll *a* concentrations in both years were higher in the area of the salinity threshold (RKM 45) as compared to down-river brackish habitats (RKM 34; Fig. 2.9). Peaks in chlorophyll *a* concentrations occurred in 2009 in early May, 2 weeks following the peak of the hatch date distribution at RKM 45 (C. Conroy, unpubl. data), while the peak in brackish waters (RKM 34) followed 2 weeks after that. In 2010, peak chlorophyll *a* concentrations occurred during July.

#### *Consequences of Migration and Differences in Habitat: Growth, Condition, and Feeding Ecology*

The recent growth index (5 mm of growth prior to collection) in brackish habitats exceeded that in freshwater in 2010 ( $n=32$ ,  $t=3.36$ ,  $df=28.0$ ,  $p<0.01$ ) but not 2009 ( $n=43$ ,  $t=0.84$ ,  $df=41$ ,  $p=0.40$ ; Fig.2.10). Condition indexed as length-adjusted weights (i.e. allometric approach) revealed no significant effects due to habitat (2009:  $n=723$ ,  $F=0.22$ ,  $df=29$ ,  $p=0.65$ ; 2010:  $n=150$ ,  $F=3.24$ ,  $df=26$ ,  $p=0.08$ ), contingent membership (2009:  $n=42$ ,  $F=2.14$ ,  $df=29$ ,  $p=0.12$ ; 2010:  $n=32$ ,  $F=0.44$ ,  $df=26$ ,  $p=0.72$ ), or hatch date (2009:  $n=43$ ,  $F=1.23$ ,  $df=29$ ,  $p=0.0.31$ ; 2010:  $n=32$ ,  $F=0.32$ ,  $df=26$ ,  $p=0.73$ ) in either year. Other measures of condition and trophic status were assessed in 2010, but not in 2009 (see Methods). No significant difference in condition (muscle C:N ratio) was

detected between habitats in this analysis ( $n=47$ ,  $F=0.71$ ,  $df=26$ ,  $p=0.41$ ). Still, C:N measured in juveniles collected in brackish habitats tended to be higher than those in freshwater (Fig. 2.11a). Similar to habitat, hatch date and contingent membership had no significant influence on C:N ( $p>0.1$ ), but a pattern of decreasing condition with increasing hatch date was clearly visible (Fig. 2.11b).

Analysis of juvenile feeding ecology identified differences in the food web attributes of fresh and brackish water inhabitants; however, measures of trophic position and niche breadth did not differ between habitats. Stable-isotope-derived carbon source  $\delta^{13}\text{C}$  values were depleted in freshwater habitats in comparison to brackish water ( $n=47$ ,  $t=5.45$ ,  $df=45$ ,  $p<0.0001$ ; Fig. 2.12). Source  $\delta^{13}\text{C}$  values followed a gradient of salinity (as represented by *RKM*), with depletion increasing as salinity at the site of fish collection decreased ( $n=47$ ,  $F=73.68$ ,  $df=32$ ,  $p<0.0001$ ; Fig. 2.13). Although carbon sources differed between habitats, the trophic position of juveniles did not differ due to habitat as calculated using both white muscle ( $n=47$ ,  $t=-0.23$ ,  $df=45$ ,  $p=0.82$ ) and liver tissue  $\delta^{15}\text{N}$  values ( $n=47$ ,  $t=-0.94$ ,  $df=17.5$ ,  $p=0.36$ ); trophic positions derived from white muscle were further enriched than those from liver tissue (Table 2.5;  $n=47$ ,  $t=-6.97$ ,  $df=92$ ,  $p<0.0001$ ). This similarity in trophic ecology between habitats corresponded to other measures of trophic characteristics; there was no difference in trophic width based on a comparison of habitat-specific variances (Levene's test,  $F=0.30$ ,  $df=45$ ,  $p=0.59$ ). Measures of niche area and trophic packing were similar between habitats, with differences limited to the already described habitat specific  $\delta^{13}\text{C}$  values (C sources) (Fig. 2.14; Table 2.7).

Stomach content analysis revealed habitat differences in both years. As measured by weight, fish larvae dominated all diets apart from juveniles collected in brackish water in 2010 (n=150), accounting for between 46% and 86% of prey item dry weight (Fig. 2.15a). In 2009 (n=62), striped bass YOY preyed mostly on Atlantic silversides *Menidia menidia*, Atlantic menhaden *Brevoortia tyrannus*, as well as alosines *Alosa spp.* in freshwater; while these remained important for juveniles in brackish water, prey species expanded to include anchovy *Anchoa spp.*, skillettfish *Gobiesox strumosus*, as well as unidentified sciaenids. Crabs, shrimp, and other crustaceans were other important contributors to brackish water diets, but were largely absent from freshwater diets. While freshwater diets in 2010 were again mostly composed of fish larvae, brackish water prey items by weight in 2010 were primarily crustaceans (89%), with mysids making up most of this proportion (22% of total diet weight). Amphipods were an important component of diets in 2010, but were largely absent from 2009 stomachs. When measured by occurrence, fish larvae remained important to juveniles collected in freshwater in 2009 (30%), but receded somewhat for 2010 and brackish habitat in 2009 (Fig. 2.15b). Brackish water diets in 2009 were well-balanced among fish larva, amphipods, and mysids. As measured by occurrence, 2010 diets were dominated by amphipods, with copepods playing an important role in freshwater. Based on measures of percent composition by weight (%W) and occurrence (%O), juveniles inhabiting freshwater depended on fish much more than those in brackish water; in both years juveniles in brackish habitats had more balanced diets, relying more on non-teleost prey than their freshwater counterparts. Diets differed significantly between habitats in both 2009 and 2010 (Monte Carlo-simulated Fisher's exact tests all resulted in  $p < 0.0001$ ). Gut fullness

did not differ between fresh and brackish habitats in 2009 ( $n=62$ ,  $t=0.50$ ,  $df=188$ ,  $p=0.62$ ); however, in 2010 freshwater juveniles had fuller stomachs than brackish juveniles ( $n=150$ ,  $t=-3.42$ ,  $df=188$ ,  $p=0.0008$ ).

### Discussion

Juvenile striped bass in the Patuxent River displayed a range of ontogenetic growth patterns that corresponded to varying extents with their spatial behaviors—possibly related to the varied habitats they occupied and traversed. Differing early growth rates between juveniles destined to adopt either resident or migratory behaviors, suggested that juvenile dispersal was a deliberate behavior, rather than a passive or random behavior based on an environmental event or fish density. Following dispersal, a few differences in growth rates between certain migratory contingents suggested some carryover effects, but overall differences were not detected, were negligible, and /or dampened towards the end of the juveniles' first growth season. A notable exception was juveniles that dispersed and returned to freshwater habitats; the return dispersal coincided with a substantial rise in growth rate. The principal classes of habitats to which juveniles arrived, freshwater and brackish water, showed only moderate differences in recent growth rate and no detectable differences in condition indices. Still trophic dependencies varied substantially between these habitats.

### *Otolith Deposition and Fish Growth Assumptions*

The relatively narrow range of sizes over which dispersal occurred in this study, provided a feasible means in which to define pre- and post-dispersal growth rates. The transition from fresh (as indicated by low Sr/Ca values) to brackish habitats (high Sr/Ca values) occurred over small ranges in size in both years, with most dispersals occurring

within a single 5 mm TL stanza (Chapter 1, this thesis). Such abrupt change in terms of length allowed us to clearly separate the portions of life history spent in each habitat for each contingent, which sets up clear comparisons for habitat-specific periods of growth. As long as our estimates of age and size were robust, the relationships between growth, migratory behaviors, and habitat effects were sound. In order to estimate past sizes and ages, several assumptions had to be made, most of which pertain to the relative growth rates between fish length and otolith size.

Otolith physiology in striped bass YOY has been studied extensively both in the laboratory and in the field (Jones and Brothers, 1987; Secor and Dean, 1989; 1992; Secor *et al.*, 1995b). The consistent formation of daily increments from an early age allows for the accurate aging of fish, particularly in that deposition rates are robust to periods of varying foraging conditions and growth (Jones and Brothers, 1987; Secor and Dean, 1992). Temperature influences when the first daily increment forms (Houde and Morin, 1990), but our ages were adjusted for this effect. Temperature and past growth histories have been shown to influence the allometry of otolith size to fish size (Mosegaard *et al.*, 1988; Secor and Dean, 1992) but the Biological Intercept Method developed by Campana (1990), used in here in our study, largely compensates for these biases. Finally, otolith growth is expected to be less variable and lag several days behind fish growth. For these reasons we used 5 mm size stanzas that incorporated at least several days of somatic growth. No known age individuals were available from either 2009 or 2010 Patuxent River year classes for validating increment interpretations. However, we were confident in our estimates of age based on the procedures followed during increment counts. Finally, the nature of the contingents identified in the profile analysis resulted in small



memberships of some groups, reducing the power of group contrasts. In binomial and multinomial contrasts, sample sizes >100 are generally preferred particularly as membership ratios decline below 20%. Additionally sampling error (e.g., inclusion of anomalous behaviors) increases at small sample size. For these reasons, our ability to detect robust seasonal and yearly changes in contingent membership was curtailed.

#### *Proximate Causes of Partial Migration*

Results supported the premise that partial migration – adoption of resident and migratory behaviors – is conditional, dependent on early growth, but also is influenced directly to some degree by extrinsic, environmental factors (Chapman *et al.*, 2011). The view that partial migration is conditional holds that different behaviors expressed within populations can arise due to individual ontogenetic trajectories that vary in condition, growth, and other traits. Thresholds that translate these trajectories into discrete spatial behaviors can confer local fitness increases to resulting contingents, or alternatively can be thought of as compensating for early trajectories of poor conditions and growth (Chapman *et al.*, 2011). Conditional partial migration in which resident behavior is linked to high pre-dispersal growth rates has been observed in congeneric white perch and other freshwater and coastal species (Forseth *et al.*, 1999; Bujold *et al.*, 2004; Kraus and Secor, 2004). Significant differences in pre-dispersal growth rates observed suggest that this conditional strategy is at work in maintaining the diversity of early striped bass migratory behaviors.

Early growth differed substantially between juveniles classified by their eventual contingent membership. Juveniles that remained resident experienced higher rates of growth over small size stanzas either immediately following hatch (2010, Fig. 2.2b) or

prior to reaching 10 mm TL (2009, Fig. 2.2a) when compared against juveniles that eventually migrated. That these higher growth rates occurred in both years of our study suggests that this is a common difference between contingents arising prior to the onset of migratory behavior. Interesting here for striped bass is the observation that pre-dispersal growth differences not only occurred for the coarse classes of contingents – resident v. migratory groups, but also occurred among migratory groups identified as small, intermediate, and large migrants, with large migrants experiencing higher pre-dispersal growth than intermediate migrants, who in turn experienced higher rates compared to small migrants (Fig. 2.3). The direction of these effects – higher pre-dispersal growth in smaller migrants v. larger migrants supports the inference that degrees of residency are favored by higher growth rates. Admittedly, these relationships were often subtle and not ubiquitous. Never-the-less across contingents it was clear that early growth had a large influence on the decision of whether to remain resident or migrate and, if so, when. This could suggest that dispersal in this partial migration system is not caused by a single threshold but a continuum of dispersal responses based on early larval and juvenile growth rates.

Increasing temperature and changing forage conditions during the spawning season should result in coincident increases in pre-dispersal growth rates during larval and early juvenile periods (Rutherford and Houde, 1995; Secor and Houde, 1995). For instance, Kerr and Secor (2010) concluded that later hatch dates tended to coincide with favorable conditions for early growth in the Patuxent River, leading to the enhanced growth of later hatched cohorts of white perch. Peaks in important larval prey items such as *Bosmina* spp. often occur in the river in May (Campfield, 2004), coinciding with latter

portions of the hatch date distribution. In concordance with this expectation, late hatched juveniles experienced greater early growth immediately following hatch in 2009 and possibly in 2010 as well, when compared to those hatched on earlier dates. But the influence of hatch date on contingent membership was not obvious. Residents tended to be hatched on later dates (>75<sup>th</sup> percentile), accounting for 25% and 44% of all late hatched juveniles in 2009 and 2010, but statistical significance could not be attached to this association.

The timing of hatch results in different early conditions for recently hatched larvae. Temperatures can change quite rapidly through meteorological forcing in the relatively shallow spawning habitats of the Patuxent River estuary. Secor and Houde (1995) identified mean temperatures below 15 C and above 20 C during the first month of life as leading to higher mortality than those within this range. In this study, the earliest hatch date quartile cohort faced weekly mean temperatures as low as 12.0 C in 2009 and 15.4 C in 2010, with lowest recorded temperatures falling to 10 C and 13 C in each year, respectively. Mean temperature during the earliest quartile of hatch dates was 13.8 C in 2009, possibly resulting in increased mortality and stress that could affect early growth for members of this early hatched cohort. Mean temperature over this same quartile period in 2010 was warmer, 16.8 C. Although temperatures differences day to day occasionally exceeded 5 C, weekly mean temperatures were fairly stable throughout the hatching and subsequent larval periods of both years in both years (Fig. 2.7).

Flow may serve as a secondary trigger for dispersal in partial migration systems. A large flow event coincided with many of the dispersals in 2009 (Fig. 2.6). Although the frequency of contingent membership did not differ between years, the timing of

migration did, with 55% of a sub-sample of aged migrants dispersing during the week of the large flow event. If flow were the principal driver of dispersal across contingents, one would predict a narrow distribution of hatch dates for each contingent, with large and intermediate migrant dispersers having earlier hatch dates than small migrants. This was clearly not observed (Fig. 2.4), indicating that contingent structuring was not exclusively dependent on this flow event in 2009. Most of the individuals that did disperse during the previously discussed high flow event in 2009 were members of the intermediate migrant contingent and were between 15 and 30 mm TL. Striped bass YOY are capable of sustained swimming speeds of  $3-4 \text{ BL}\cdot\text{s}^{-1}$  once they reach 10 mm TL (Meng, 1993), which should allow them to actively swim 2-8 km per day. Thus, complete passive transport of YOY between 10 and 25 mm TL seems unlikely. A form of directed passive transport has been identified in Atlantic salmon (Davidsen *et al.*, 2005); salmon fry take advantage of high flow conditions to accomplish physical transport with minimal energetic waste. The large number of migrants in a short period of time may indicate similar opportunistic use of flow events. Under this scenario, striped bass that pass a migration threshold could be prompted to disperse under certain flow conditions; and during a high flow event, a large proportion of juveniles experience the same high flow conditions, resulting in mass migration. Note that despite the large flow event, a certain fraction of juveniles remained resident and the same general classes of migratory contingent behaviors was observed in 2010 absent a large flow event.

Ultimately, migratory behavior is likely influenced by both intrinsic and extrinsic factors. There may be other components of migration that were not tested here, including intra-population interactions such as competition for food or habitat (cohort density),

behavioral interactions leading to adoption of migration behaviors, and possible sub-population genetic structure leading to heritable migratory tendencies. For instance, the identification of larval dispersers and their widely varying early growth rates and hatch dates seems to suggest that this phenomenon was not the result of pre-dispersal growth and an associated threshold. Rather, these individuals may be among the few survivors of striped bass larvae advected down-river. If this is the case, their contingent likely faced high mortality in occupied brackish habitats. For instance, releases of  $>10^5$  hatchery produced striped bass larvae in brackish water resulted in no recaptures, despite subsequent recapture of larvae released above the salt front (Secor *et al.* 1995a). In past ichthyoplankton surveys of the Patuxent River, capture of wild striped bass larvae below the salt front are very rare ( $<1\%$  of samples) (Secor *et al.*, 1995b). However, in the Upper Bay (Chesapeake Bay) larvae are more frequently observed in brackish water. For instance, Shideler (2011) found 55% of feeding stage larvae below the salt front. The incidence of dispersed larvae surviving to the YOY juvenile period was unexpected, but noteworthy as it occurred in both years of the study.

Despite the potential role played by other factors such as flow, evidence points towards partial migration being largely dependent on early growth, which in turn is affected by environmental conditions and the timing of hatch. However, in contrast to the congeneric white perch, the timing of dispersal was highly variable and dependent on local conditions. This would suggest that striped bass employ a conditional strategy, where environmentally-influenced early growth triggers migratory behaviors, which are ultimately influenced by the interplay of vital rates and local conditions such as temperature and flow. Based simply on pre-migratory growth rates and presumed higher

survival in the natal habitat, one might speculate that later hatch dates and residence would be favorable strategies for striped bass YOY. However, in terms of juvenile production, the pre-dispersal period of striped bass YOY is only half of the story. Important changes in vital rates also accompanied migratory behaviors after their initial dispersal.

#### *Consequences of Partial Migration and Habitat Differences*

The early benefits of high growth experienced by residents did not persist past the period of initial dispersal (Fig. 2.2; 2.3). Rather, improved post-dispersal growth was observed for some, but not all migratory contingents. This would seem to align with the expectation that brackish habitats provide better conditions for juvenile growth than freshwater due to factors such as osmotically favorable salinity conditions and available forage (Boynton *et al.*, 1981; Secor *et al.*, 2000). In this study we observed that recent growth rates of juvenile striped bass collected from brackish water habitats was greater than those from freshwater in both years, albeit no significant difference was detected in 2009. The connection between hatch date and migratory behavior may have led to a small gradient in decreasing lipid content with hatch date, identified in the directed analysis in 2010. Despite these hints of a carryover effect of contingent membership on later growth and condition, these effects were apparently swamped by the more immediate influences of habitat occurrence.

The pre- and post-dispersal growth dynamics of the small migrant contingent gave some evidence of compensatory growth, where poor freshwater growth led to early dispersal and accelerated growth in brackish water. Such a connection between migration and growth compensation has been made in the congeneric white perch (Kerr

*et al.*, 2010). The lack of accelerated growth following migration in intermediate and large migrants could indicate a relatively low scope for growth due to higher pre-dispersal growth rates. Compensation generally follows a period of low growth, usually due to some nutritional limitation (Metcalf and Monaghan, 2001). This could also explain the marked increases in the growth of returning migrants upon reinvasion of freshwater, possibly occupying areas that experienced reductions in density due to mortality and migration. In the case of these migrants as well as larval dispersers in both years, rapid increases in growth occurred late during their first growth season.

Partial migration should only persist where individuals expressing different behaviors experience fitness advantages based on their specific physiological or behavioral status (Chapman *et al.*, 2011). In the case of striped bass YOY, both residence and migration behaviors should offer specific benefits, which we sought to test through trophic comparisons. In chapter 1, we demonstrated stable differences in the salinity structure of the Patuxent River estuary, over which larvae and juvenile striped bass disperse across a relatively narrow salinity range. An important functional attribute of freshwater and brackish habitats are differences in their food web structure and availability of appropriate prey. Freshwater represented a combination of aquatic and terrestrial production as well as emergent vegetation (Fig 2.12; 2.13; Michener and Lajtha, 2007); as expected, the brackish water food web had a strong marine signal. Despite these differences in carbon source and previous evidence that striped bass diets differed between brackish and freshwater (Boynton *et al.*, 1981), trophic position did not differ between habitats in our study. Indeed, based on direct diet analysis, freshwater inhabitants fed more often on high energy, high trophic level fish larvae than their

brackish water counterparts (Fig. 2.15). The failure to detect a difference in trophic position between habitats might be related to the turnover rate of  $\delta^{15}\text{N}$  in fish tissue. However turnover would likely affect carbon as well as, and  $\delta^{13}\text{C}$  showed strong differences between habitat (Fig. 2.12; 2.13). The similar trophic breadths and feeding success of juveniles collected in both habitats (Table 2.5) suggest similar opportunities for generalist predators in both habitats regardless of the direct evidence of stomach contents, which may have been too limited in how it represented summer-time diets. Based on diet and trophic measures, it would appear that brackish habitats did not offer obvious opportunities for improved growth. However, the increased post-migration growth of contingents that experienced the poorest pre-migration growth suggests subtle fitness advantages that are dependent on the states of individuals, perhaps following a gradient related to size-at-dispersal.

#### *Larger Implications and Future Work*

The realized early benefit (enhanced growth) of some migrant contingents, but small differences in feeding ecology between habitats suggests that the post-dispersal habitat differences may not always drive early dispersal decisions. Rather, migration may mostly benefit those that are experiencing poor growth in the natal habitat. Benefits to small migrants following migration were clear. Similarly, growth was accelerated for returning migrants that reinvaded freshwater. In both these instances, partial migration may be “making the best of a bad situation” (Chapman *et al.*, 2011). Larger migrants experienced no obvious benefits of moving into brackish habitats, but were part of a gradient of delayed dispersal related to higher growth rates in the natal habitat. Such gradients in growth may reveal important differences between striped bass and white



perch YOY. Migrant white perch YOY experienced increases in rates of growth following dispersal and also tended to occupy those non-natal habitats consistently throughout their adult lives (Kerr *et al.*, 2009). The less obvious differences in pre- and post-dispersal growth rates by juvenile striped bass could result in less consistent separation of contingents during the later juvenile period. Indeed, most striped bass YOY (n=26 of 27 total) collected in October 2009 were found to have dispersed at some point prior to collection, including those collected in the freshwater reaches of the estuary (Chapter 1, this thesis). Low growth may be an impetus for movement throughout the juvenile phase.

The connections between migration and early growth that influences migratory behaviors may have effects that continue into fully recruited adult striped bass. Kerr *et al.* (2011) investigated the early migratory behaviors of white perch throughout a number of Chesapeake Bay estuaries and found differing contingent patterns based on local conditions. The interplay between early environmental conditions in certain estuaries, cohort-specific growth, and migratory behaviors may be estuary-specific. Due their more limited lifetime migration behaviors, identifying the natal estuaries of fully recruited white perch is straightforward when compared to the highly migratory striped bass. Secor and Piccoli (2007) found that upwards of 50% of males and 75% of females sampled in the Chesapeake Bay (Maryland) undertook ocean migrations. However, given the anadromous origins of both white perch and striped bass (Williams *et al.*, 2012), the expression of migratory tendencies of adults may have a similar basis in early growth. Examining adult otoliths for evidence of migrations and growth rates during the first year of life may offer important insight into the how partial migration influences

overall population dynamics. As estuaries change due to the influences of climate change and continued human growth, freshwater and brackish habitats in natal nurseries will be greatly but differentially influenced. Establishing carryover effects between juvenile contingent behaviors and adult abundances and migration behaviors will be important in understanding the influence that shifting estuaries to striped bass and other estuarine dependent species.

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Tables

Site	RKM	Mean Site Parameters			Mean Site Growth			% Increase in Dry Weight			
		Shell Depth (mm)	Shell Length (mm)	Shell Width (mm)	Shell Depth (mm)	Shell Length (mm)	Shell Width (mm)	Model 1	Model 2	Model 3	Model 4
CBL Pier	3	18.69	53.44	44.25	8.18	22.10	19.61	262%	426%	177%	939%
Broome's Island	18	18.70	53.94	42.77	8.19	22.60	18.13	270%	441%	182%	905%
SeaBreeze Restaurant	23	20.01	57.44	44.23	9.50	26.10	19.59	331%	558%	218%	1043%
Eagle Harbor	43	20.25	54.26	44.92	9.74	22.92	20.28	275%	451%	185%	982%
King's Landing	49	13.64	39.98	30.69	3.13	8.64	6.05	80%	113%	59%	268%

Model	Source	Location	Model
1	Harding et al. 2007	Chesapeake Bay	$\log DW = 2.41 \cdot \log SH - 4.32$
2	Harding et al. 2007	Chesapeake Bay	$\log DW = 3.11 \cdot \log SH - 5.62$
3	Drexler 2011	Tampa Bay, FL	$DW = 3.0 \cdot 10^{-4} \cdot SH^{1.9072}$
4	Newcombe 1950	York River, VA	$DW = 4.422 \cdot 10^{-4} \cdot SL \cdot SW - 0.2665$

*DW* tissue dry weight (g)  
*SH* shell height (mm)  
*SL* shell length (mm)  
*SW* shell width (mm)

Table 2.1. Oyster growth as determined by published oyster shell size-to-oyster mass relationships. (a) Site-specific measurements and growth in 3 oyster shell dimensions and percent increase in translated dry mass during equilibration in the Patuxent River. (b) Size-to-mass relationships as well as their published sources and study locations.

	Total Length Stanzas	Larval Dispersers						Small Migrants						Intermediate Migrants								
		0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm	0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm	0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm
Residents	0 - 5 mm	ns						ns						ns								
	6 - 10 mm		ns						←						←							
	11 - 15 mm			ns						ns						ns						
	16 - 20 mm				ns						ns						ns					
	21 - 25 mm					ns						ns						ns				
	26 - 30 mm						ns						ns							ns		
	31 - 35 mm							ns						ns								ns
Larval Dispersers	0 - 5 mm							ns						ns								
	6 - 10 mm								ns						ns							
	11 - 15 mm									ns						ns						
	16 - 20 mm										ns						ns					
	21 - 25 mm											ns						ns				
	26 - 30 mm												ns							ns		
	31 - 35 mm													ns								ns
Small Migrants	0 - 5 mm													ns								
	6 - 10 mm														ns							
	11 - 15 mm															ns						
	16 - 20 mm																ns					
	21 - 25 mm																	ns				
	26 - 30 mm																		ns			
	31 - 35 mm																				ns	

Table 2.2a. Differences in instantaneous growth ( $g$ ) between contingents in 2009 for the primary sample of juvenile striped bass (0-35 mm).  $g$  has been determined over 5 mm stanzas. Arrows ( $\uparrow/\leftarrow$ ) indicate significant differences and point to the contingent with the higher growth rate ; “ $ns$ ” indicates not significant. Tests performed using least square means comparisons ( $\alpha=0.05$ ).

	Total Length Stanzas	Larval Dispersers							Small Migrants							Intermediate Migrants									
		0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm	0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm	0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm			
Residents	0 - 5 mm	←							←																
	6 - 10 mm		ns							ns															
	11 - 15 mm			ns							ns														
	16 - 20 mm				ns							←							←						
	21 - 25 mm					ns							ns							ns					
	26 - 30 mm						ns							ns							ns				
	31 - 35 mm							ns							ns							ns			
Larval Dispersers	0 - 5 mm							ns							ns										
	6 - 10 mm								ns							ns									
	11 - 15 mm									ns							ns								
	16 - 20 mm										ns							ns							
	21 - 25 mm											ns							ns						
	26 - 30 mm												ns							ns					
	31 - 35 mm													ns							ns				
Small Migrants	0 - 5 mm														ns										
	6 - 10 mm															ns									
	11 - 15 mm																ns								
	16 - 20 mm																	ns							
	21 - 25 mm																		ns						
	26 - 30 mm																			ns					
	31 - 35 mm																					ns			

Table 2.2b. Differences in instantaneous growth ( $g$ ) between contingents in 2010 for the primary sample of juvenile striped bass (0-35 mm).  $g$  has been determined over 5 mm stanzas. Arrows ( $\uparrow/\leftarrow$ ) indicate significant differences and point to the contingent with the higher growth rate ; “ $ns$ ” indicates not significant. Tests performed using least square means comparisons ( $\alpha=0.05$ ).

Least Square Means Comparisons of Growth between Adjacent Size Stanzas						
	0-5mm → 6-10mm	6-10mm → 11-15mm	11-15mm → 16-20mm	16-20mm → 21-25mm	21-25mm → 26-30mm	26-30mm → 31-35mm
<b>Contingent</b>						
<b>Intermediate Migrant</b>	$t = 4.96$ $p < 0.0001$	ns	$t = 2.80$ $p = 0.0054$	ns	$t = 3.49$ $p = 0.0006$	ns
<b>Small Migrant</b>	$t = 3.34$ $p = 0.0010$	ns	ns	ns	ns	ns
<b>Larval Migrant</b>	n/a <sup>§</sup>	n/a	n/a	n/a	n/a	n/a
<b>Resident &amp; Large Migrant</b>	ns*	$t = 2.83$ $p = 0.0049$	ns	ns	ns	ns

† ns indicates non-significant t-test results without Bonferroni adjustment  
§ n/a indicates insufficient contingent size to justify means comparisons

Table 2.3a. Results of least square means comparisons of instantaneous growth rates between successive periods of growth for the primary sample (6-35 mm TL) of 2009 striped bass juveniles. Significant differences indicate increases or decreases in contingent-specific growth. Due to sample size constraints, some contingents were not analyzed.

Least Square Means Comparisons of Growth between Adjacent Size Stanzas						
	0-5mm → 6-10mm	6-10mm → 11-15mm	11-15mm → 16-20mm	16-20mm → 21-25mm	21-25mm → 26-30mm	26-30mm → 31-35mm
<b>Contingent</b>						
<b>Intermediate Migrant</b>	ns*	ns	ns	$t = 2.20$ $p = 0.0287$	ns	ns
<b>Small Migrant</b>	ns	$t = 2.94$ $p = 0.0036$	ns	ns	ns	ns
<b>Larval Migrant</b>	n/a <sup>§</sup>	n/a	n/a	n/a	n/a	n/a
<b>Resident &amp; Large Migrant</b>	$t = 3.08$ $p = 0.0023$	ns	$t = -2.24$ $p = 0.0260$	$t = 2.71$ $p = 0.0074$	ns	ns

<sup>†</sup> ns indicates non-significant t-test results without Bonferroni adjustment

<sup>§</sup> n/a indicates insufficient contingent size to justify means comparisons

Table 2.3b. Results of least square means comparisons of instantaneous growth rates between successive periods of growth for the primary sample (6-35 mm TL) of 2010 striped bass juveniles. Significant differences indicate increases or decreases in contingent-specific growth. Due to sample size constraints, some contingents were not analyzed.

	Larval Dispersers						Small Migrants						Intermediate Migrants						Large Migrants						Returning Migrants																	
	Total Length Stanzas						Total Length Stanzas						Total Length Stanzas						Total Length Stanzas						Total Length Stanzas																	
	0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm	36 - 40 mm	41 - 45 mm	46 - 50 mm	0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm	36 - 40 mm	41 - 45 mm	46 - 50 mm	0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm	36 - 40 mm	41 - 45 mm	46 - 50 mm	0 - 5 mm	6 - 10 mm	11 - 15 mm	16 - 20 mm	21 - 25 mm	26 - 30 mm	31 - 35 mm	36 - 40 mm	41 - 45 mm	46 - 50 mm		
Residents	0 - 5 mm	ns								ns											ns																					
	6 - 10 mm	ns	ns							←											ns																					
	11 - 15 mm		ns	ns							ns											←																				
	16 - 20 mm			ns	ns							ns																														
	21 - 25 mm				ns	ns							ns																													
	26 - 30 mm					ns	ns							ns																												
Larval Dispersers	31 - 35 mm					ns	ns																																			
	36 - 40 mm						ns	ns																																		
	41 - 45 mm							ns	ns																																	
	46 - 50 mm								ns	ns																																
	0 - 5 mm									ns																																
	6 - 10 mm										←																															
Small Migrants	11 - 15 mm																																									
	16 - 20 mm																																									
	21 - 25 mm																																									
	26 - 30 mm																																									
	31 - 35 mm																																									
	36 - 40 mm																																									
Intermediate Migrants	41 - 45 mm																																									
	46 - 50 mm																																									
	0 - 5 mm																																									
	6 - 10 mm																																									
	11 - 15 mm																																									
	16 - 20 mm																																									
Large Migrants	21 - 25 mm																																									
	26 - 30 mm																																									
	31 - 35 mm																																									
	36 - 40 mm																																									
	41 - 45 mm																																									
	46 - 50 mm																																									

Table 2.4. Differences in instantaneous growth ( $g$ ) between contingents for the secondary sample of larger juvenile striped bass (0-50 mm) in 2009.  $g$  has been determined over 5 mm stanzas. Arrows ( $\uparrow/\leftarrow$ ) indicate significant differences and point to the contingent with the higher growth rate ; “ $ns$ ” indicates not significant. Tests performed using least square means comparisons ( $\alpha=0.05$ ).

		Least Square Means Comparisons of Growth between Adjacent Size Stanzas								
		0-5mm → 6-10mm	6-10mm → 11-15mm	11-15mm → 16-20mm	16-20mm → 21-25mm	21-25mm → 26-30mm	26-30mm → 31-35mm	31-35mm → 36-40mm	36-40mm → 41-45mm	41-45mm → 46-50mm
<b>Contingent</b>										
Intermediate Migrant	$t = 3.39$ $p = 0.0008$	ns	ns	ns	ns	ns	ns	ns	ns	ns
Small Migrant	$t = 2.53$ $p = 0.0118$	ns	ns	ns	ns	ns	ns	ns	ns	ns
Larval Migrant	$n/a^{\S}$	$n/a$	$n/a$	$n/a$	$n/a$	$n/a$	$n/a$	$n/a$	$n/a$	$n/a$
Resident & Large Migrant	ns*	ns	ns	ns	ns	ns	ns	ns	ns	ns
Large Migrant	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Returning Migrant	$t = 2.68$ $p = 0.0078$	ns	ns	$t = 2.03$ $p = 0.0430$	ns	ns	ns	ns	ns	$t = -6.81$ $p < 0.0001$
		<sup>‡</sup> ns indicates non-significant t-test results without Bonferroni adjustment <sup>§</sup> $n/a$ indicates insufficient contingent size to justify means comparisons								

Table 2.5. Results of least square means comparisons of instantaneous growth rates between successive periods of growth for the secondary sample (6-50 mm TL) of 2009 striped bass juveniles. Significant differences indicate increases or decreases in contingent-specific growth. Due to sample size constraints, some contingents were not analyzed. No significant differences were identified in the secondary sample of 2010 striped bass.



	Total Length Stanzas	Middle 50% Hatch Dates						Latest 25% Hatch Dates							
		0-5mm	6-10mm	11-15mm	16-20mm	21-25mm	26-30mm	31-35mm	0-5mm	6-10mm	11-15mm	16-20mm	21-25mm	26-30mm	31-35mm
Earliest 25% Hatch Dates	0-5mm	ns							↑						
	6-10mm		ns							↑					
	11-15mm			↑							↑				
	16-20mm				ns							ns			
	21-25mm					ns							ns		
	26-30mm						ns							ns	
	31-35mm							ns							ns
Middle 50% Hatch Dates	0-5mm								↑						
	6-10mm									↑					
	11-15mm										ns				
	16-20mm											ns			
	21-25mm												ns		
	26-30mm													ns	
	31-35mm														ns

Table 2.6. Differences in instantaneous growth ( $g$ ) between hatch date quartiles (2<sup>nd</sup> and 3<sup>rd</sup> quartiles combined for this analysis) in 2009 for the primary sample of juvenile striped bass (0-35 mm TL).  $g$  has been determined over 5 mm stanzas. Arrows (↑/←) indicate significant differences and point to the contingent with the higher growth rate ; “ $ns$ ” indicates not significant. Tests performed using least square means comparisons ( $\alpha=0.05$ ).

Trophic Niche Metrics	Freshwater		Brackish water	
	White Muscle	Liver	White Muscle	Liver
$\delta^{15}\text{N}$ Mean $\pm$ SE	18.07 $\pm$ 0.16	16.95 $\pm$ 0.18	17.30 $\pm$ 0.14	15.99 $\pm$ 0.13
$\delta^{13}\text{C}$ Mean $\pm$ SE	-25.01 $\pm$ 0.57	-	-20.91 $\pm$ 0.44	-
Trophic Position $\pm$ SE	3.03 $\pm$ 0.02	2.70 $\pm$ 0.01	3.01 $\pm$ 0.01	2.63 $\pm$ 0.01
Convex Hull Area	15.14	-	15.69	-
Mean Dist to Centroid	2.16	-	2.31	-
Mean Nearest Neighbor Distance	0.73	-	0.49	-
Standard Deviation of NND	0.43	-	0.35	-

Table 2.7. 2010 habitat-and tissue-specific trophic niche metrics and, where applicable, standard errors (SE) of juvenile striped bass collected in the Patuxent River estuary. Convex hull area, mean distance to centroid, mean nearest neighbor distance and standard deviation of NND are measures of stable isotope bivariate space ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ).

*Figures*

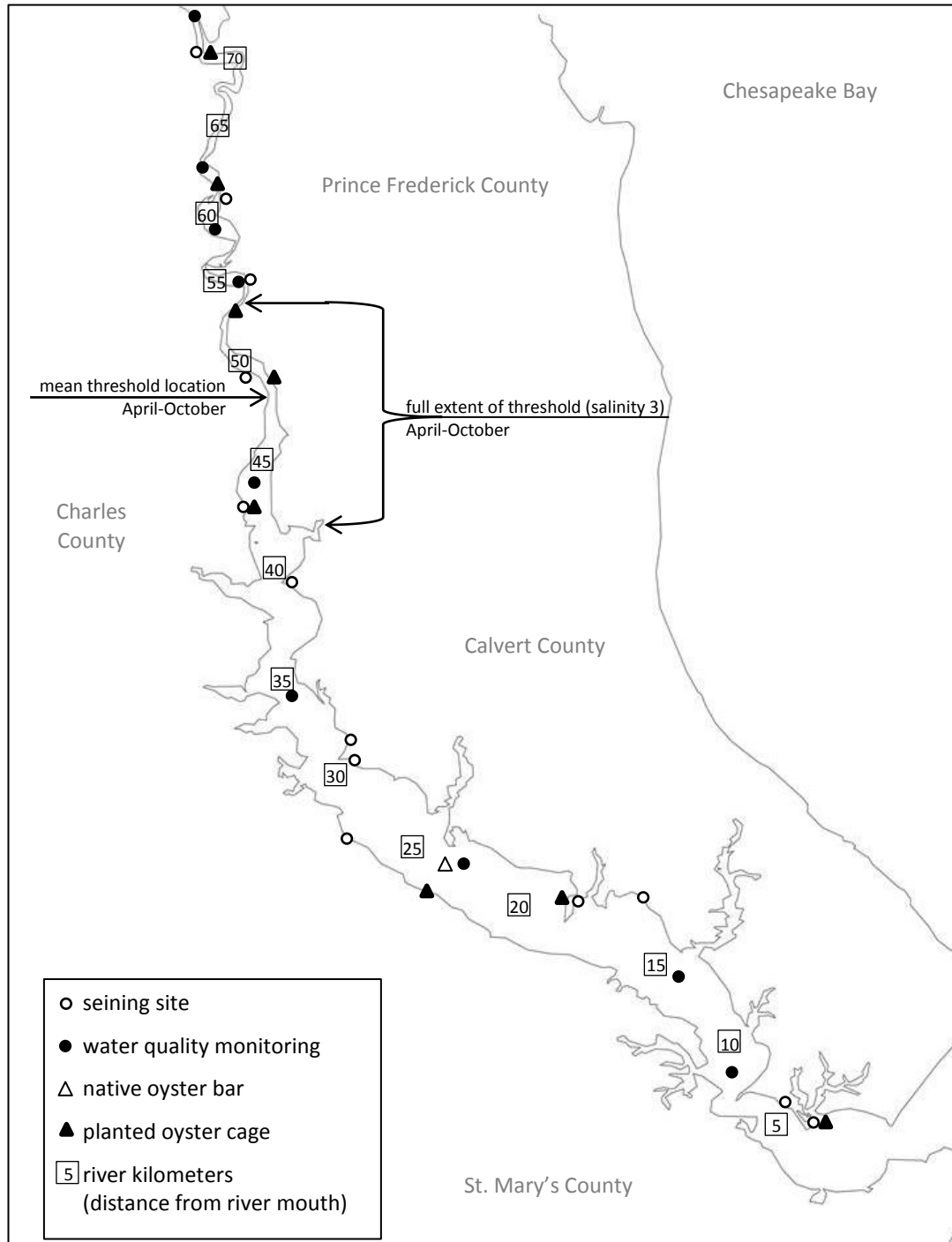


Figure 2.1. Map of the study area, the Patuxent River tidal estuary, Chesapeake Bay. Sites where striped bass were collected via seine are indicated (○), as well as the locations of long-term water quality monitoring (●). The positions of introduced oyster cages (▲) and harvested native oysters (△) are also shown. RKM are listed for reference.

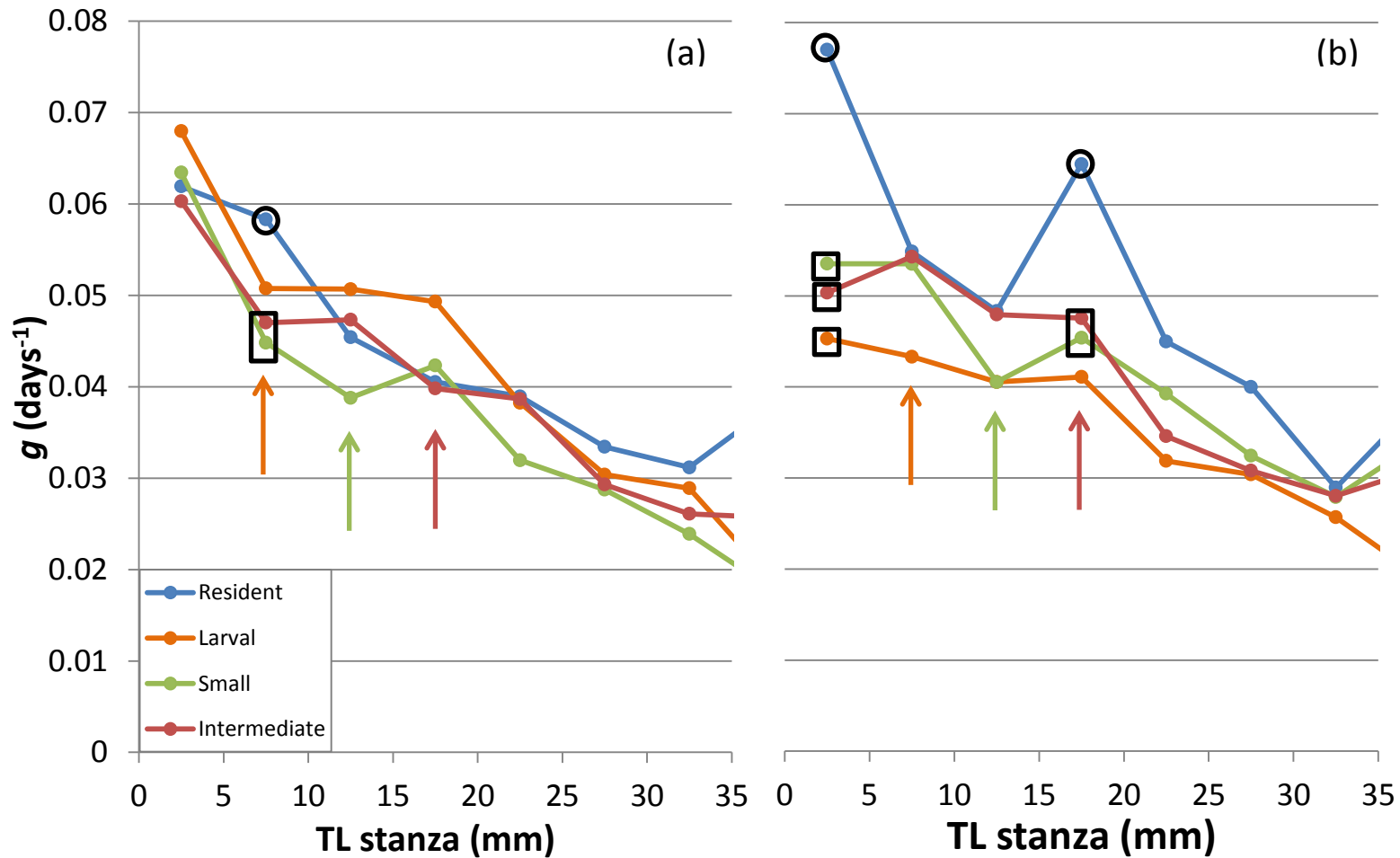


Figure 2.2. Instantaneous growth rates ( $g$ ) for the primary sample (6-35 mm TL) of juvenile striped bass; 5 mm stanzas for 2009 (a) and 2010 (b). Arrows ( $\uparrow$ ) indicate the size of mean dispersal for each migratory contingent. Significant differences between contingents (as determined by LS means comparisons  $\alpha=0.05$ ; see Table 2.2) are indicated circles ( $\circ$ , higher values) and boxes ( $\square$ , lower values).

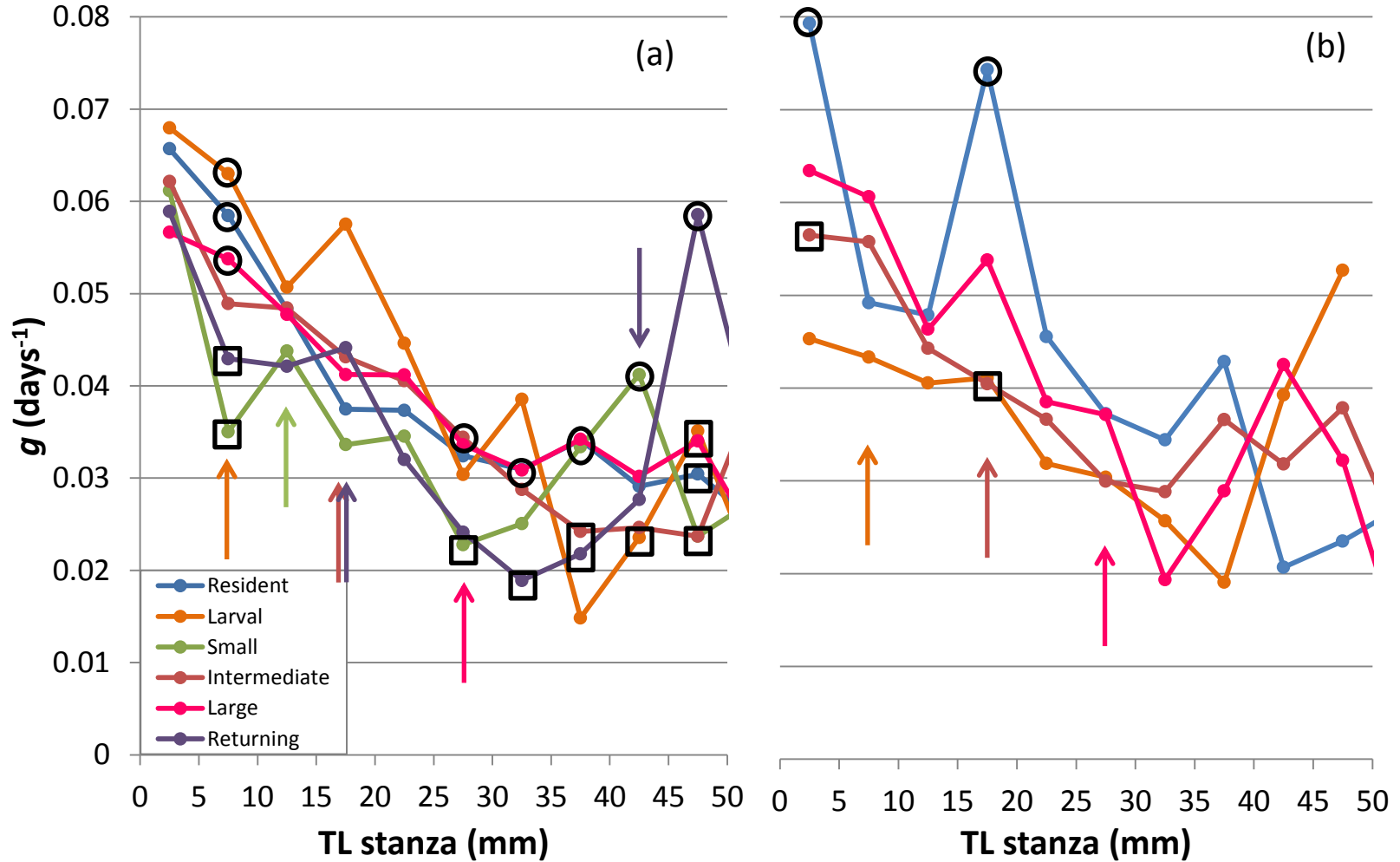


Figure 2.3. Instantaneous growth rates ( $g$ ) for secondary sample including larger individuals of juvenile striped bass (6-50 mm TL); 5 mm stanzas for 2009 (a) and 2010 (b). Arrows indicate the size of mean dispersal from ( $\uparrow$ ) and return to ( $\downarrow$ ) freshwater for each migratory contingent. Significant differences between contingents (as determined by LS means comparisons  $\alpha=0.05$ ; see Table 2.3) are indicated circles ( $\circ$ , higher values) and boxes ( $\square$ , lower values).

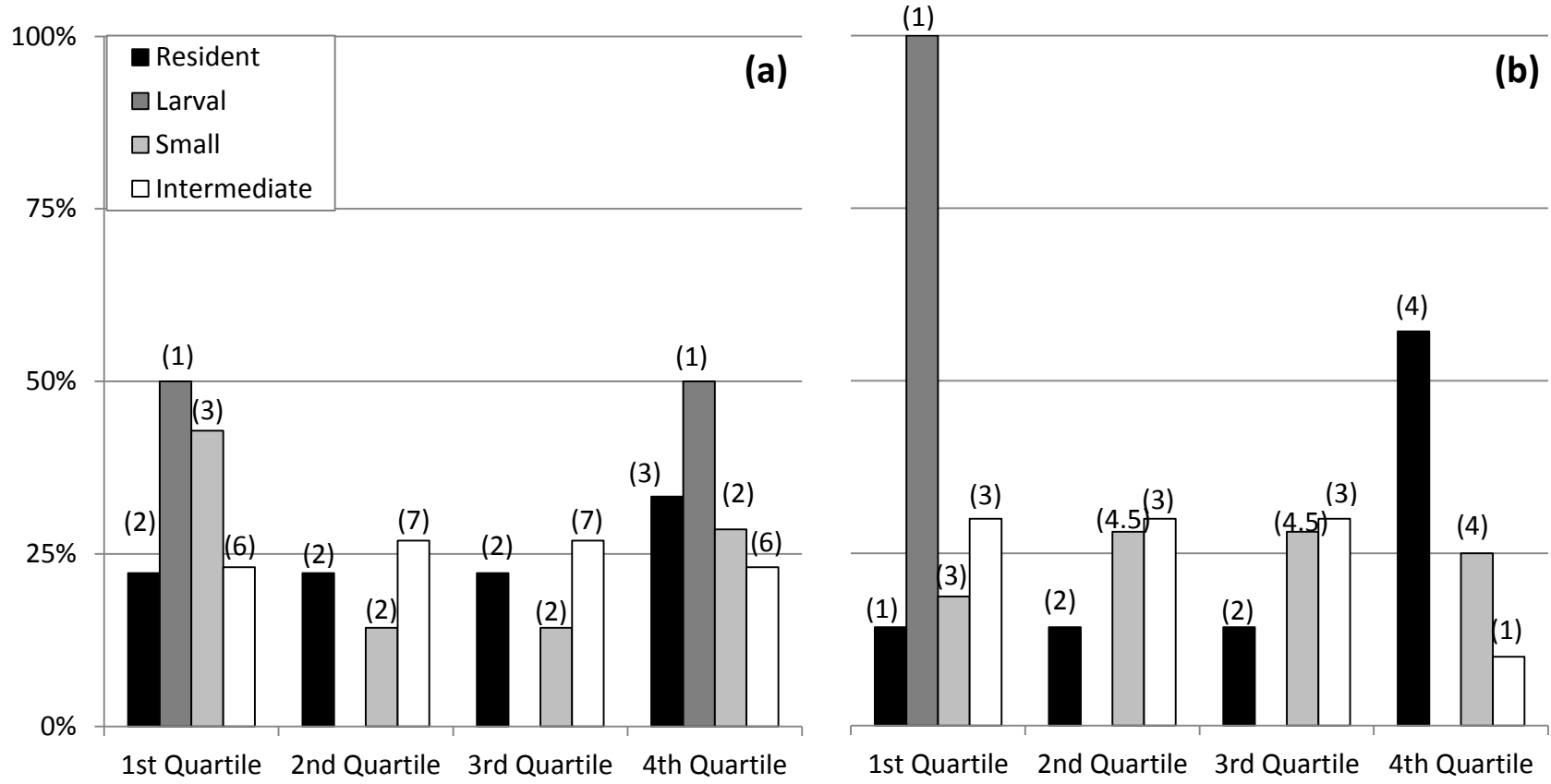


Figure 2.4. Histogram of contingent-specific hatch date quartiles of juvenile striped bass in 2009 (a) and 2010 (b). Number of individuals are in parentheses above each quartile.

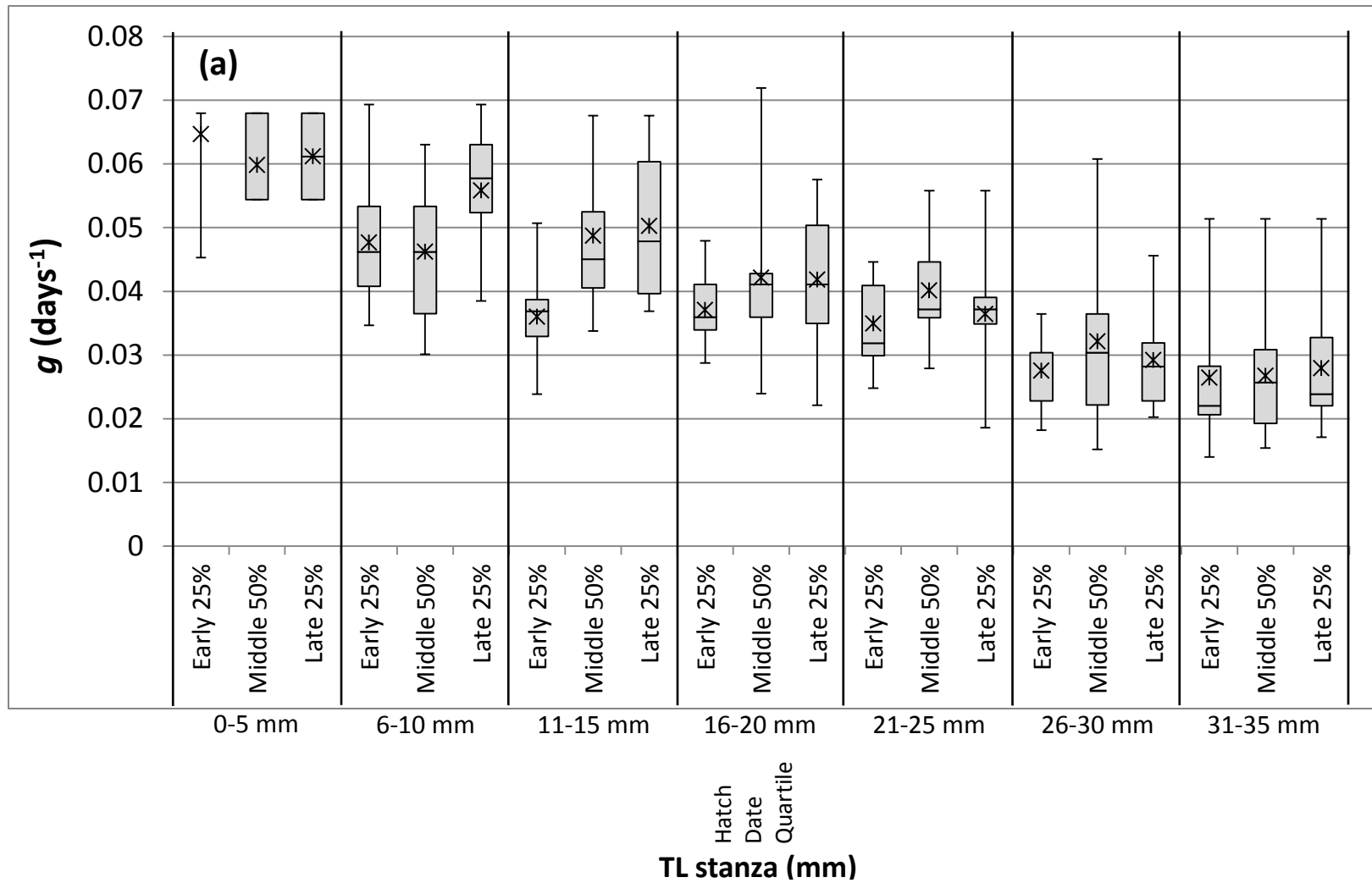


Figure 2.5a. Box plots of instantaneous growth rates ( $g$ ) for the primary sample of juvenile striped bass in 2009; 5 mm stanzas by hatch date quartiles. Hatch date quartiles are shown in each column: Early 25%, Middle 50%, and Late 25%. Here and in subsequent figures, boxplots indicate 25<sup>th</sup>, 50<sup>th</sup> (median), and 75<sup>th</sup> percentiles, whiskers indicate minimum and maximum observed values, and stars (\*) indicate means.

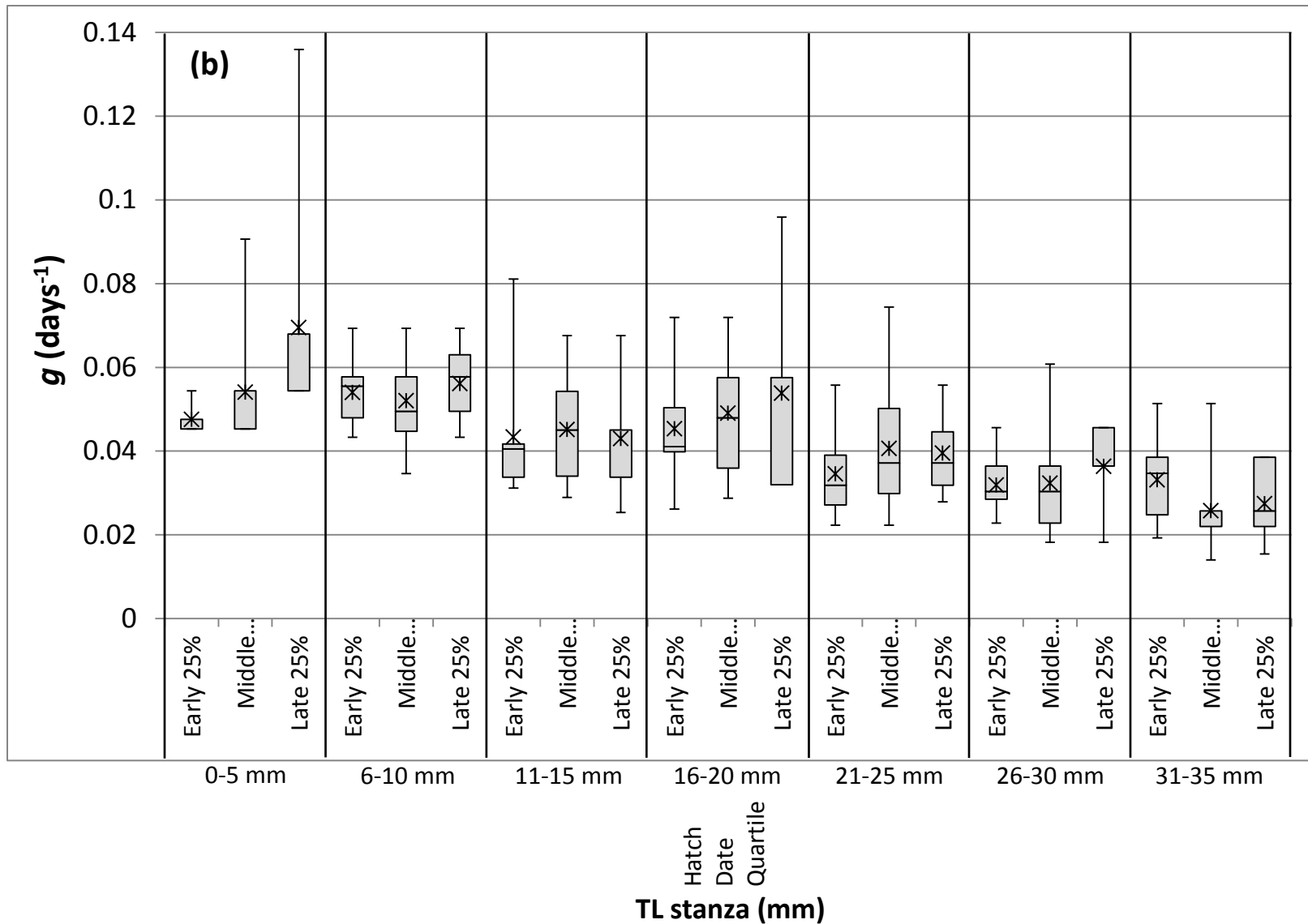


Figure 2.5b. Box plots of instantaneous growth rates ( $g$ ) for the primary sample of juvenile striped bass in 2010; 5 mm stanzas by hatch date quartiles. Hatch date quartiles are shown in each column: Early 25%, Middle 50%, and Late 25%.



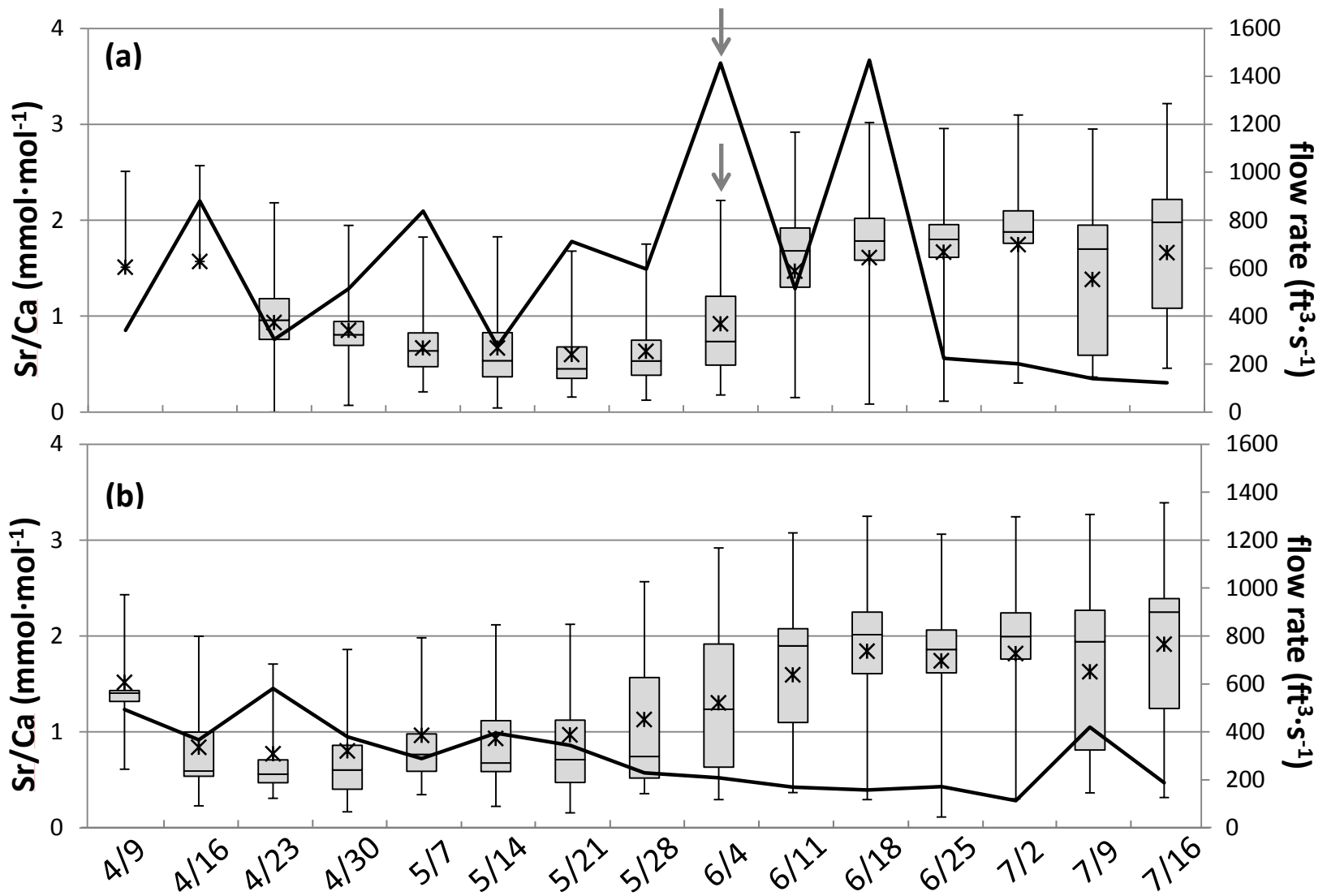


Figure 2.6. Patuxent river flow rate (line) and boxplots of weekly mean otolith Sr/Ca of juvenile striped bass in 2009 (a) and 2010 (b). Arrows ( $\downarrow$ ) indicate coinciding migration and flow events in 2009.

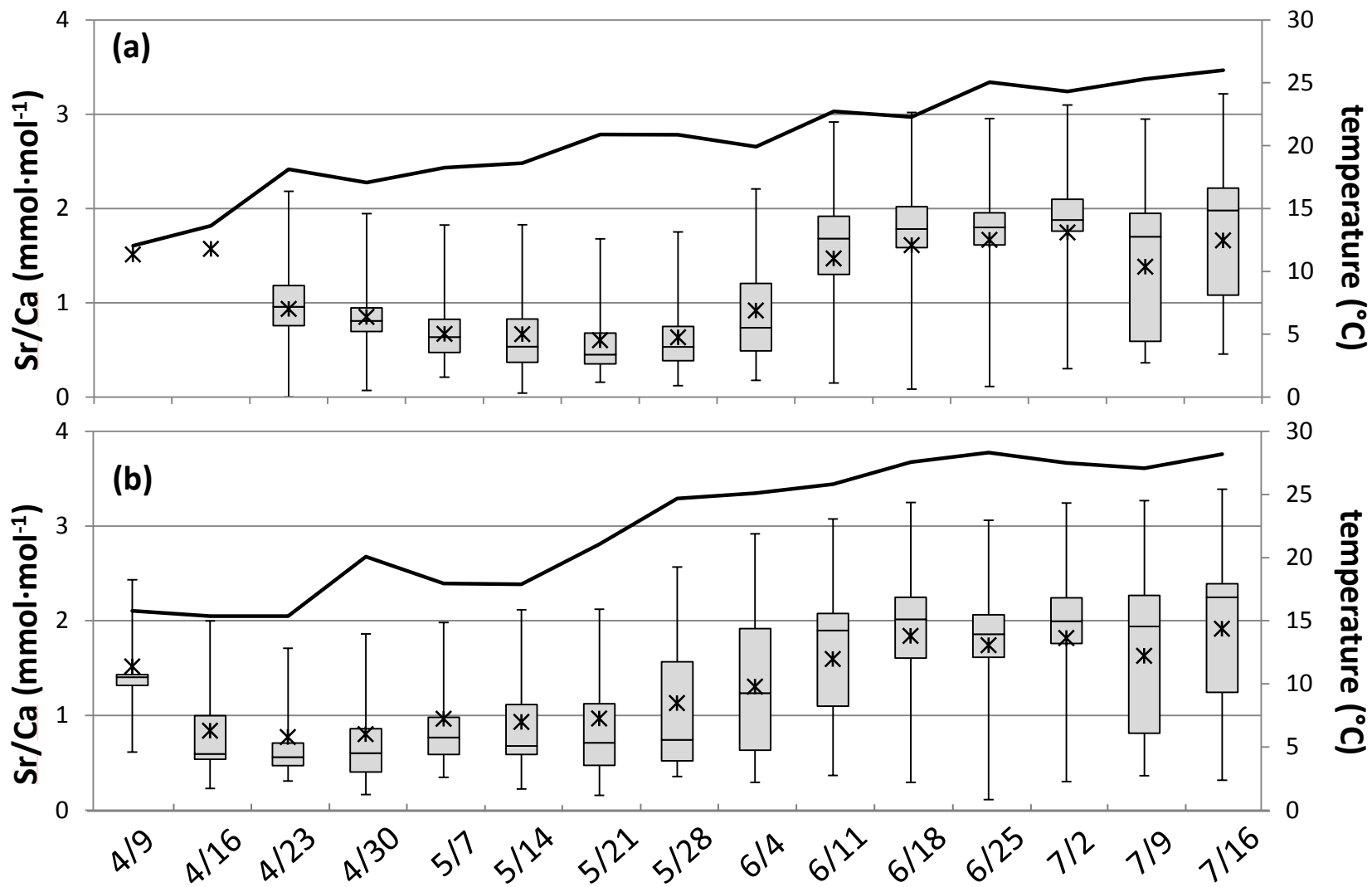


Figure 2.7. Patuxent river temperature (line) and boxplots of weekly mean otolith Sr/Ca of juvenile striped bass and in 2009 (a) and 2010 (b).

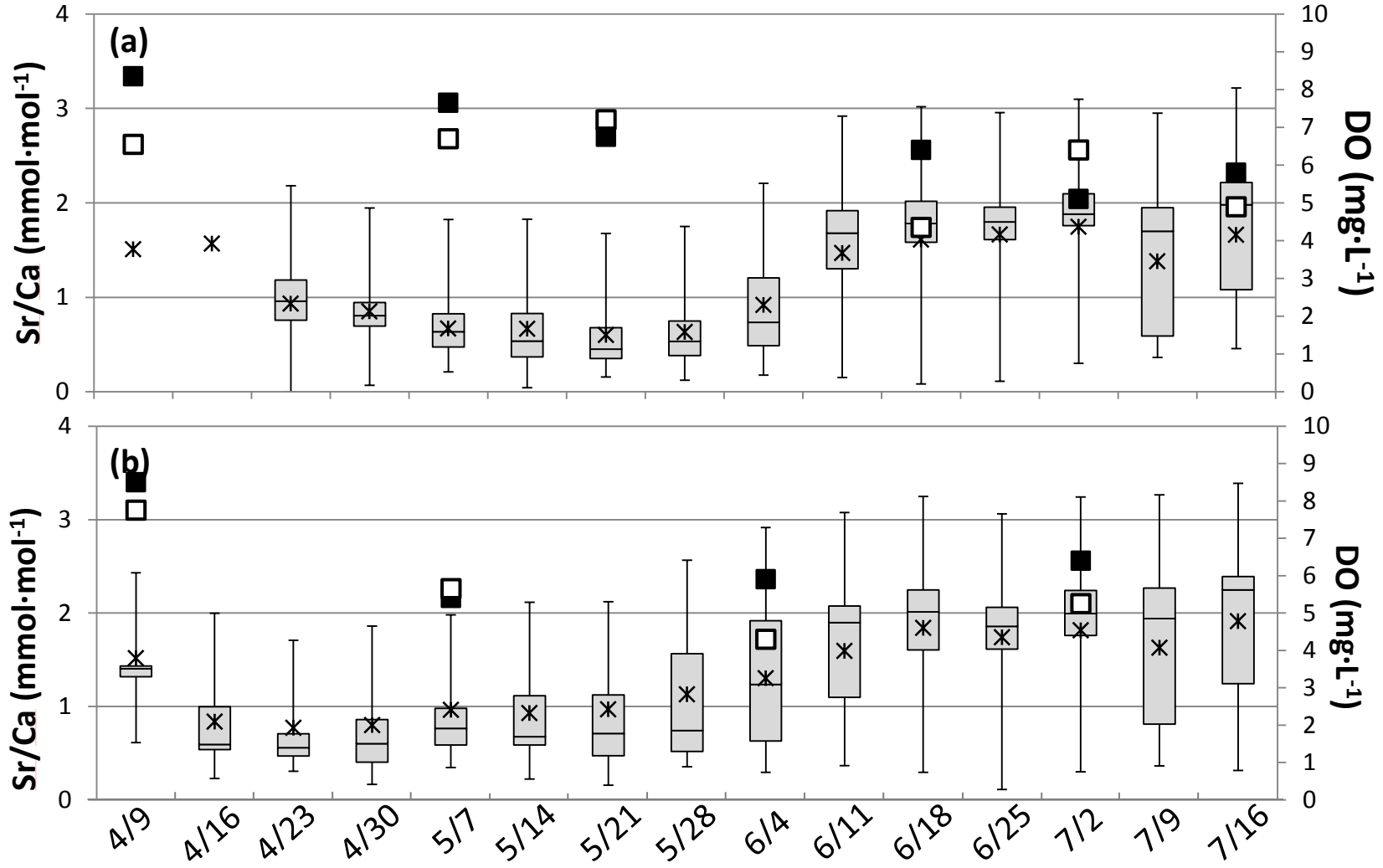


Figure 2.8. Dissolved oxygen (DO) concentrations at *RKM* 34 (□) and 45 (■) and boxplots of weekly mean otolith Sr/Ca of juvenile striped bass in 2009 (a) and 2010 (b).

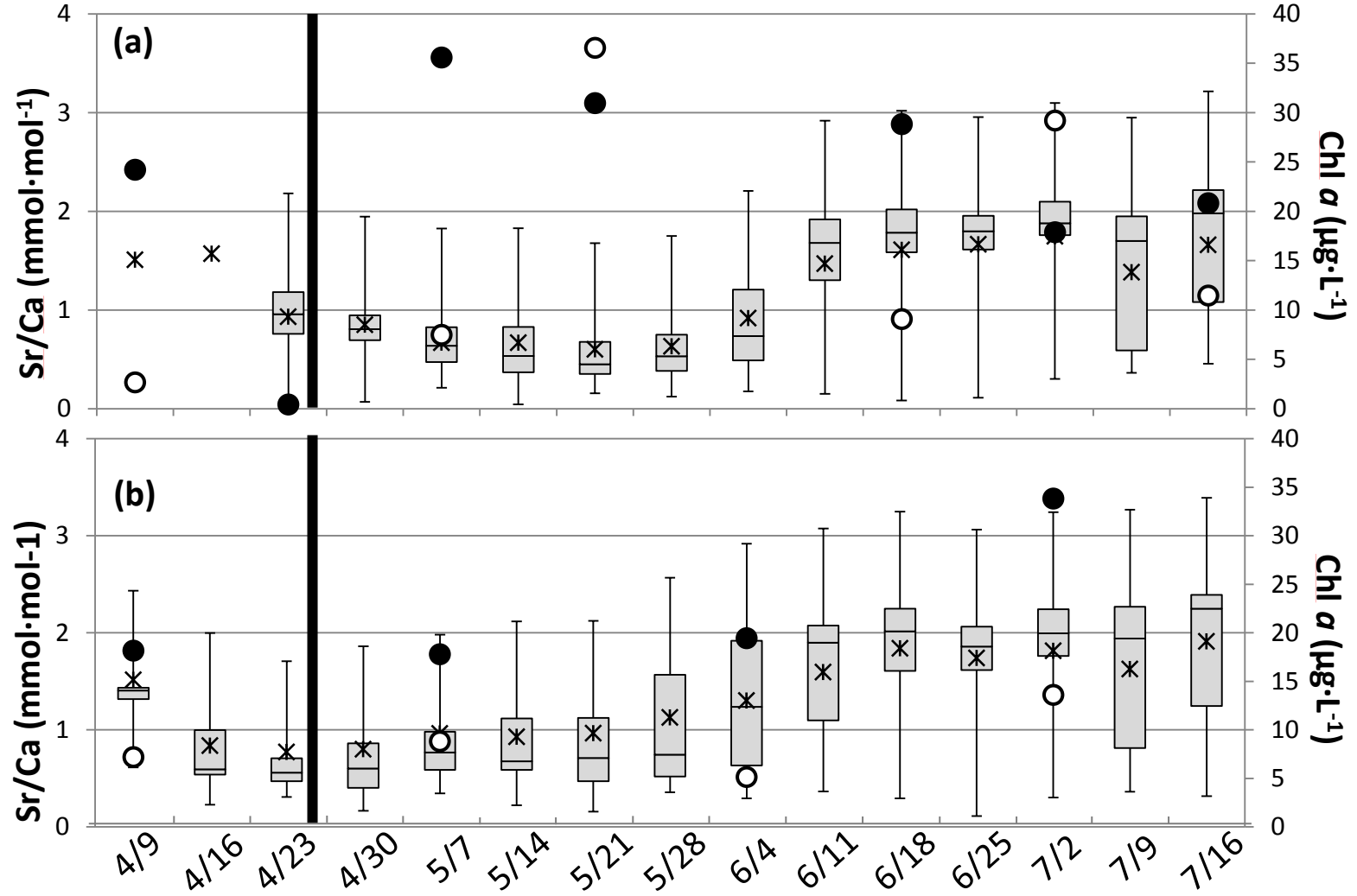


Figure 2.9. Chlorophyll *a* concentrations at *RKM* 34 (○) and 45 (●) and boxplots of weekly mean otolith Sr/Ca of juvenile striped bass in 2009 (a) and 2010 (b). Black bars indicate the peak (2009) and median (2010) of hatch date distributions.

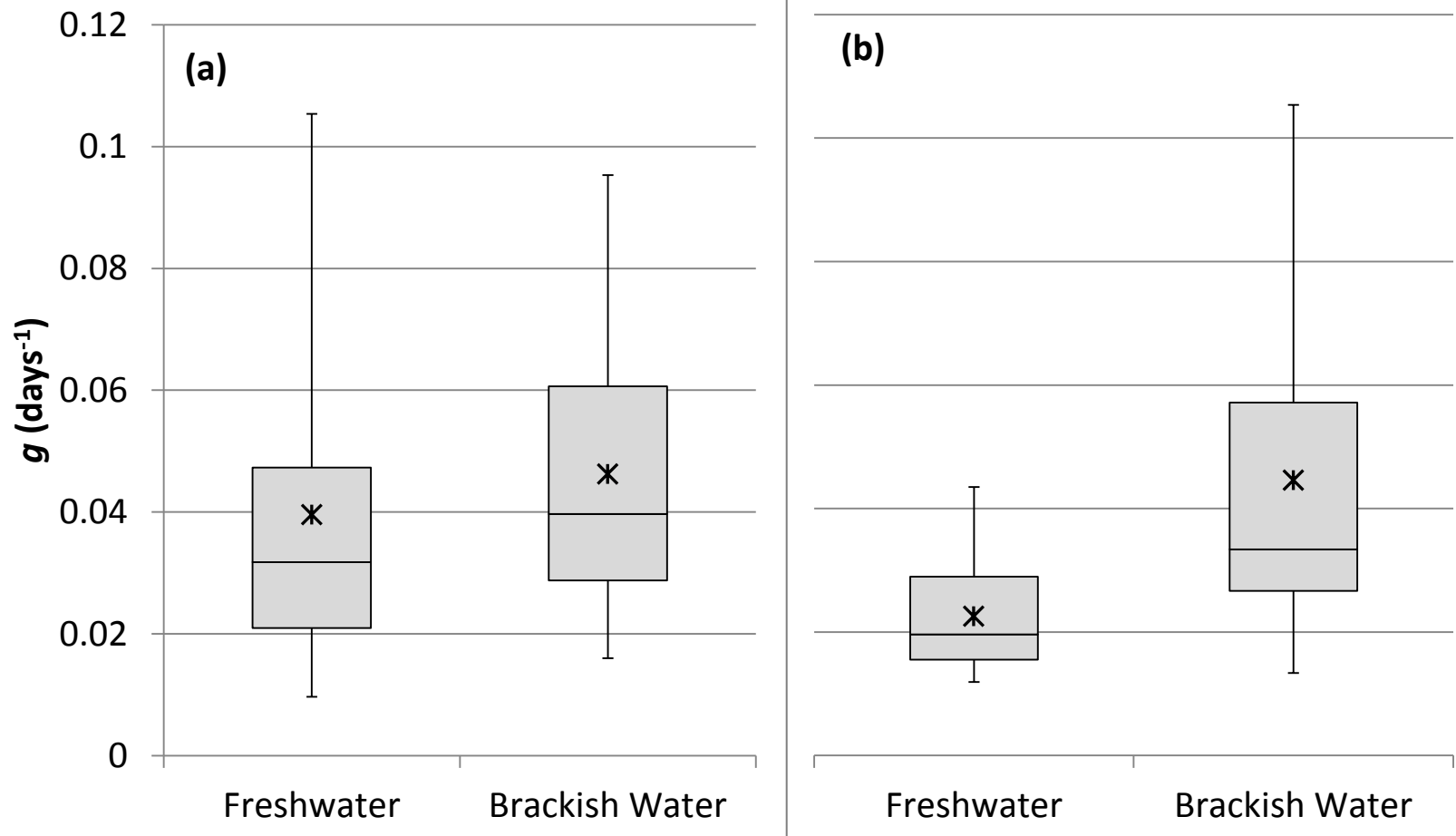


Figure 2.10. Boxplots of recent growth (over last 5mm prior to collection) by habitat of juvenile striped bass collected in 2009 (a) and 2010 (b).

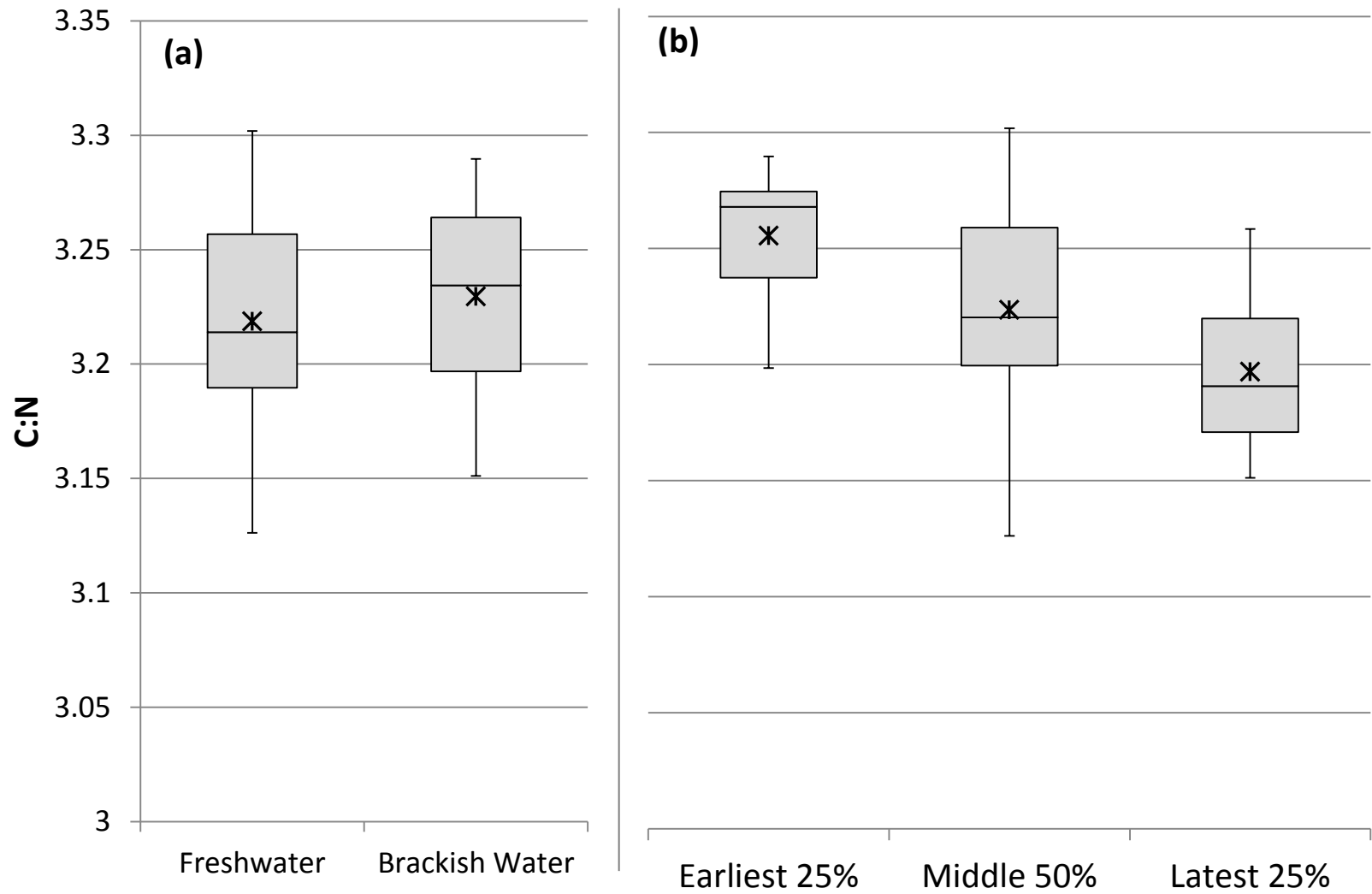


Figure 2.11. Boxplots of condition (as measured by C:N) by habitat of juvenile striped bass collection (a) and hatch date quartile (b) in 2010.

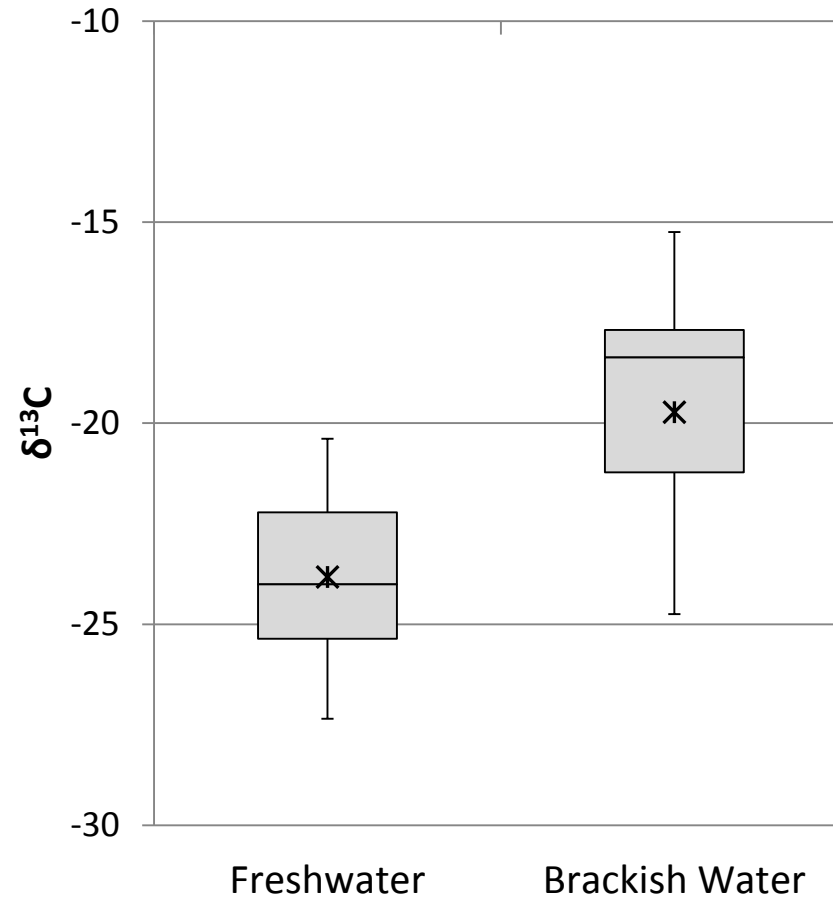


Figure 2.12. Boxplots of carbon-source  $\delta^{13}\text{C}$  by habitat of juvenile striped bass collection in 2010.

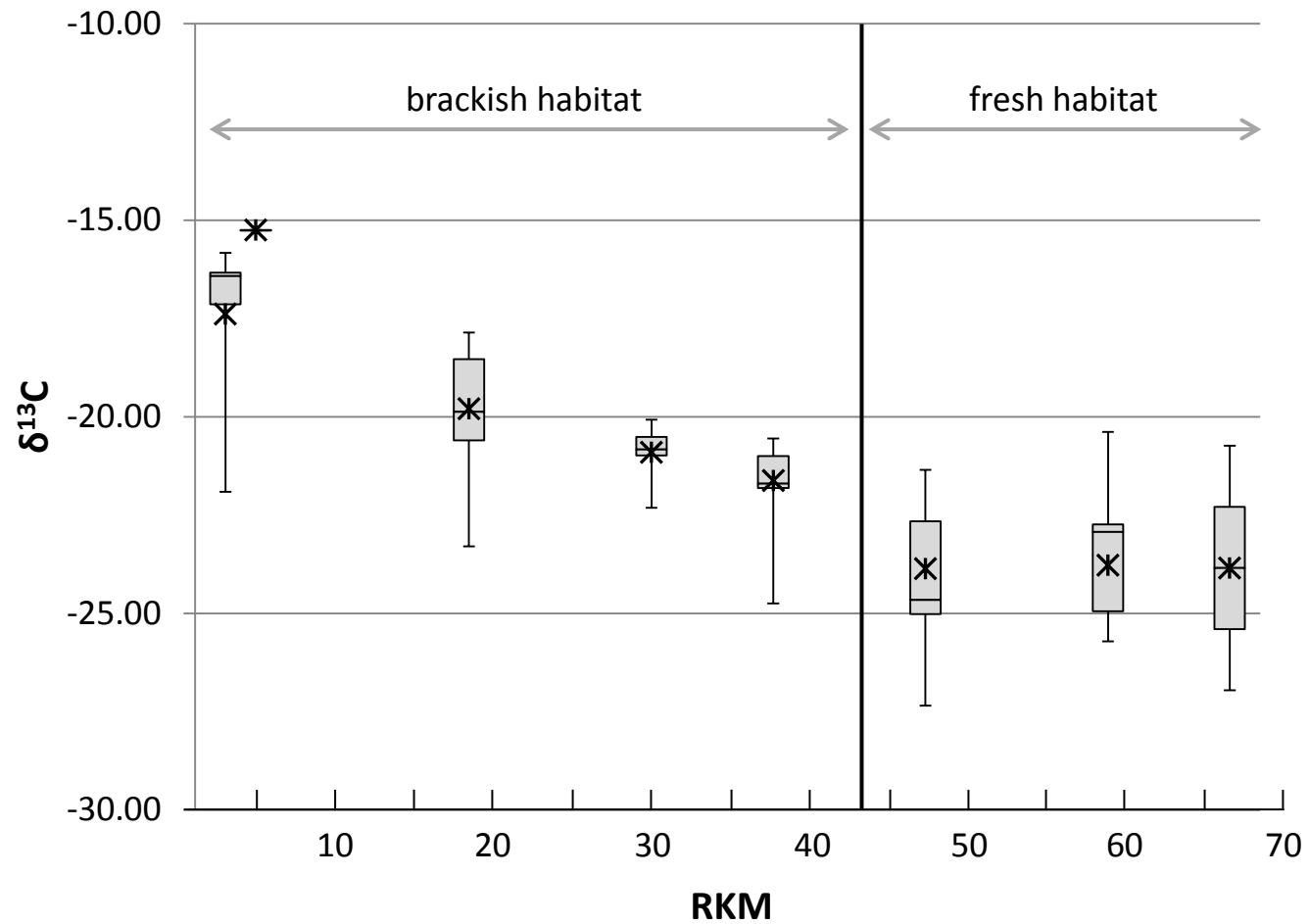


Figure 2.13. Boxplots of carbon-source  $\delta^{13}\text{C}$  (as determined using  $\delta^{13}\text{C}$  measurements of juvenile striped bass white muscle) by *RKM* at collection in 2010. Black bar (|) indicates location of transition from fresh to brackish habitat (salinity 3).



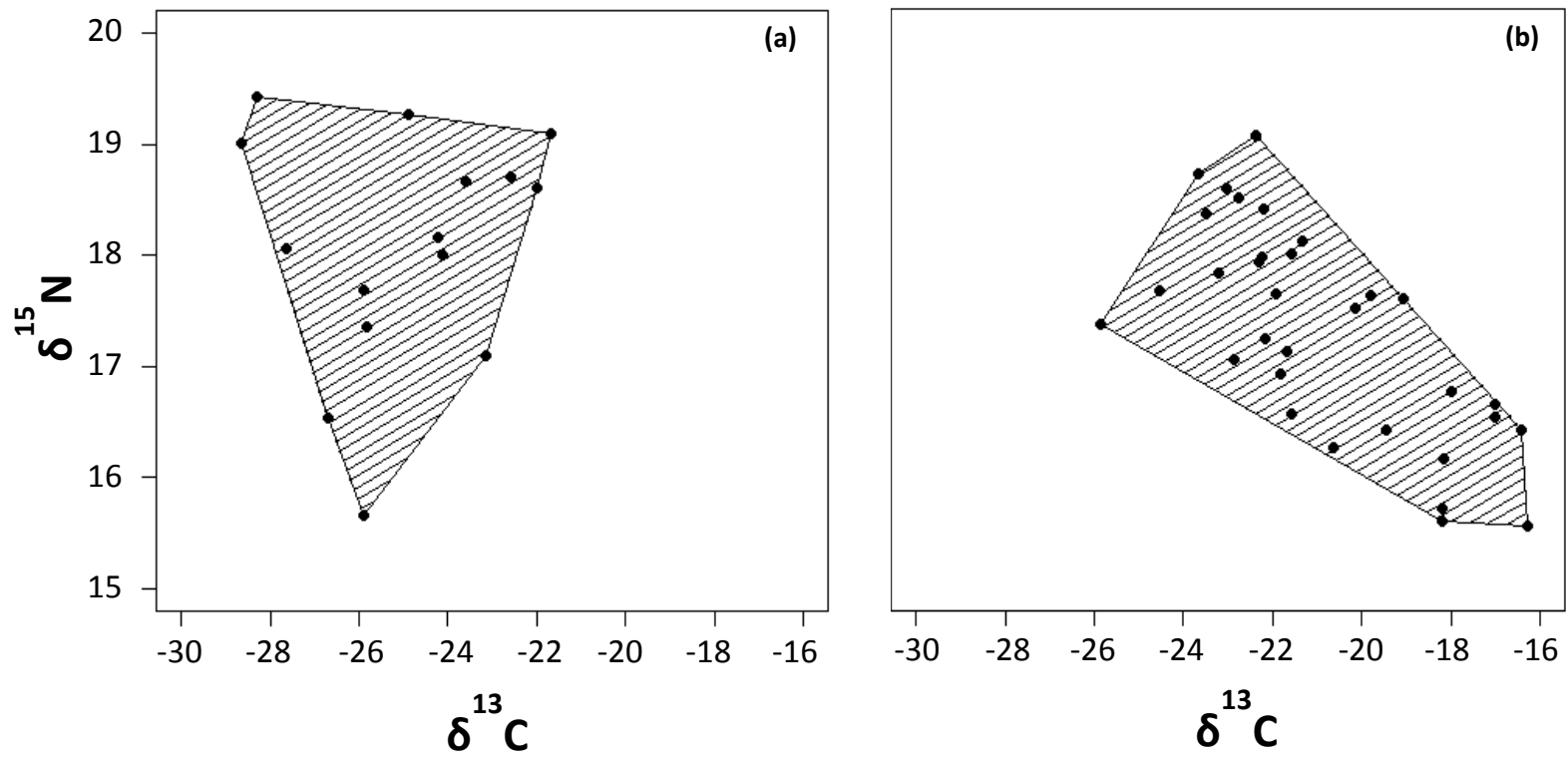


Figure 2.14. Convex Hull of freshwater (a) and brackish water (b) stable isotope bivariate space for white muscle from juvenile striped bass collected in 2010.

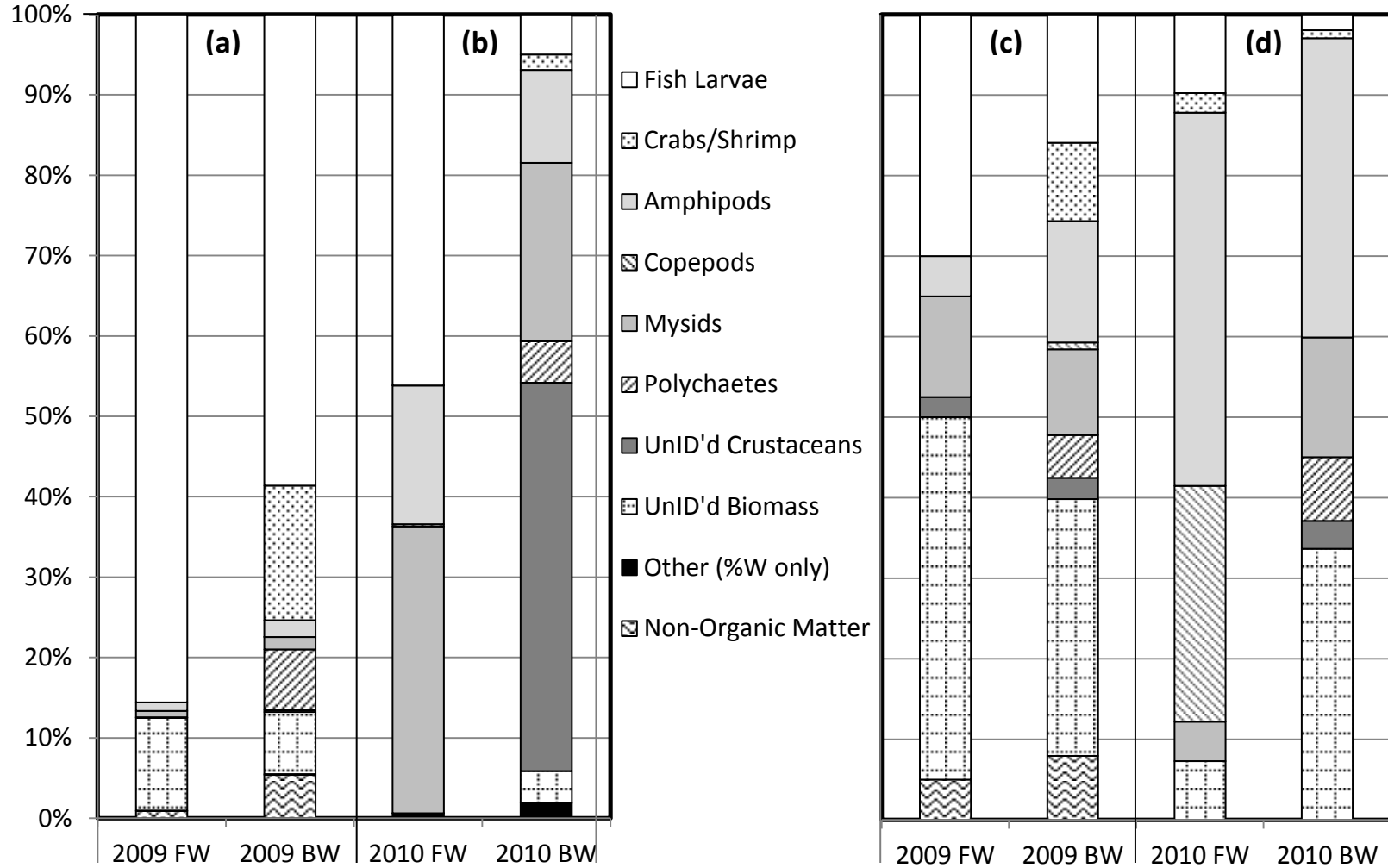


Figure 2.15. Bar graphs of diet percent composition by weight (%W; a,b) and occurrence (%O; c,d) for juvenile striped bass in 2009 (a,c) and 2010 (b,d).

## Chapter 3: Future work on early partial migration in estuarine fishes

During the course of any study, limitations are identified in the approach to the populations of interest. Additionally, potential future projects addressing both questions newly identified within the current system or applications of techniques to new systems are developed. During field work, laboratory procedures, data analysis, and writing, I identified changes to the design of this study, as well as further research that may improve understanding of ontogenetic partial migration and its role in the persistence of striped bass populations as well as its potential importance in other estuarine species. This chapter is a summary of these ideas for use in future endeavors.

### Expansion of Current Study

As discussed in chapters 1 and 2, inherent in using the approaches employed during this study are limitations in the scope of inference. Under circumstances of unlimited budgets and resource availability, I would have made several adjustments to our sampling and study approach. The most easily addressed issue I faced during this research was sample size. As discussed in Chapter 1, due to resource limitations sampling in 2010 was much more limited than in 2009. Based on some of the interesting migration behaviors I identified and the changes in membership frequency discovered during 2009, a substantial increase in sampling intensity would be warranted in future studies. Sampling efforts of the complete river conducted biweekly starting at the beginning of June and continuing through October would provide a larger sample population and finer temporal representation of the year class. This would enable clearer interpretation of changes in contingent frequency, like that observed between July and

October in 2009. Additionally, larger sample sizes would allow for more powerful analyses comparing contingent vital rates as well as clearing up any question about the relative sizes of contingents, especially for those with small rates of occurrence (<15% in the current study).

Concurrent to sampling, laboratory and in situ experimentation might afford beneficial validation to the identified partial migration. As part of a study of early migratory behaviors in white perch YOY, Kraus and Secor (2004b) kept caged individuals at a number of sites located throughout the Patuxent River. Samples taken from these cages periodically led to the validation of both the relationship between Sr/Ca and salinity in white perch as well as the chemical Sr gradient within the estuary. Using a similar approach would provide in situ validation of this relationship that has been determined in laboratory and mesocosm experiments in striped bass YOY by Secor *et al.* (1995). The non-linear relationship between Sr/Ca and salinity and the coarse nature of otolith-chemistry-implied habitat use precludes the elucidation of site-specific differences within freshwater and much of brackish water habitat. The use of caged juveniles would also provide finer scale measurements of habitat-specific differences in early growth rates. A large number of manipulations would be possible, including staggered introductions of cages to more closely examine the effects of hatch-date on early vital rates and installing cages at a number of depths to test for the importance of vertical distribution.

Additional sampling would aid in understanding the importance of habitat use. Near-shore depth-stratified sampling using fish traps and deeper sampling with depth-specific Tucker trawls would help clarify the vertical distribution of individuals and

potential differences in size, behavior, and growth with depth. Direct sampling of available prey would provide selectivity of striped bass juvenile feeding as well as direct measures of prey item trophic positions. Limited sampling of available near shore habitats that were not sampled in this study would also help; these include bottom types not conducive to seining as well as tributary streams within the estuary.

*Expansions and Elaborations of this Study in Striped Bass and Other Estuarine Fishes*

Otolith chemical analysis resulted in the identification of unexpected Sr/Ca patterns. Larval dispersal was completely unexpected; although rare, this early movement may play an important role in population persistence. Despite my conviction that these dispersals were played out physically along the salinity gradient within the estuary, further work is required to validate this phenomenon. The low rate of larval dispersal may reflect the high mortality of just-hatched striped bass in brackish habitats, but it could indicate a small proportion of juvenile fish whose chemical absorption and otolith accretion differ substantially from the established normal processes of most individuals. Whether the inferred movement is real or the result of natural variation, further study is warranted and will clarify otolith chemistry for future ecological interpretation. Additionally, the large range of initial Sr/Ca values (in size-based profiles hatch-5 mm TL) deserves further exploration. In a study of Atlantic herring and sprat, Brophy *et al.* (2004) identified elevated concentrations of manganese in fish primordia compared to the rest of tested otolith material using laser ablation. The authors posited that these peaks in Mn were due either to maternal effect, a relationship that has been confirmed in Pacific salmon (Volk *et al.*, 2000), or to physical factors in the initial formation of the otolith's crystalline structure. Work on biomineralization in corals has

identified similar inconsistencies in crystalline structures formed in solutions (De Yoreo and Vekilov, 2003). Previous analysis of striped bass otoliths did not detect influences due to maternal contributions to the embryo's otolith composition (Kalish, 1990; Secor, 1992). In order to support ecological interpretations of otolith chemistry during the earliest periods of life, the cause of this variability must be identified.

The early life history of successfully recruited adults can be used to establish the importance certain aspects of ontogeny. Kraus and Secor (2004a) and Kerr *et al.* (2009) examined the first year of recruited white perch in the Patuxent River estuary. They established that in this system, migratory behaviors tended to persist throughout adulthood and were also able to link specific contingents to rates of recruitment. Further work in other estuaries identified important differences in the relationships of year-class strength and residency between systems (Kerr and Secor, 2011). Although such an approach would be complicated in the highly and variably migratory striped bass, similar efforts might still prove useful. Even if system of origin cannot be specifically identified, differences in important vital rates, such as growth, can be measured at specific points during life history. Additionally, any effect on age- and size-at-maturity as well as migratory tendencies as adults may be determined. Examining the dynamics of specific natal estuaries may require looking at the early behaviors of striped bass yearlings. Over-winter mortality of age-0 striped bass is high and survival through the first year represents an important milestone on the way towards eventual adult recruitment (Martino, 2008). Yearlings are more likely to remain in close proximity to their natal estuaries and have not undertaken the long coastal migrations of adults (Secor and Piccoli, 2007). Using otolith microstructure and elemental analysis, early migratory

behaviors might be connected to survival rates over the first winter and year-class strength for specific systems.

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