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# FULLY EQUIPPED TO SUCCEED: MIGRATORY CONTINGENTS SEEN AS AN INTRISIC POTENTIAL FOR STRIPED BASS TO EXPLOIT AN HETEROGENEOUS ENVIRONMENT EARLY IN LIFE

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ABSTRACT (150 to 200 words)

Migratory contingents, groups of individuals belonging to the same population that adopt different migratory patterns, have been identified in numerous Striped Bass (*Morone saxatilis*) populations along North American East Coast. We tested the hypothesis that migratory contingents may develop early in life to maximize the exploitation of the variety of habitats faced by a recently introduced fish population. Using the discriminatory power provided by otolith chemistry, we studied early life history stages of Striped Bass in a recently reintroduced population in the St. Lawrence Estuary. Migratory patterns were inferred using multivariate analysis of four otolith trace elements (Sr, Ba, Mn and Mg) on juveniles (0+ and 1+). Three migratory contingents were identified during early life history stages: freshwater residents, oligohaline migrants and mesohaline migrants. This study demonstrates the rapid establishment, in less than 10 years since initial stocking, of three migratory contingents initiated early in life among the St. Lawrence Striped Bass population. We postulate that diversification provided by the establishment of distinct migratory contingents among early life history stages promotes the rapid colonization of new environments through the exploration and exploitation of an increased number of nursery habitats. This would potentially leads to self-sustaining contingents compared to a single population exhibiting a unique, hard-wired, migratory pattern.

Keywords: Migratory contingent; Striped Bass; otolith chemistry; LA-ICP-MS; split-moving window

## 1 INTRODUCTION

Several anadromous and catadromous fishes exhibit intra-population variations in habitat (Dodson et al. 2013; Secor et al. 2001; Tsukamoto et al. 1998). Recent methodological advances and theoretical considerations revealed that migration in fishes is a complex trait deserving more attention (Arai et al. 2004; Chapman et al. 2012; Tzeng et al. 2002). Divergent life-history tactics, including partial migration, are well known among animal populations (Morais et al. 2011; Tzeng et al. 2002; Zimmerman et al. 2012). Partial migration can be defined as the presence of some resident (non-migratory) individuals within a migratory population (Chapman et al. 2011b). Partial migration was first identified in avian fauna, but it is known to occur within anadromous fishes (mostly salmonids; Jonsson and Jonsson 1993; Nordeng 1983) and the estuarine-dependent white perch (*Morone americana*; Kerr et al. 2009). Partial migration can create, in a single population, relatively stable subdivisions known individually as distinct migratory contingents (Secor 1999).

The concept of contingent was introduced by pioneer fisheries scientists such as Hjort (1914). Clark (1968) hypothesized the presence of contingents based on movements of discrete Striped Bass groups within the Hudson River (NY, USA). He used the term contingent to describe "a group of fish that engage in a common pattern of seasonal migration among feeding, wintering, and spawning areas". More recently, contingents have been described across several taxa including Japanese Eel (*Anguilla japonica*; Tsukamoto et al. 1998), Green Sturgeon (Acipenser medirostris; Lindley et al. 2011), Black Bream (*Acanthopagrus butcheri*; Elsdon and Gillanders 2006), and Striped Bass (*Morone saxatilis*; Secor et al. 2001). Contingents were believed to be relevant management units when identified within a population (Secor 1999). In this case, management plans should take into account the unique ecological conditions experienced by each contingent. Knowing which habitats are used and the migratory patterns present within a population is mandatory to quantify the severity of the anthropogenic alterations and the fishing pressure imposed on each contingent. Moreover, such information allows the identification of areas requiring special consideration (e.g. no-take zone, restoration, protection).

Incorporation of trace elements in otoliths from ambient waters provides a natural tag for every fish (Campana 1999; Secor et al. 1995). Studies of chemical variation recorded along the life of fish have become increasingly used to infer fish migrations (Kerr et al. 2009; Secor and Piccoli 1996; Volk et al. 2010). Strontium has been widely used to investigate diadromous fish migrations, since the concentration of this element in water changes with salinity according to a dilution curve (Secor et al. 1995). In addition, other stable elements incorporated in otoliths, such as barium, magnesium or manganese, could be associated with migratory movements into a water mass harboring distinct characteristics (Elsdon and Gillanders 2005; Mercier et al. 2012). Concentration of these elements are used in stock identification, their natural variability providing elemental "fingerprints" of production zones (Campana et al. 1995). Assignment to the population of origin (Rooker et al. 2001) of individuals from a mixed sample (or fishery) is achieved by discriminant analysis (Rooker et al. 2001). Despite its potential utility, multivariate analysis of elemental fingerprints has seldom been used to study migration; a very small percentage of studies use elements other than Sr and Ba concentrations in otoliths (e.g., Arai et al. 2004; Secor and Piccoli 2007; Tzeng et al. 2002).

Several authors highlighted the power gained by using quantitative methods for interpreting elements in otolith chemical profiles (Gemperline et al. 2002; Phillis et al. 2011) over classical methods (e.g., threshold values; Jessop et al. 2002). Hedger et al. (2008) suggested several methods to analyze elemental profiles including split-moving window analysis (SMW), which was developed to identify discontinuities in univariate or multivariate ecological series (Webster 1973). SMW is based on the calculation of a dissimilarity index (e.g., Mahalanobis generalized distance) along an otolith profile between two halves of a "moving window" of a predetermined width. The greatest dissimilarities are representative of discontinuities in the ecological series. Hedger et al. (2008) used SMW to objectively interpret Sr variation within otoliths, however, the procedure can also be performed with multivariate data (i.e., multiple elements from otoliths; Webster 1973).

The St. Lawrence population of Striped Bass (Québec, Canada), once the northernmost population along the North America East Coast, was extirpated in the late 1960s after experiencing heavy fishing pressure, habitat degradation, and pollution (Robitaille et al. 2011).

Following improvements in water quality in the early 1990s (St. Lawrence Centre 1996) and stabilization of forage fish populations, a program to reintroduce Striped Bass in the St. Lawrence Estuary was initiated (Robitaille et al. 2011). Individuals from the Miramichi River population (New Brunswick, Canada) were used to initiate the breeding stock. Since 2002, the fish farm (Baldwin Mills fish hatchery, Québec, Canada) has supplied 14,000 juveniles and 27 million larvae for stocking. Natural reproduction for this population was first observed in 2008 (Pelletier et al. 2011), and larvae from natural spawning events were sampled for the first time in 2010 (Lecomte et al. unpubl). The capture of juvenile Striped Bass throughout the St. Lawrence Estuary (ranging from Montreal to Saguenay River, Fig. 1) suggests the existence of distinct migratory contingents, one associated with freshwater habitats and at least one additional contingent associated with more saline waters. Considering the low abundance of adults compared with historical numbers (Robitaille et al. 2011), the St. Lawrence Striped Bass population is still considered to be in the colonization phase and as such, fishing is still prohibited. We thus presume that density dependence does not play a major role yet in the biology of the introduced population. Thus, habitat utilization observed in the St. Lawrence may reflect the full intrinsic potential of an unexploited, expanding, population that began to exploit a productive, yet heterogeneous, estuarine landscape.

The general objective of this study was to describe the migratory patterns inferred from early life stages of Striped Bass in the St. Lawrence estuary. More specifically, we aimed at (1) identifying the presence of migratory contingents among early life stages using multivariate otolith chemistry and SMW analysis, and (2) identifying the population's spawning sites.

## 2 MATERIALS AND METHODS

### 2.1 Study Site

The St. Lawrence River drains a catchment area of 1.6 × 106 $km^2$ and connects the Great Lakes to the Gulf of St. Lawrence (St. Lawrence Centre 1996). The St. Lawrence Estuary (SLE) is an important part of this system. The upper limit of the estuarine turbidity maximum (ETM) is located 15 km upstream of the first detection of salinity in surface waters and extends 70 km downstream, where surface salinity is approximately 12 (Bewers and Yeats 1978). The ETM is a highly productive area used as a nursery area by several species (Dauvin and Dodson 1990; Dodson et al. 1989; Sirois and Dodson 2000). In the St. Lawrence, as waters become progressively more marine along the longitudinal axis, the SLE exhibits a steep elemental gradient, ideal for studying migration patterns using otolith chemistry (Cossa and Poulet 1978; Yeats and Loring 1991).

## 2.2 Sampling

Samples were obtained through different sources: a monitoring network of the *Ministère du des Forêts, de la Faune et des Parcs du Québec* , commercial by-catch (eel fishing weir), and from experimental beach seine surveys. In 2011, 54 1+ juvenile Striped Bass were captured between June and November at nine sites, two upstream of the salt front and seven downstream (Fig. 1). Between September $4^{th}$ and $17^{th}$ 2012, 64 0+ juveniles were captured at 18 different sites, seven upstream of the salt front and 11 downstream. Each fish was measured (total length = TL) and aged (by scale analysis). In 2011, 1+ fish were frozen immediately after capture; in 2012, 0+ fish were fixed in 95% ethyl alcohol that was replaced after 24h.

## 2.3 Otolith preparation

Sagittal otoliths were extracted and cleaned of organic tissue before being rinsed three times in ultrapure water. Otoliths were allowed to dry under a laminar flow fume hood for 24 h then stored in dry, acid-washed polyethylene vials. Otoliths were handled only with clean plastic forceps previously washed in 10% nitric acid (Trace metal grade 67-70%, Fisher Scientific, QC, Canada, diluted with ultrapure water) for 24 hours and rinsed three times in ultrapure water before drying under a class 100 laminar flow fume hood for 24 h.

The right sagittal otolith was embedded in two-part epoxy resin (Miapoxy 100, Freeman, OH, USA) and cut in transversal sections 1 mm thick with a slow-speed diamond bladed saw (Isomet saw; Buehler, IL, USA). After sectioning, the otolith core was exposed with polishing paper (2000 grit Wetordry$^{TM}$, 3M$^{TM}$) and lapping film (1 and 5 µm lapping film, 3M$^{TM}$). Sagittal sections were mounted on a petrographic microscope slide with thermoplastic glue (CrystalBound$^{TM}$ 509; Aremco$^{TM}$ products, NY, USA). Otoliths were sonicated in ultrapure water for 5 min, dried under a laminar flow fume hood for 24 h, and then stored in slide boxes before laser ablation.

## 2.4 Otolith laser ablation

Otolith trace element concentrations were determined using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS; Agilent 7700x ICP-MS coupled to a Resonetics Resolution M-50 Excimer (193nm) ArF laser). Laser ablations were realized in a profile analysis, a continuous line from one edge to the other, passing through the core. The laser beam diameter was set to 20 μm with a frequency of 15 hz and energy of 4 mJ, and the stage transit speed was 5 $\mu m*sec^{-1}$. Since preliminary measurements showed that Striped Bass otolith daily increments had a mean width of approximately 5 μm (data not shown), resolution was estimated as less than 5 days per second of ablation. This method allows the detection of 22 elements or isotopes ($^{7}$Li, $^{23}$Na, $^{24}$Mg, $^{25}$Mg, $^{29}$Si, $^{31}$P, $^{39}$K, $^{43}$Ca, $^{44}$Ca, $^{55}$Mn, $^{57}$Fe, $^{61}$Ni, $^{63}$Cu, $^{69}$Ga, $^{71}$Ga, $^{86}$Sr, $^{87}$Sr, $^{88}$Sr, $^{136}$Ba, $^{137}$Ba, $^{138}$Ba, $^{139}$La). Three standard materials (SRM-610 purchased from NIST, MD, USA; GP4-A and MACS-3 obtained from USGS, CO, USA) were assessed for 60 s after every five otoliths (roughly every 1.5 h). Calcium ($^{44}$Ca) was used as an internal standard and was assumed to be 40.0% of the otolith mass. Element concentrations were calculated from conversion of isotope counts and expressed in ppm.

## 2.5 Data analysis

The relevance of the information provided by the estimated concentration of all elements was assessed using the limits of detection (LOD) and the limits of quantification (LOQ). LOD was calculated as three times the standard deviation ($SD_{blank}$) of the gas blank divided by the sensitivity of the instrument signal. Similarly, LOQ was defined as 10 times $SD_{blank}$ * sensitivity$^{-1}$ (Lazartigues et al. 2014). By definition, concentration values below LOD cannot be considered "detected" and were replaced by zeros. Because subsequent analyses relied on variations of element concentrations, elements with values below LOQ were not considered. Of the 22 elements quantified by ICP-MS, three did not meet the minimal threshold defined by the established LOD ($^{63}$Cu, $^{71}$Ga and $^{139}$La). Based on noticeable variations along otolith profiles, four elements ($^{24}$Mg, $^{55}$Mn, $^{88}$Sr, and $^{138}$Ba) were selected for subsequent analysis (see Table 1). The isotopic masses used for each element were set to the most abundant natural isotope and assumed to be representative of the total concentration of that element in the otolith. For simplification, no mass numbers will be presented in the text (e.g., Mn = $^{55}$Mn).

For SMW multivariate analysis, trace element concentrations along profiles were transformed to their standardized principal component (PCA) to produce synthetic, uncorrelated variables. Variables not satisfying normality assumptions were natural log transformed (Quinn and Keough 2002), which is best suited for multivariate fingerprint analysis (Campana 2005). The number of principal components used for the SMW was determined by the "eigenvalues equal one" rule by a visual interpretation of a Scree plot (Quinn and Keough 2002).

SMW analysis was then conducted on the two first principal components of the entire otolith profile (from the core to the edge along the longer otolith radius). The window width was determined by autocorrelation analysis, as suggested by Webster (1973). Significant habitat transition was identified as the window position where the Mahalanobis distance was greater than the profile mean distance + one standard deviation (SD). When several adjacent window positions met this criterion, only the position with the highest calculated Mahalanobis distance was considered as the "habitat transition". Data exploration and PCA were done using the R packages *base* and *stats* (R Core Team, 2012), whereas the SMW was done using the smw.R procedure (Rossiter unpubl.).

Since each "habitat transition" represents a change between two constant multivariate chemical fingerprints, the elemental signal between two transitions was considered as representative of a period of uniform chemical deposition on an otolith. The habitat fingerprint was then represented by the mean value of the four selected element concentrations between two transitions. Their positions were converted to "relative age positions", the ratio of the distance (µm) from the core to the habitat transition on the profile length representing the total growth season (µm). Variation in the chemical composition of an otolith can be the result of migratory movements, physiology or habitat condition. We assume that most of this variation is induced by true migratory movement. Hence, only discriminant function analysis (DFA) can identify a transition with enough magnitude to be related to migratory movement.

SMW-delimited elemental fingerprints were classified by DFA generated using otolith margin fingerprints. Mean values of the last 20 analysis points (corresponding to ~ 30 µm with the parameters used for the laser) of a profile were assumed to be representative of the element concentrations of the area where the fish was captured. Capture site fingerprint identities were assigned to one of the three SLE zones, which were defined according to water salinity and grouped following the modified Venice classification (Bulger et al. 1993). From upstream to downstream, zones were designated as freshwater (F; salinity 0 to 4), oligohaline (O; salinity 2 to 14), and mesohaline (M; salinity 11 to >18). The modified Venice classification is a biologically based (i.e., based on species distribution) separation encompassing natural variability of estuarine waters. Prior to DFA, homogeneity of the within–group variance–covariance matrices was tested by plotting the scores of the first two discriminant functions and checking for homogeneity as suggested by Tabachnick and Fidell (1996). Migration behavior is described as the successive occupation of distinct zones identified along the otolith profile (e.g. F, O or M), and according to the pattern detected, for each individual assigned a general behavior (e.g. resident, oligohaline-migrant, mesohaline-migrant). Successive identification of the same zone along a profile (ex. two transitions identified as freshwater) was considered as residency in this zone.

Time spent in each habitat was estimated using back-calculated lengths during habitat transitions and the individual average growth rate. The biological intercept procedure was used to back-calculate length at each habitat transition (Campana 1990). Based on laboratory observations, the biological intercept in the back-calculation equation was set to a TL of 5 mm and an otolith radius of 15 µm. Individual growth rates were calculated assuming a length of 5 mm at hatching and an average birth date on May 24$^{th}$ (Lecomte et al. unpublished). Time spent in each habitat was then calculated for each fish and for each length interval between habitat transitions.

Otolith core fingerprints were used to characterize the spawning sites where individuals originated. Mean values for the four elements selected in the first 20 analysis points of the profile were considered as the core fingerprint, representing water characteristics of the spawning site. Core fingerprints were classified with DFA using 2011 and 2012 fingerprints separately to create the discriminant function. However, to confirm that differences were due to spawning location and not from a potential maternal effect (Kalish 1990; Secor 1992)), we compared the results from the previous definition of the "core fingerprints" with an area more distant from the otolith core (i.e., after yolk-sac absorption). We assumed that all Striped Bass larvae had completely absorbed their yolk-sac at a maximum TL of 7.5 mm (Wallus and Simon 2006). This is a conservative value compared to the average minimal value observed (TL = 6 mm) in North American populations (Wallus and Simon 2006). According to two classical studies on otolith–length relationships (Dickey et al. 1997; Secor and Dean 1989), a 7.5 mm TL Striped Bass larva has an otolith radius of between 40 to 60 µm, depending on the growth ratio (between 15 and 30 µm for 6 mm TL larvae). We conducted DFA classification and PCA ordination of the 20 analysis points between 40 to 60 µm of the laser profile (post yolk-sac), which assures a signature representative of the first habitat used without maternal contribution. All the DFA and PCA ordinations were done with PRIMER 6 (PRIMER-E Ltd.).

# 3 RESULTS

## 3.1 Habitat utilization and migratory contingents identification

The first two principal components that were estimated on each fish for SWM analysis accounted on average for 75.1 ± 8.09% (mean±SD) of the variance. The window size was set for each individual and varied between 49 and 400 units (220 ± 82 units; mean±SD) depending on the autocorrelation analysis. The SMW analysis successfully detected on average 6.4 segments on each otolith profile (min 2, max 13). Mean values for the four elements in each segment were assumed to be representative of the exploited habitat and two adjacent segments identified by the SMW analysis may be assigned to the same habitat. Hence, each fish did on average 1.4 habitat transitions during its entire life (min 0, max 5). For the 118 otoliths analyzed, a total of 753 otolith profile segments and 162 habitat transitions were identified.

Element concentrations at the otolith margin were significantly different among zones in 2011 (MANOVA 2011: $F_{2,51} > 29.50$, $p < 0.001$; Fig. 2). In 2012, only Mn variation was not significant; otherwise, the remaining element concentrations were significantly different among zones (MANOVA 2012: $F_{2,61} > 22.09$, $p < 0.001$; Fig. 2). Fingerprints were classified by DFA according to the chemical composition representing the various estuarine zones (F, O or M). Since the variance–covariance of the 2012 dataset was not homogeneous, it was necessary to use quadratic discriminant function analysis (QDFA); the 2011 variance–covariance was homogeneous, allowing the use of linear discriminant function analysis (LDFA). Classification success was 93.8% for 1+ Striped Bass (2011) and 95.3% for (2012) 0+ Striped Bass (Fig. 3). Three similar patterns of habitat utilization were recurrent and grouped as migratory contingents (Fig. 4).

The first contingent includes all juvenile Striped Bass that spent their entire life before capture in freshwater; they were thus referred to as "freshwater resident". The second contingent, "Oligohaline migrant", grouped individuals that moved between freshwater and oligohaline zones at least one time. Finally, the "mesohaline migrant" group included Striped Bass that made at least one movement into the mesohaline zone. Most of the individuals in the analysis (90.8%) had a freshwater fingerprint identified as the first habitat occupied, 7.6% had first used the oligohaline zone, while only 1.6% (n=2) had the mesohaline zone as their first habitat used. To observe the maintenance of contingents before and after the first winter for the 1+ Striped Bass (i.e., individuals that spent two summers in the SLE), the contingent to which they belonged for their first year of life was also identified (Fig. 5). The proportion of contingents in the sample did not vary much between years. During their first year, 27.8% were freshwater residents, 48.1% were oligohaline migrants, and 24.1 % were mesohaline migrants (Fig. 5). The proportion remained fairly similar during their second year (22.2% freshwater residents, 40.7% oligohaline migrants, 37.1% mesohaline migrants). For the 2012 cohort (0+ Striped Bass), freshwater residents dominated with 45.3%, followed by oligohaline migrants (34.3%) and mesohaline migrants (20.3%; Fig. 5).

As previously defined, freshwater residents for both years utilized the freshwater zone 100% of the time. Oligohaline migrants sampled in 2011 and 2012 had similar habitat utilization of freshwater (ca 75%) and oligohaline (ca 25%) habitats (Fig. 6). However, frequency of the habitat utilization by mesohaline migrants was variable. In 2011, Striped Bass predominantly used mesohaline habitats (45%), whereas fish sampled in 2012 favored freshwater (68%; Fig. 6).

### 3.2 Spawning sites identification

The origins of Striped Bass identified with otolith core fingerprints were classified as freshwater or oligohaline; freshwater origin was more frequent than oligohaline, and there was no otolith core classified in the mesohaline habitat (Table 2, Fig. 7). On the other hand, all three habitats were represented in the fingerprints from post-yolk-sac analysis in 2011 and 2012. The freshwater habitat dominated the post-yolk-sac origin (89% in 2011 and 66% in 2012). A smaller proportion of individuals were assigned to oligohaline (9% in 2011 and 33% in 2012) or mesohaline (2% in 2011 and 2012) habitat (Fig. 7). The similar ordination between the core and post-yolk-sac areas suggests that otolith core fingerprints successfully represented the signature of the water mass rather than a potential maternal effect in Striped Bass larvae.

The major spawning zone for all contingents within the St. Lawrence Estuary is clearly located within the freshwater portion of the estuary. However, spawning sites located within the oligohaline zone are also used to a certain degree. There is no link between the spawning site habitat (freshwater or oligohaline) and the future migratory contingent expression.

## 4 DISCUSSION

### 4.1 Habitat utilization and migratory contingents identification

As hypothesized, the extensive distribution of early-life stages of Striped Bass within varied habitats of the St. Lawrence appear as a consequence of the expression of divergent migratory contingents. Results showed that distinct migratory patterns were common in the newly introduced Striped Bass population in the St. Lawrence and such observation appeared recurrent among cohorts. Observed contingents were similar to those observed in many native Striped Bass populations along the North American East Coast (Secor and Piccoli 2007; Wingate et al. 2011;

Zlokovitz et al. 2003). The main difference lies in the fact that migratory behaviors established earlier in life within St. Lawrence River Striped Bass than elsewhere. Identification of contingents in a recently reintroduced population underlines the adaptable nature of the species. Striped Bass are described as an estuarine opportunist (Ray 2005), the expression of a partial migratory behavior leading to contingents (Chapman et al. 2011a; Chapman et al. 2012).

As early as the middle of their first growing season, 0+ individuals from a relatively homogenous origin are already exhibiting divergent patterns in habitat utilization. In both cohorts we sampled, downstream movements occurred when Striped Bass were > 40 mm in total length (data not shown). At this length, Striped Bass have acquired swimming capability (Mansueti 1958) and are able to circumvent passive drift imposed by estuarine circulation. The precocious expression of contingents is an unusual behavior for the species, which is not believed to exhibit migratory behavior until 2-4 years of age when multiple contingents (migratory and resident) coexist (Rulifson and Dadswell 1995; Secor and Piccoli 1996). Comparable observations of precocious migratory behavior have also been made in the southern Gulf of St. Lawrence (the source population), where all young-of-the-year exhibit downstream migration from late June to September (Robichaud-LeBlanc et al. 1998; Robinson et al. 2004). No distinct migratory contingents are known from this southern population.

The population from which this St. Lawrence population was derived is known for its strict migratory behavior within the Miramichi estuary (Douglas et al. 2009). Young-of-the-year undertake a downstream migration toward coastal waters or other nearby estuaries between June and September (Robichaud-LeBlanc et al. 1998; Robinson et al. 2004). Virtually no juveniles remain residents in freshwater during their first year of life. Moreover, as far as we know adults make a direct migration to upstream spawning grounds and stay there for 1–2 weeks before returning downstream, with no observed freshwater residency (Douglas et al. 2009; Hanson and Courtenay 1995). While neither partial migration nor multiple contingents are known in the source population, the newly reintroduced St. Lawrence Striped Bass almost instantaneously exhibited a wide spectrum of migratory behavior similar to large populations of the central East Coast of North America. In less than 10 years of initial reestablishment, Striped Bass appears to have colonized most available habitats, ranging from the freshwater portion to the more saline (salinity >18) part of the middle estuary. It seems that this colonization was achieved through divergent life-cycle pathways. The reintroduced population exploits an area believed to be more than two times greater than the one occupied by the extirpated (historical) St. Lawrence Estuary population (Robitaille et al. 2011). This newly reintroduced population can be assumed to be relatively genetically homogenous. However, individuals exhibit contrasting early-life histories not representing this homogeneity. It appears that contingent membership is determined mainly during the first growing season and not by natal origin.

## 4.2 Spawning site identification

The first spawning site identified for the reintroduced SLE population was located upstream of the estuarine salt front near the mouth of du Sud River (Montmagny, QC; Lecomte et al. submitted). Our study suggests that spawning does not take place exclusively at this site. While the dominant freshwater origin can be attributed to recruitment from the du Sud River, the oligohaline fingerprints indicate the existence of an additional spawning site. Interestingly, in June 2013, a second important spawning site was identified with the capture of ripe individuals, during the spawning season, in the downstream portion of the Ouelle River. This river flows into the oligohaline portion of the St. Lawrence (Fig. 1).

The concordance between core and post-yolk-sac fingerprints suggests that the maternal contribution to the otolith's chemical signature in Striped Bass larvae is negligible, as also observed by Secor (1992). Rapid absorption of vitelline reserves (Eldridge et al. 1981), short incubation time, and precocious exogenous feeding (Eldridge et al. 1982; Tsai 1991; Wallus and Simon 2006) by Striped Bass larvae probably reduce the maternal effect on otolith chemistry. The common maternal effect on otolith fingerprints of salmonids (Kalish 1990; Zimmerman and Reeves 2002) is attributed to higher vitelline reserves (Peterson et al. 1996) and the corresponding longer period of time needed to absorb them. To exemplify this, the total length of salmonid larvae triples during yolk-sac absorption, whereas Striped Bass larvae gain only 50% of their total length during this phase. Our study suggests that core fingerprints could safely be used to represent spawning ground signatures for Striped Bass.

### 4.3 Multivariate profile analysis

The effectiveness of the method used herein was optimized by the conservative behavior of numerous chemical elements related to salinity in estuarine ecosystems (Subramanian and D'Anglejan 1976). The use of several elements (fingerprints) improved the accuracy of habitat transition identification and the reconstruction of past life history by identifying habitats that may have been missed otherwise. For example, it appears that fingerprints of some otoliths with Sr concentrations high enough to be within the range of those from mesohaline habitats (Fig. 3B; Sr concentration in oligohaline habitat) were nevertheless classified as oligohaline thanks to the added discriminatory power provided by the other elements (Ba, Mg, and Mn). While SMW is a powerful and robust method, discontinuities occurring at the ends of a profile are easily missed since the distance criteria cannot be calculated (i.e., separate portions of the window need to be equal in length: for a 100-point window, the last 50 points of the laser ablation profile are not included in SMW). This limitation can lead to small discrepancies between first or last identified habitat and core or margin values. To overcome this limitation, we separately defined elemental fingerprints of the otolith margin and core. This allowed us to include all the parts of the otolith in the analysis and avoid this limitation of the SMW.

### 4.4 Concluding remarks

Investigation of the migratory behaviour of a recently reintroduced population of Striped Bass reveals the adaptive potential of the species. Evidence shows the establishment of three distinct migratory contingents within the population, less than a decade after first introduction. The rapid formation of a relatively stable migratory structure takes place even if these contingents were unknown in the population used to reintroduced Striped Bass in the St. Lawrence. Results shed some light on the rapid success of the reintroduction program, mainly by showing that Striped Bass was rapidly able to exploit, even early during their life cycle, habitats available within the estuary. This observation matches the previous report of the “explosive” population burst, following Striped Bass colonization of the estuaries along the west coast of North America (Smith and Kato 1979; Stevens et al. 1985). As shown for the unexploited, expanding St. Lawrence Striped Bass population, such species may in fact possess intrinsic adaptive capacities to fully exploit heterogeneous, unpredictable, yet highly productive estuarine environments. Maintenance of this “adaptiveness” can be attributed to phenotypic plasticity driven by a switch mechanism, like the threshold traits model (Pulido 2011) or the plasticity-relaxation-mutation (Hughes 2012). Considering the ecology of the species, conservation of this plasticity can give selective advantage. Striped Bass populations are subjected to highly variable inter-annual environmental and biotic conditions (Martino and Houde 2010; North and Houde 2003), and individuals that are extensively mobile can cope with these variable habitats. The reintroduction program of Striped Bass can then be considered as a large-scale experiment of colonization. This opens opportunities to study the intrinsic potential of adaptation of estuarine Striped Bass.

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TABLES

Table 1. Mean (with SD) limits of detection (LOD) and limits of quantification (LOQ) of selected trace elements

| Elements | LOD (ppm) | LOQ (ppm) |
|---|---|---|
| $^{24}Mg$ | 0.18 ± 0.45 | 0.61 ± 1.51 |
| $^{55}Mn$ | 8.52 ± 0.69 | 29.0 ± 4.00 |
| $^{88}Sr$ | 0.05 ± 0.12 | 0.17 ± 0.38 |
| $^{138}Ba$ | 0.03 ± 0.02 | 0.10 ± 0.05 |

Table 2. Origin (in percentage) of freshwater resident (FR), oligohaline migrant (OM), and mesohaline migrant (MM) estimated from the otolith core elemental fingerprint

| | 2011 1+ sample (n=54) | | | 2012 0+ sample (n=64) | | |
|---|---|---|---|---|---|---|
| Origin | FR | OM | MM | FR | OM | MM |
| Freshwater habitat | 100% | 92.3% | 66.7% | 65.5% | 59.0% | 53.8% |
| Oligohaline habitat | 0% | 7.7% | 33.3% | 34.5% | 41.0% | 46.2% |
| Mesohaline habitat | 0% | 0% | 0% | 0% | 0% | 0% |

FIGURES CAPTIONS

**Fig. 1** Sampling sites along the St. Lawrence Estuary. White open circles are 2011 sample sites and black solid circles are 2012 sample. The black lines show the approximate limits of the defined salinity zones, corresponding to a modified Venice classification. Salinity range associated with each salinity zone is shown in parentheses

**Fig. 2** Mean element concentrations (ppm) in 2011 and 2012 for three identified zones. Different letters indicate a significant difference (Tukey's HSD) among zones for all otoliths of a same year

**Fig. 3** Ordination of the discriminant function analysis for 2011 (upper panel) and 2012 (lower panel) otolith profile segments

**Fig. 4** Trace element (Mg, Mn, Sr, and Ba) concentrations (in ppm) during the first growing season (0+) as determined from otolith profile (back-calculated age in days) from the otolith's core to edge. Individuals typical (a) of a freshwater resident, (b) of an oligohaline migrant, and (c) of a mesohaline migrant. Vertical lines show habitat transitions determined by SMW and capital letters identify DFA classification of inhabited zones: F= freshwater, O = oligohaline, and M = mesohaline

**Fig. 5** Proportion of contingent for 1+ fish sampled in 2011 first and second year (upper panel) and for 0+ fish sampled in 2012 (lower panel)

**Fig. 6** Mean of relative habitat utilization by contingent of 1+ striped bass captured in 2011 (upper panel) and 0+ Striped Bass captured in 2012 (lower panel), error bars shows standard deviation (SD)

**Fig. 7** Spawning site elemental fingerprints in Striped Bass at hatching (core) and after yolk resorption (post-yolk-sac) for both year. Different symbols represent group reclassification by DFA

FIGURE 1

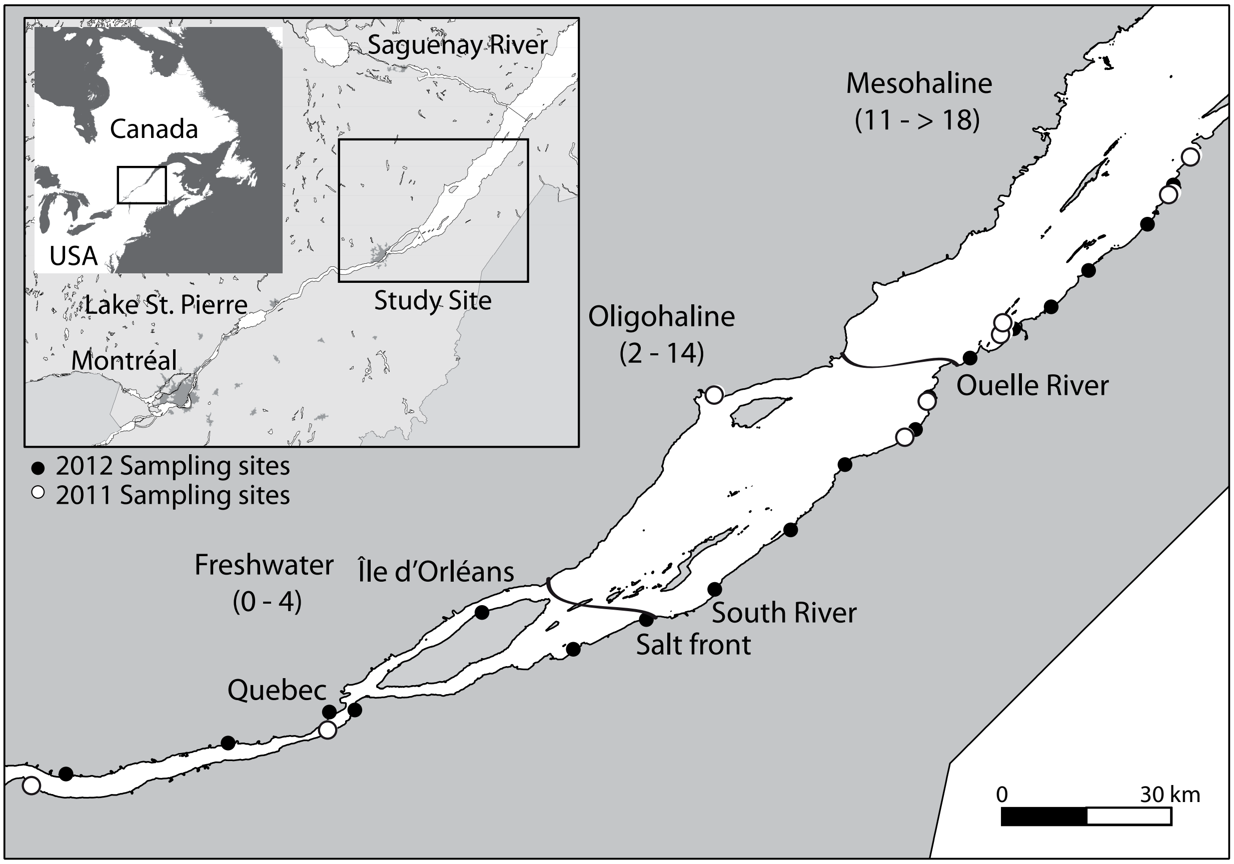
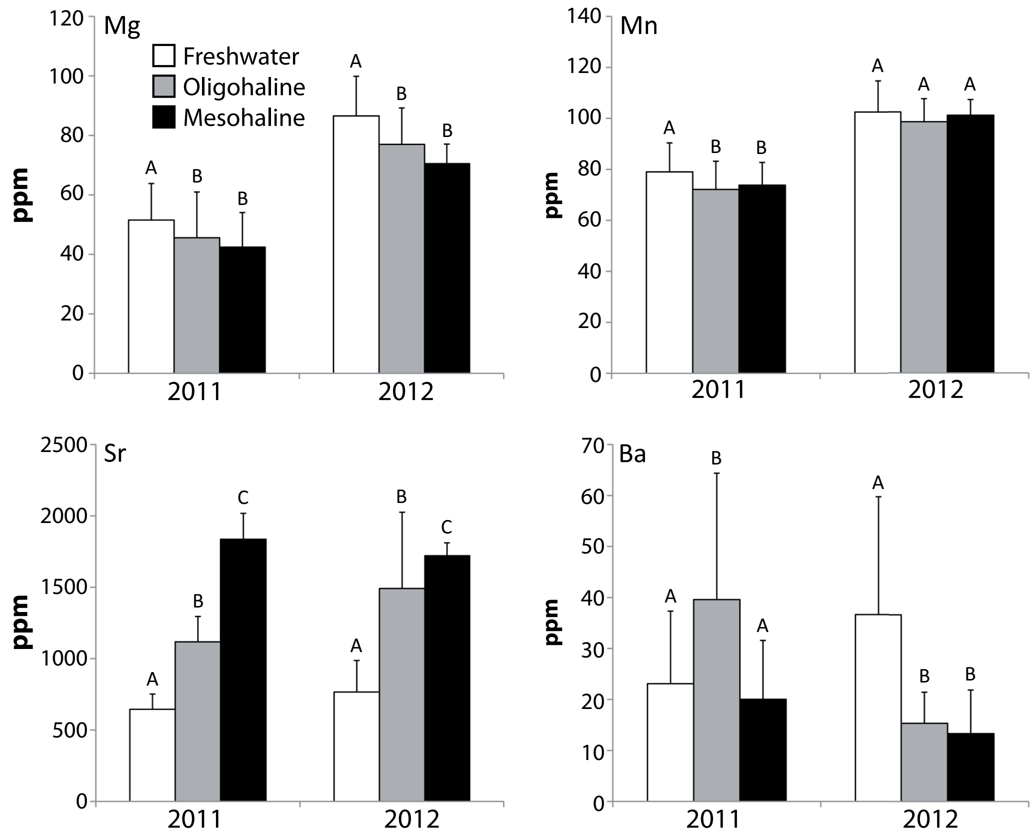

Saguenay River
Canada
USA
Lake St. Pierre
Study Site
Montréal
Mesohaline
(11 - > 18)
Oligohaline
(2 - 14)
Ouelle River
2012 Sampling sites
2011 Sampling sites
Freshwater
(0 - 4)
Île d'Orléans
South River
Salt front
Quebec
0
30 km

FIGURE 2



Mg
Freshwater
Oligohaline
Mesohaline
ppm
120
100
80
60
40
20
0
A
B
B
A
B
B
2011
2012
Mn
140
120
100
80
60
40
20
0
A
B
B
A
A
A
2011
2012
Sr
2500
2000
1500
1000
500
0
A
B
C
A
B
C
2011
2012
Ba
70
60
50
40
30
20
10
0
A
B
A
A
B
B
2011
2012

FIGURE 3

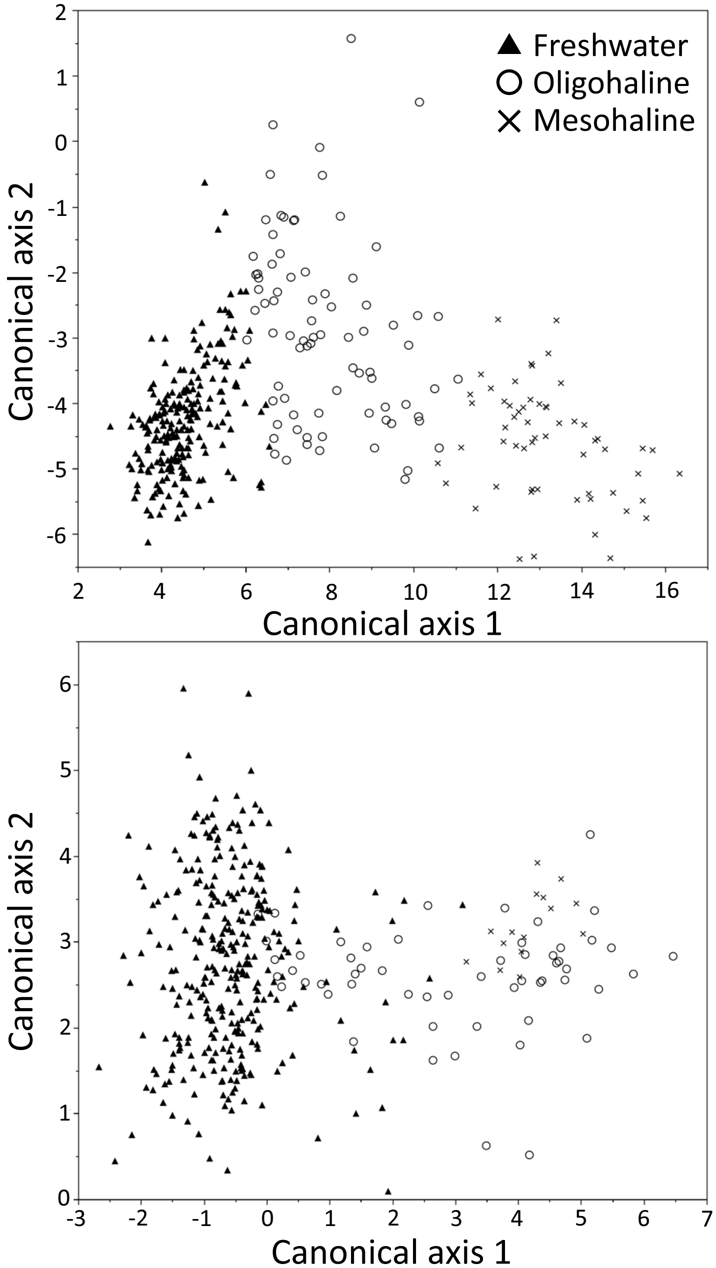

Freshwater
Oligohaline
Mesohaline
Canonical axis 2
Canonical axis 1
2
1
0
-1
-2
-3
-4
-5
-6
2
4
6
8
10
12
14
16
Canonical axis 2
Canonical axis 1
6
5
4
3
2
1
0
-3
-2
-1
0
1
2
3
4
5
6
7

FIGURE 4

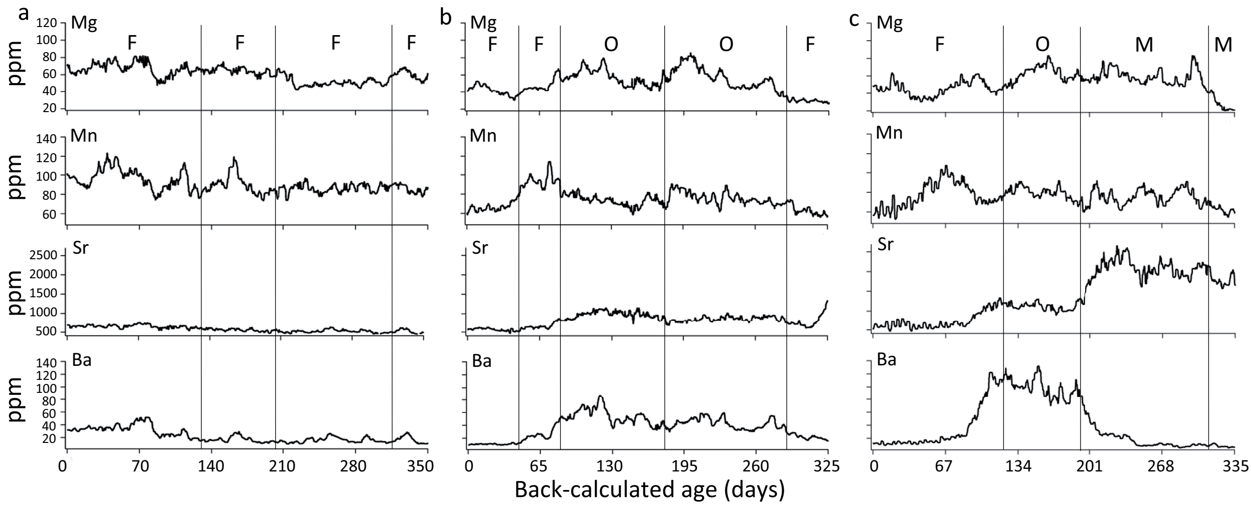

a
b
c
Mg
Mn
Sr
Ba
ppm
F
O
M
0
70
140
210
280
350
65
130
195
260
325
67
134
201
268
335
Back-calculated age (days)

FIGURE 5

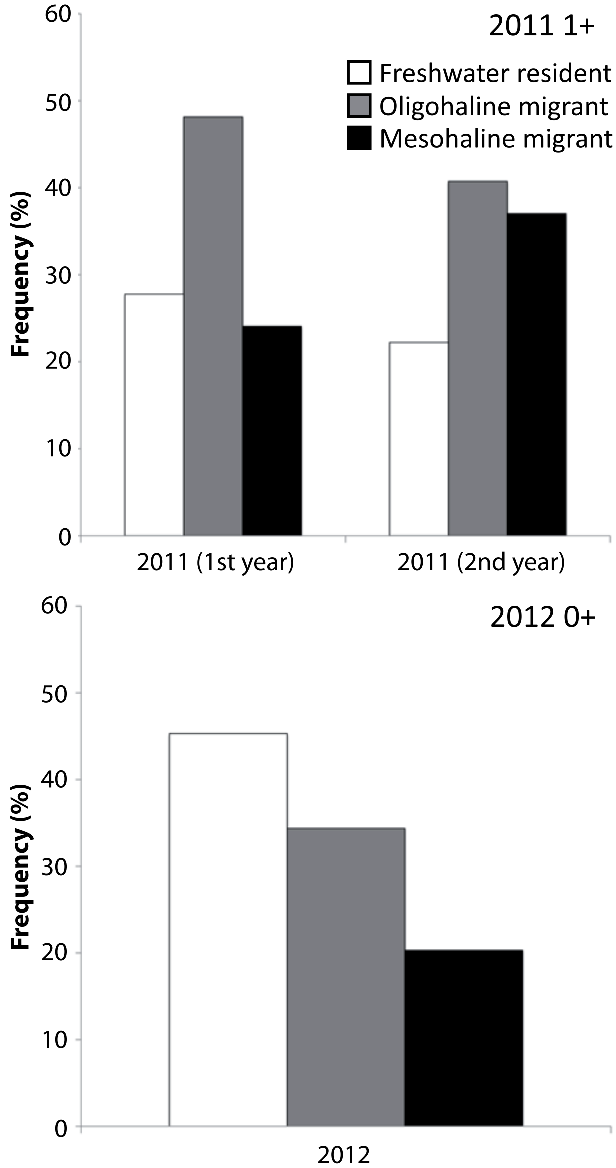

2011 1+
Freshwater resident
Oligohaline migrant
Mesohaline migrant
Frequency (%)
0
10
20
30
40
50
60
2011 (1st year)
2011 (2nd year)
2012 0+
Frequency (%)
0
10
20
30
40
50
60
2012

FIGURE 6

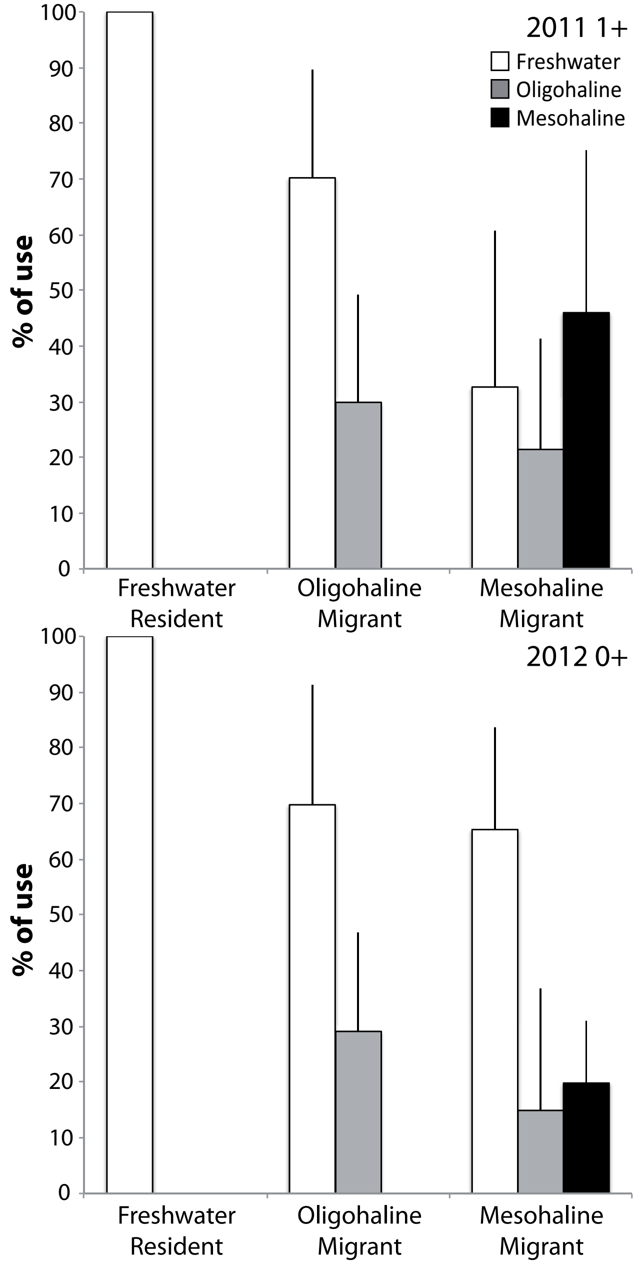
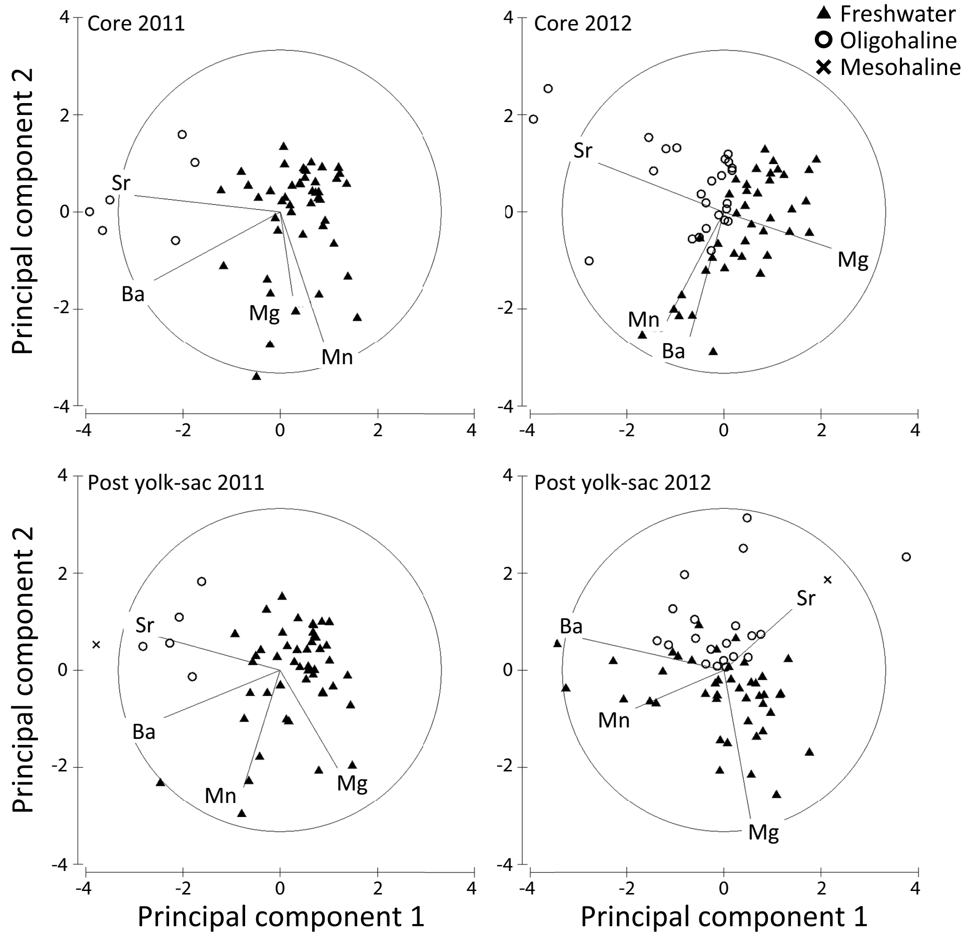

2011 1+
Freshwater
Oligohaline
Mesohaline
% of use
100
90
80
70
60
50
40
30
20
10
0
Freshwater Resident
Oligohaline Migrant
Mesohaline Migrant
2012 0+
% of use
Freshwater Resident
Oligohaline Migrant
Mesohaline Migrant

FIGURE 7



Core 2011
Core 2012
Post yolk-sac 2011
Post yolk-sac 2012
Freshwater
Oligohaline
Mesohaline
Principal component 2
Principal component 1
Sr
Ba
Mg
Mn