

University of Maryland Center for Environmental Science
Chesapeake Biological Laboratory
P. O. Box 38
Solomons, MD 20688-0038

FINAL REPORT

EFFECT OF MIGRATION ON POLYCHLORINATED BIPHENYL CONCENTRATIONS IN HUDSON RIVER STRIPED BASS

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SUBMITTED TO:

Dr. Dennis J. Suszkowski
Science Director
Hudson River Foundation
40 West 20th Street, Ninth Floor
New York, N.Y. 10011

PRINCIPAL INVESTIGATORS:

David H. Secor and Joel E. Baker
University of Maryland Center for Environmental Science
Chesapeake Biological Laboratory
P.O. Box 38
Solomons, MD 20688-0038

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EXECUTIVE SUMMARY

Since 1976, the commercial striped bass fishery in the Hudson River (NY) has been closed due to high levels of total polychlorinated biphenyls (*t*-PCBs) concentrations in edible tissues. PCB contamination in sediments is high in the Hudson River Estuary, due in part to historical loadings. From the mid 1940s to the mid 1970s, the Hudson River estuary received over 2.5×10^5 Kg of PCBs largely as a result of industrial discharges above the Troy Dam at Ft. Edward and Hudson Falls. Sedimentary PCB inventories reveal a considerable concentration gradient down-estuary due to advective, dispersive and dilution effects. Although concentrations in edible portions of striped bass declined significantly after the termination of direct discharge in the upper estuary in 1978, annual averages still exceed the 2 $\mu\text{g/g}$ (ppm) action limit promulgated by the US Food and Drug Administration (FDA) (Sloan et al. 1995).

We investigated the expectation that variable habitat use by striped bass caused differential exposure to and contamination by PCBs in the Hudson River Estuary. We used electron microprobe analysis of strontium in otoliths, which estimates salinity in the fish's environment, as a method for estimating recent and life-time habitat use by striped bass. This report is structured on four aims: 1) to relate total PCB levels in striped bass to recent habitat use in the Hudson River Estuary and Long Island Sound (Chapters 1 and 2); 2) to use PCB congener patterns in striped bass as an index of near-source habitat use and relate these to migration patterns (Chapter 2); 3) to develop a novel analytical tool, elemental fingerprinting of striped bass otoliths, for measuring patterns of habitat use to verify interpretations on Hudson River striped bass migration patterns (Chapter 3); and 4) based upon theoretical considerations, to begin to examine the causes and consequences of divergent migrations in striped bass and other fishes as revealed by otolith composition analyses (Chapter 4).

Recent habitat use was a strong determinant of PCB contamination for striped bass collected during fall and spring months ($n = 88$). Total PCB body burden was inversely correlated with mean salinity encountered during the most recent growth season prior to capture. ANOVA and regression tests showed that PCB levels were strongly and negatively related to recent salinities at which striped bass grew, independent of effects due to of season of capture, sex, site of collection, or fish size. All individuals with highly contaminated PCB levels (mean PCB ≥ 9 ppm) showed freshwater resident behavior, rarely experiencing salinities >5 ppt. Results supported the expectation that fish inhabiting highly contaminated freshwater regions during the growth season prior to capture will not be able to significantly reduce body burden due to growth dilution.

Fish with recent exposure to mesohaline salinities showed high variability in PCB body burdens (0.4 - 9.0 ppm), suggesting a local source of PCB contamination in the New York Harbor region. In some cases, microprobe analysis revealed that fish which shifted from coastal or brackish habitats to up-estuary freshwater habitats were likely to show high PCB levels. However, the converse was not always true: fish which shifted from freshwater to brackish marine habitats did not always reduce their PCB levels, again indicating the possibility of a mesohaline source of PCBs. These results corroborate recent observations of relatively high mean PCB levels in fish collected in the New York Harbor region.

Seventy-one fish collected throughout the Hudson River estuary and Long Island Sound were analyzed for congener specific PCBs. Similar to work based upon *t*-PCB body burden estimates provided by the Hazleton laboratory, our estimates of *t*-PCB also showed an inverse correlation with salinity in recently experienced habitats. In general, striped bass permanently residing in fresh and oligohaline portions of the estuary adjacent to known PCB sources had higher *t*-PCB levels. Fish utilizing the 0 to 5 ppt salinity range had congener patterns, with higher proportions of lower chlorinated congeners (di-, tri-, and tetrachlorobiphenyls) from those utilizing down-estuary salinity ranges. Patterns dominated by lower chlorinated congeners were indicative of lifetime exposure to unweathered PCBs in the fresh to oligohaline waters of the upper estuary (Troy Dam) while patterns shifted to more highly chlorinated congeners down-estuary. Striped bass recently using the salinity range 20 to 25 ppt showed considerable variability in the concentration of *t*-PCBs possibly suggesting exposure to a local source of PCBs. Moreover, within this salinity range, there were several fish that displayed source-like patterns, even though their individual lifetime salinity chronologies suggested that they had not been in fresh to oligohaline (0 to 5 ppt) waters recently (i.e., the last three years) or for their entire lives. Although there is evidence supporting additional PCB sources in the lower Hudson River Estuary (e.g., New York Harbor), the current limited resolution of otolith electron microprobe analysis in identifying exact locations based on salinity ranges within the lower Hudson River curtailed full evaluation of this issue.

While otolith Sr (salinity) is an important scalar in the patterns of variable migration of Hudson River striped bass, otoliths contain other elements which might record more subtle environmental gradients, and thereby more precisely define habitat use. Elemental fingerprints of otoliths have been used recently as a means to identify natal source and evaluate migration patterns for several coastal and oceanic species. Elemental fingerprints of otoliths from 21 Hudson River striped bass *Morone saxatilis* were used to define resident, estuarine, and coastal migratory contingents which had previously been determined by otolith microanalysis of Sr. Using bulk chemistry inductively coupled plasma mass spectrometry (ICP-MS), thirteen alkali and transition metals were detected. Discriminate analysis of elements other than Sr (deliberately excluded) showed a high degree of separation among the three migratory contingents. Transition metals Co, Cu, and Cd and the alkali Rb were higher in otoliths from the freshwater contingent. Zinc was higher in otoliths of the estuarine contingent and alkali metals Ca, K and Mg were higher in the coastal contingent. Identification of contingents by the ICP-MS bulk chemistry method indicated divergent lifetime migratory patterns for Hudson River striped bass. ICP-MS and electron microprobe measures of Sr were directly compared and showed 95% precision. Identification of contingents by the ICP-MS bulk chemistry method indicated that a discrete set of lifetime migration patterns exist for Hudson River striped bass. Future studies employing otolith elemental analyses will provide a unique opportunity to examine the causes and consequences of sub-population migration behaviors.

In a past study on seasonal striped bass migration in New York Harbor and Long Island Sound, Clark (1968) showed a strong "clustering effect," where tagging location influenced recapture location. Striped bass tagged in New York Harbor exhibited little dispersal in all seasons, tending to be recaptured in New York Harbor or western Long Island Sound. Fish tagged in eastern Long Island Sound were more dispersive but tended to be recaptured throughout Long Island Sound and off of Cape Cod. Clark concluded that these two groups, plus an additional migratory Atlantic group were "contingents," each contingent defined by a unique seasonal migration:

"Variations in migration patterns, shown by differences of seasonal distribution of tag recaptures, suggest that different contingents of striped bass occupied the area of our study during the course of each year. We have attempted to identify these and to describe their migratory characteristics. We do not argue that these contingents are genetically distinct, but that they are separate components of the Atlantic population. They may have formed simply by the accident of being brought together in one nursery area as juveniles. However, a contingent may be formed; once established it appears to maintain its integrity by engaging in a distinct pattern of seasonal migrations not shared by fish of other contingents." (Emphasis added).

Our otolith microprobe analyses supported this hypothesis, revealing three discrete migration patterns in Hudson River striped bass: 1) a resident group, inhabiting freshwater and oligohaline regions of the Hudson River; 2) a lower estuary "mesohaline" group, inhabiting mesohaline and polyhaline regions (Harbor-LI System); and 3) a coastal migratory group. Combining our results with Clark's, there is evidence for contingents centered in the Hudson River, New York Harbor, Western Long Island Sound, and coastal Atlantic.

An intriguing question is, if such contingents exist, then how are they controlled and regulated? Using frameworks for understanding smoltification in salmonids and ontogenetic niche shifts, I hypothesize that early life decisions regarding energy allocation lead to later divergence in habitat shifts (migration). This mechanism results in the maintenance of "retentive" and "exploratory" behaviors and contributes to features of population regulation including persistence, range contraction and expansion, and colonization. Examples of divergent migration tactics exist for a diverse array of teleosts and has significant bearing on how we manage fish stocks and understand environmental effects on fish populations. Because the current meaning of stock is synonymous with biological population, factors which affect accessibility to human impacts (i.e. contingent dynamics) remain unspecified. We recommend that the stock concept should be modified to incorporate a hierarchy of biological levels which evaluate both lineage (subpopulation - population - metapopulation - subspecies - species) and accessibility (individual - brood - school/shoal - yearclass - contingent).

Research and Management Recommendations

Previous models of the long-term behavior of PCBs in striped bass were biased towards coastal habitat use in adult striped bass and under-represented PCB burdens in the overall Hudson River population. The fraction of the population which is resident (or spends parts of their life in the New York Harbor region) is unknown and would be expected to vary on an annual and generational time-frame based upon changes in recruitment and exploitation on the more migratory contingents of the population. The high degree of variability and unpredictability in spatial dynamics the Hudson River striped bass prescribes more intensive monitoring of migration patterns and meta-population and individual-based modeling approaches to predict future rates of PCB loss.

Striped bass collected in the upper estuary (river km >90) during the fall months are likely to be resident fish which are highly contaminated with PCBs. Fishing in the upper estuary should continue to be restricted. Further, health warnings could be revised to reflect the increased likelihood of contaminated striped bass collected in upestruary regions during fall. Evidence from our study also suggests that some but not all striped bass utilizing New York Harbor - W. Long Island Sound encounter local sources of PCB contamination which should be identified and regulated in the near future.

CHAPTER 1. Effect of Habitat Use on PCB Body Burden in Hudson River Striped Bass (*Morone saxatilis*)

Erik R. Zlokovitz and David H. Secor

ABSTRACT

The Hudson River commercial striped bass fishery has been closed since 1976 due to high PCB contamination. Accurate forecasting of PCB levels in striped bass has been confounded by high variance in contamination among individuals. We investigated the relationship between habitat use and PCB contamination in Hudson River and Long Island striped bass, using electron microanalysis of otolith strontium to generate time series of individual salinity habitation. Males with highly contaminated levels (mean PCB = 9 ppm) showed freshwater resident behavior, rarely experiencing salinities >5 ppt. Several individuals showed large habitat shifts. Shifts from brackish or marine habitats to freshwater habitats were often associated with high PCB levels. A third pattern was apparent in large females, where polyhaline/euhaline salinity habitation was associated with lower PCB levels. Total PCB body burden was inversely correlated with mean salinity encountered during the most recent growth season prior to capture. Fish with recent exposure to mesohaline salinities showed high variability in PCB body burdens (0.4 - 9.0 ppm), suggesting a local source of PCB contamination in the New York Harbor region.

INTRODUCTION

The Hudson River commercial striped bass fishery has been closed since 1976 due to high levels of polychlorinated biphenyl (PCB) contamination (Limburg 1986; Brown et al. 1985). The mean PCB body burden in Hudson River striped bass continues to exceed the current U.S. Food and Drug Administration (FDA) action limit of 2.0 ppm (Bush et al. 1989; Fabrizio et al. 1991). Closure of the Hudson River fishery in 1976 and the Long Island coastal fishery in 1985 due to PCB contamination has resulted in an estimated annual loss of \$0.75 - 3.7 million to the New York striped bass fishery (Kahn and Buerger 1994). In addition, recreational striped bass fishermen have been issued annual fish consumption health advisories since 1976 (Sloan et al. 1986).

A total of 2.7×10^5 kg PCBs were discharged into the Hudson River estuary from approximately 1947 to 1987 (Thomann et al. 1991). The majority of PCB contamination to the Hudson River estuary resulted from a solvent washing process at the General Electric capacitor facility above the Troy Dam (river km 246) (Bush et al. 1989). High levels of PCBs (mean 18.1 ppm total PCB) were found in the edible flesh of the striped bass in 1978 (Horn and Sloan 1985; Bush et al. 1989). As a condition of the 1975 Settlement Agreement signed by General Electric Corporation (GE) and the New York State Department of Environmental Conservation (NYDEC), discharge of PCBs from the GE capacitor manufacturing plant was terminated in June 1977 (Hetling et al. 1978;

Armstrong and Sloan 1988). PCB concentrations in striped bass initially declined with the significant reduction in upstream loadings. However, concentrations through the 1980's showed little decline and have persisted above levels considered unsafe for human consumption (Sloan et al. 1995).

High discharge events and dredging projects in the up-estuary region have exacerbated contamination throughout the Hudson River by re-introducing buried contaminants. This has resulted in a PCB gradient within the biota which is positively related to river kilometer (Limburg 1986; Bush et al. 1989). For instance in 1993, total PCB concentrations in striped bass were highest (mean = 6.41 ppm wet weight) in the Albany/Troy region (river km [Rkm] 246) and concentrations decreased with distance downstream to about 1.9 ppm in the Tappan Zee region (river km 40) (Sloan et al. 1995). Mean PCB levels in striped bass have been typically <2.0 ppm in Long Island Sound and New York's marine district.

Levels of PCB contamination are expected to be affected by patterns of habitat use by striped bass which often undertake coastal migrations away from the Hudson River system. The current model of the long term behavior of PCBs in Hudson River striped bass assumes that striped bass >2 years old occur in coastal habitats during summer months and use coastal habitats for the majority of the year by age 6 (Thomann et al. 1989). Using otolith microanalysis to investigate migrations, Secor and Piccoli (1996) observed a contingent of resident fish in the upper estuary near Troy Dam (Rkm 246) which did not participate in coastal migrations. They hypothesized that these fish were most vulnerable to PCB contamination because they fed and grew in close proximity to the most highly contaminated sediments in the Hudson River. Conversely, we expected that fish which participated in regular coastal migrations, or fish which established long-term residence in polyhaline/euhaline habitats would have lower PCB body burdens due to growth dilution in relatively "clean" habitats.

The objective of this study was to use otolith microanalysis to: 1) verify the proposed link between habitat use and PCB body burden in Hudson River striped bass (i.e. resident fish should have high PCB body burden); and 2) examine the effects of season, sex, and place of collection on habitat use and PCB body burden.

METHODS

New York State Department of Environmental Conservation has routinely sampled striped bass in the Hudson River, south shore of Long Island, and Long Island Sound for PCB contamination since 1976. Most fish are collected by beach haul seine (100 m long X 3 m deep) although some coastal samples were provided by angling. Fish selected for PCB analysis were filleted (skin not removed) and then frozen. Muscle tissue from fillets were shipped to Hazleton Laboratories America, Inc. in Madison, Wisconsin for gas chromatography PCB analysis (Aroclor© method). We used total PCB (PCB) values, based upon wet weight (measured in ppm), which is a sum of major Aroclors.

We subsampled 1994 and 1995 samples to represent season, sex, collection site, and PCB level as homogeneously as possible (Table 1). Individuals with PCB burden ≥ 1.8 ppm were considered "hot;" those <1.8 ppm were considered "cold." This criterion was close to FDA's action limit and represented the 50% percentile in PCB levels in the striped bass analyzed for otolith Sr (Figure 1). Adult females (n = 21) and males (n = 18) were sampled from the Troy dam region (river

km 246), Catskill (Rkm 179), Poughkeepsie (Rkm 122), Haverstraw Bay (Rkm 64), Tappan Zee bridge (Rkm 43), Manhattan (Rkm 19), New York City Harbor, eastern Long Island Sound, and Long Island's south shore (Figure 2; Table 1). Females ranged in size from 463-1007 mm total length, age 3-15 years. Males ranged in size from 457-858 mm, age 3-16 years (Table 1).

Sagittal otoliths were removed from striped bass carcasses which had been sampled previously for PCB analysis. Otoliths were cleaned with 10% bleach solution and embedded in Spurr low-viscosity resin. Otoliths were sectioned transversely (sections were approximately 1 mm thick) through the otolith cores using a low speed, diamond metallurgical wafering saw. Sections were mounted on glass slides, polished initially with wet 600-grit sandpaper to remove major marks and scratches, and then polished in a slurry of 0.3 μm alumina until their surfaces were free of pits and abrasions. This polishing method was used to minimize artifacts in microprobe analysis (Kalish 1990). Finally, sections were rinsed with deionized water and placed in an ultrasonic cleaner to remove any residue resulting from the polishing procedure.

Annuli in striped bass otoliths have been verified to form at an annual rate, and precision in age determination was estimated to exceed 95% (Secor et al. 1994). Each annulus comprised a narrow opaque zone and a wide translucent zone when viewed under transmitted light microscopy. Annuli were counted once for each fish under light microscopy (magnification 60X or 150X), along the sulcal ridge in transverse sections by a single reader.

Electron probe otolith microanalysis of Sr and Ca was performed by X-ray wavelength dispersive spectrometry using a JEOL JXA-840A microprobe (Center for Microanalysis, University of Maryland, College Park, MD). Measurement of atomic weights of strontium and calcium was standardized using strontianite (SrCO_3) and calcite (CaCO_3) standards (Secor 1992). We routinely used two transects per otolith, spacing each point of measurement 25 μm apart for the initial transect which ran from the first to fifth annulus. The second transect traversed narrower annuli corresponding to older ages; spacing between points was set at 13 μm . Each point was approximately 5 μm in diameter. To reduce error between machine runs Sr was expressed as a ratio, Sr:Ca. Backscatter electron micrographs for each analyzed otolith showed series of low atomic weight (dark) zones that corresponded to the optically opaque zones of annuli. Each 5 μm measured "point" was visible in electron micrographs. These points were related to the distance from succeeding opaque zones. Points directly within an opaque zone were considered to represent early spring, prior to spawning (Secor et al. 1994), and were thus the last points associated with a given year of life. Points immediately succeeding the opaque zone were considered to form just after the spawning season and represent the first part of a given year of life (i.e., spring). Points between opaque zones were assumed to sample age in linear proportion. For example, if four points were measured from annulus 7 to 8, then points were assigned ages 7.0, 7.25, 7.50, and 7.75.

Time series data of Sr:Ca were compiled for each striped bass. Based upon laboratory and field experiments Secor et al. (1995) developed a logistic relationship between salinity and otolith Sr:Ca:

$$\text{Salinity Habitation (ppt)} = 40.302 (1 + 56.337 e^{-1523.310(\text{Sr/Ca})})^{-1}; r^2 = 0.94; n = 54$$

This model was used to convert Sr:Ca values to salinity chronologies. Salinity habitation estimated

the salinity inhabited for the period of time represented by each Sr:Ca datum. Residuals from the logistic model indicated that Sr:Ca typically predicted salinity habitation with a precision error $< \pm 6$ ppt.

Mean salinities of the most recent growth season, the last two growth seasons, and the last three growth seasons were used as a measures of recent habitat use. These variables were regressed against PCB level and contrasted using sequential sums of squares. The most recent growth season's habitat history explained most variance in PCB level and this response was used to test season, sex, and site effects. To conduct a nested analysis of variance, fish were sampled across seasons (fall-winter vs. spring), sexes (males vs. females), PCB levels (< 1.8 ppm vs. ≥ 1.8 ppm), and zone (< 90 Rkm vs. ≥ 90 Rkm). Fish analyzed from New York City Harbor, Long Island Sound, and the south shore of Long Island were only collected in fall and thus were excluded from the nested ANOVA. This reduced sample size from 90 to 63. The nested design directed the analysis of variance to occur in hierarchal order at four levels:

$$\gamma_{ijklm} = \mu + \gamma_i + \beta_{j(i)} + \gamma_{k(ij)} + O_{\lambda(ijk)} + \xi_{(ijkl)m},$$

where γ_{ijklm} = the salinity experienced by an individual during its last growth season;

μ = overall mean;

γ_i = the effect of the i th season;

$\beta_{j(i)}$ = the effect of the j th sex

$\gamma_{k(ij)}$ = the effect of the k th zone;

$O_{\lambda(ijk)}$ = the effect of the ℓ th PCB level; and,

$\xi_{(ijkl)m}$ = the random error component.

Statistical significance for factors was accepted at $\alpha = 0.05$ (type-I sum of squares for type-I error).

Analysis of covariance was also performed to examine effects of season, sex, and site on the relationship between total PCB body burden and recent salinity history. Site categories were Troy/Catskill/Poughkeepsie (≥ 90 Rkm), Haverstraw/Tappansee (≥ 20 , < 90 Rkm), Manhattan/NYC Harbor (< 20 Rkm), and Long Island (coastal). The response variable was \log_{10} transformed to normalize residuals.

RESULTS

Salinity chronologies from individual striped bass showed three distinct migratory behaviors. All fish captured during fall and winter in the upper estuary in the vicinity of the Troy Dam had high PCB levels. Fish were predominately resident, inhabiting salinities of 5 ppt or less throughout their lives (Figure 3). A single female (PCB = 7.3 ppm) sampled from this region during fall also exhibited resident behavior. Resident behaviors associated with high PCB contamination also occurred for spring-collected males and females but was less dependent upon site of collection. In some individuals, salinity chronologies indicated a habitat shift from either low to high or high to low salinity (Figure 4). One individual captured in the Troy region (river km 246) with PCB level = 10.5 ppm used mesohaline habitats early in life, then suddenly shifted to freshwater/oligohaline habitats.

Alternatively, an individual with low PCB body burden (0.4 ppm) inhabited fresh water for its first two growth seasons and then emigrated to marine or mesohaline habitats for the remainder of its life. Shifts from low to high salinity were not always associated with low PCB body burdens. A Long Island captured fish with a relatively high body burden of PCB (2.7 ppm) inhabited freshwater/oligohaline habitats early in life, then shifted to polyhaline/euhaline regions for most of the remainder of its lifetime (Figure 3). A third pattern in migration was annual cycles from fresh to marine habitats, indicating possible spawning migrations (Secor and Piccoli 1996). Two such migrating females showed strong cyclic behavior (Figure 5); the female with higher PCB body burden (7.2 ppm) inhabited lower salinity waters over its lifetime.

Salinity records for each individual were used to compute lifetime means, an overall index of an individual's past habitat use. Frequency distributions of lifetime salinities showed that fish classified as cold (<1.8 ppm) tended to grow in mesohaline/polyhaline environments (Figure 6). Individuals classified as hot (≥ 1.8 ppm) and highly contaminated (≥ 5 ppm) tended to predominately use freshwater and oligohaline environments throughout their lives.

Salinity history over the most recent growth season explained slightly more variance in PCB level than other measures of recent habitat use and was used as an index of recent habitat history (Figure 7). The PCB classification effect on recent habitat history was highly significant, explaining 22% of model variance. There was a significant, albeit highly variable, effect of total length ($p = 0.03$) on recent salinity history. Therefore, total length was included in the ANOVA as a covariate. Analysis of variance showed significant effects due to all factors except season (Table 2). Therefore, the nested analysis showed that PCB level was significantly influenced by recent habitat history regardless of effects due to size, sex, or site of collection. Site of collection explained most variance (36%), where fish are collected was largely influenced by where they had recently occurred.

PCB body burden was strongly and inversely related recent salinity history ($r = -0.71$; $p < 0.001$). There was no significant effect of season on the relationship between recent salinity history and total PCBs (Figure 7). In an analysis of variance using salinity history as a covariate, sex did not significantly affect total PCBs ($p < 0.42$). Similarly, no season effect was observed on the relationship between recent habitat history and total PCBs ($p > 0.32$) (Figures 7 and 8). Site did significantly influence the relationship between total PCBs and recent habitat history ($p = 0.05$). The site effect was due to fish collected in the upper Hudson Estuary (≥ 90 Rkm) which showed resident behaviors and high PCB contamination (Figure 8).

DISCUSSION

A previous model of PCB contamination in Hudson River striped bass (Thomann 1991) assumed that the entire population of striped bass began emigrating into coastal environments following sexual maturity. However, salinity chronologies determined for 1994-1995 collected striped bass corroborate recent findings (Secor and Piccoli 1996) which indicated that Hudson River striped bass migratory behavior is highly variable. We observed a resident contingent of fish, predominately males, in the upper Hudson estuary which were apparently susceptible to high PCB contamination. This trend is supported by the close proximity of this contingent to the most highly contaminated sediments in the Hudson estuary. Important forage fish for striped bass, blueback herring and alewives congregate below Troy dam and may play a role in the resident behavior of

striped bass and their high contaminant levels (pers. comm, K. Hattala, NYSDEC, New Paltz, NY). Sloan and Armstrong (1988) reported total PCB levels of 2 to 5 ppm for these species from 1980 collections.

In our application of otolith microanalysis, we assumed that Sr in striped bass otoliths was reflective of where the fish lives. This assumption is based upon laboratory and field studies (Secor et al. 1995) which showed a strong positive relationship between salinity and Sr:Ca in striped bass otoliths. We have also assumed that otolith microanalysis sampled only growth seasons. For instance, otolith growth probably slows or ceases during midwinter months. Therefore, we are not sampling each season equally. Nevertheless, because PCB uptake is expected to occur primarily in growing fish, we believe that otolith microanalysis serves as a useful measure of habitat history in contaminant studies.

Recent habitat use was a strong determinant of PCB contamination. ANOVA and regression tests showed that recent salinities at which striped bass grew were strongly and negatively related to PCB levels independent to any effects due to of season, sex, site of collection, or fish size. Results supported the expectation that fish inhabiting highly contaminated freshwater regions during the growth season before capture will not be able to significantly reduce body burden due to growth dilution. In some cases, otolith microanalysis revealed that fish which shifted from coastal or brackish habitats to up-estuary freshwater habitats were likely to show high PCB levels. However, the converse was not always true: fish which shifted from freshwater to brackish marine habitats did not always reduce their PCB levels, again indicating the possibility of a mesohaline source of PCBs. This result corresponds to recent observations of relatively high mean PCB levels in fish collected in the New York Harbor region. For instance, in 1993 mean PCB level for this region was 3.38 (Sloan et al. 1995), a level much higher than adjacent upestry regions. This level is in contrast to the overall pattern of down-estuary dilution of PCBs and suggests alternate sources of PCBs in the Hudson River estuary.

Unlike commercial fishing in the Hudson River, recreational angling for striped bass has become an increasingly important industry over the past decade. At present, NYDEC allows anglers possession of two fish of at least 71 cm total length. High fishing effort by charter, party, and private vessels as well as shore angling exists in the Hudson River estuary, and along both coasts of Long Island (B. Young, NYDEC, pers. comm). Striped bass collected in the upper estuary (river km >90) during the fall are likely to be resident fish which are highly contaminated. Fishing in the upper estuary should continue to be restricted. In addition, health warnings could be revised to reflect the increased likelihood of contaminated striped bass collected in upestry regions during fall. Fishing effort in the lower estuary (river km 0-60) and Long Island Sound predominantly targets fish which are part of a more highly migratory contingent. Therefore, fish captured in these regions are less likely to be highly contaminated.

Previous models of the long-term behavior of PCBs in striped bass were biased towards coastal habitat use in adult striped bass and under-represented PCB burdens in the overall Hudson River population. The fraction of the population which is resident (or spends parts of their life in the New York Harbor region) is unknown and would be expected to vary on an annual and generational timeframe based upon changes in recruitment and exploitation on the more migratory contingents of the population. The high degree of variability and unpredictability in spatial dynamics the Hudson

River striped bass prescribes more intensive monitoring of migration patterns and individual-based modeling approaches (Van Winkle et al. 1993) to predict future rates of PCB loss.

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REFERENCES

- Armstrong, R. W. and R. J. Sloan. 1988. PCB patterns in Hudson River fish. In: Smith, C.L.(ed.). Fisheries research in the Hudson River, Hudson River Environmental Society. State University of New York Press.
- Bush, B., Streeter, R. W. and R. J. Sloan. 1989. Polychlorobiphenyl (PCB) congeners in striped bass (*Morone saxatilis*) from marine and estuarine waters of New York state determined by capillary gas chromatography. Arch. Environ. Contam. Toxicol. 19:49-61.
- Brown, M. P., M. B. Werner, R. J. Sloan and K. W. Simpson. 1985. Polychlorinated biphenyls in the Hudson River. Environ. Sci. Technol. 19:656-661.
- Fabrizio, M. C., R. J. Sloan and J. F. O'Brien. 1991. Striped bass stocks and concentrations of polychlorinated biphenyls. Trans. Am. Fish. Soc. 120:541-551.
- Hetling, L. J., E. Horn and T. J. Tofflemire. 1978. Summary of Hudson River PCB study results. New York State Department of Environmental Conservation. Technical Paper 52, 88 pp.
- Horn, E. G. and R. J. Sloan. 1985. PCB in Hudson River striped bass-1984. Division of Fish and Wildlife, New York State Department of Environmental Conservation. Albany, NY, 6 pp.
- Kahn, J. R. and R. B. Buerger. 1994. Valuation and the consequences of multiple sources of environmental deterioration: the case of the New York striped bass fishery. Journ. Environ. Man. 40:257-273.
- Kalish, J. M. 1990. Use of otolith microchemistry to distinguish progeny of sympatric anadromous and non-anadromous salmonids. Fish. Bull. US. 88:657-666.
- Limburg, K. E. 1986. PCBs in the Hudson River. pp.83-130, In: Limburg, K.E., Mosan, M.A., McDowell, W.H. (eds.). The Hudson River Ecosystem. Springer-Verlag, New York.
- Secor, D. H. 1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass, *Morone saxatilis*. Fish. Bull. U.S. 90:798-806.

Secor, D. H., T. M. Trice and H. T. Hornick. 1994. Validation of otolith-based aging in Chesapeake Bay striped bass by mark-recapture with a comparison of otolith and scale-based aging. *Fish. Bull. US*. 93:186-190.

Secor, D. H., A. Henderson-Arzapalo and P. M. Piccoli. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? *Jour. Exp. Mar. Bio. Eco.* 192:15-23.

Secor, D. H. and P. M. Piccoli. 1996. Age and sex dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. *Estuaries* 19:778-793.

Skinner, L. C., S. J. Jackling, G. Kimber, J. Waldman, J., Shastay, Jr. and A. J. Newell. 1996. Chemical residues in fish, bivalves, crustaceans and a cephalopod from the New York-New Jersey Harbor Estuary: PCB, organochlorine pesticides, and mercury. New York State Dept. of Environmental Conservation. New York, NY, 150 pp.

Sloan, R. J., E. G. Horn, B. Young, B., Zawacki and A. Foti. 1986. PCB in striped bass from the Marine District of New York-1985, and Contaminants in Hudson River striped bass: 1978-1985. Tech Rep 86-1(BEP), New York State Department of Environmental Conservation, Albany, NY, 21 pp.

Sloan, R. J. and R. W. Armstrong. 1988. PCB patterns in Hudson River fish: II. Migrant and marine species. pp. 325-350, *In*: Smith, C. L. (ed.), *Fisheries Research in the Hudson River*. State Univ. NY Press, Albany, NY.

Sloan, R. J. and K. A. Hattala. 1991. Temporal and spatial aspects of PCB contamination in Hudson River striped bass. New York State Department of Environmental Conservation, Albany, NY, 97 pp.

Sloan, R., B. Young, D. McKown and V. Vecchio. 1991. PCB in striped bass from New York Marine waters. New York State Department of Environmental Conservation, Stony Brook, N.Y. 61 pp.

Sloan, R. J. 1994. A brief report on PCB in Hudson River striped bass. New York State Department of Environmental Conservation, Albany, NY, 63 pp.

Sloan, R., B. Young and K. Hattala. 1995. PCB paradigms for striped bass in New York state. New York State Department of Environmental Conservation, Division of Fish and Wildlife, Division of Marine Resources. Technical Report 95-1 (BEP).

Thomann, R. V., J. A. Mueller, R. P. Winfield and C. Huang. 1989. Mathematical model of the long-term behavior of PCBs in the Hudson River estuary. Hudson River Foundation Report.

Thomann, R. V., J. A. Mueller, R. P. Winfield and C. Huang. 1991. Model of fate and accumulation of PCB homologues in the Hudson estuary. *J. Environ. Engin.* 117:161-178.

Van Winkle, W., K. A. Rose and R. C. Chambers. 1993. Individual-based approaches to fish population dynamics. Trans. Am. Fish. Soc. 122:397-404.

Waldman, J. R., D. J. Dunning, Q. E. Ross. and M. T. Mattson. 1990. Range Dynamics of Hudson River Striped Bass along the Atlantic Coast. Trans. Am. Fish. Soc. 119:910-919.

Table 1. Sample of spring and fall-collected Hudson River striped bass.

Fall (August - December, N = 47)

	Female				Male			
	"Hot" (≥ 1.8 ppm)		"Cold" (< 1.8 ppm)		"Hot" (≥ 1.8 ppm)		"Cold" (< 1.8 ppm)	
	\geq RK 90	<RK 90	\geq RK 90	<RK 90	\geq RK 90	<RK 90	\geq RK 90	<RK 90
TCB (ppm)	7.6 ± 0.68	3.54 ± 0.59		0.49 ± 0.08	8.34 ± 1.10	4.64 ± 0.80		0.51 ± 0.04
N	3	9	0	13	8	8	0	6
TL (cm)	872.67 ± 53.48	711.89 ± 42.78		641.08 ± 47.27	588.25 ± 22.25	700 ± 35.27		561.67 ± 41.23
Wt (g)	7476.67 ± 969.64	4138.89 ± 686.77		3080.77 ± 725.92	2093.75 ± 299.31	4031.25 ± 726.82		2295 ± 616.76
Age (yr)	12.33 ± 1.67	8.00 ± 1.03		6.15 ± 1.10	7.63 ± 0.82	9.13 ± 0.93		4.33 ± 0.33
Lipid (%)	4.98 ± 1.01	5.12 ± 0.64		3.77 ± 0.54	3.41 ± 0.76	5.41 ± 1.45		5.82 ± 0.52

Spring (April - June, N = 41)

	Female				Male			
	"Hot" (≥ 1.8 ppm)		"Cold" (< 1.8 ppm)		"Hot" (≥ 1.8 ppm)		"Cold" (< 1.8 ppm)	
	\geq RK 90	<RK 90	\geq RK 90	<RK 90	\geq RK 90	<RK 90	\geq RK 90	<RK 90
TCB (ppm)	4.88 ± 1.00	0	1.07 ± 0.09	1.03 ± 0.17	6.78 ± 1.31	2.51 ± 0.01	0.86 ± 0.09	0.7312 ± 0.03
N	3		10	5	10	2	6	5
TL (cm)	664.33 ± 58.67		787.8 ± 26.12	682 ± 75.37	617.7 ± 17.54	583.0 ± 62.0	639.17 ± 35.0	610.0 ± 21.48
Wt (g)	3206.67 ± 719.48		5926.9 ± 701.76	4262.8 ± 1806.09	2740 ± 219.63	2650.0 ± 450.0	3000.0 ± 480.64	2528.0 ± 324.32
Age (yr)	6.33 ± 0.88		7.8 ± 0.55	6.6 ± 1.36	8.5 ± 1.14	6.5 ± 1.5	5.67 ± 0.76	5.00 ± 0.32
Lipid (%)	6.34 ± 0.66		4.50 ± 0.37	5.842 ± 1.09	6.33 ± 1.08	7.08 ± 1.42	5.56 ± 0.65	5.49 ± 0.93

Table 2. Nested analysis of variance of season, sex, site of collection, and level of PCB contamination effects on recent salinity history (n = 63). Fish total length was used as a covariate in the analysis. Season levels were fall and spring; site levels were ≥ 90 km (river km) and < 90 km; and PCB levels were < 1.8 ppm and ≥ 1.8 ppm. Factors in parentheses indicate the nesting procedure. For example, "PCB" (Season-Sex-Site) refers to variance explained by PCB level nested with combinations of season, sex, and site.

Type of Variable	Variable	df	Sum of Squares	Significance Level (P)
Covariate	Total length	1	336.1	0.002
Class variables	Season	1	394.6	0.001
	Sex (season)	2	155.9	0.11
	Site (season-sex)	4	790.8	0.001
	PCB (season-sex-site)	6	487.7	0.04

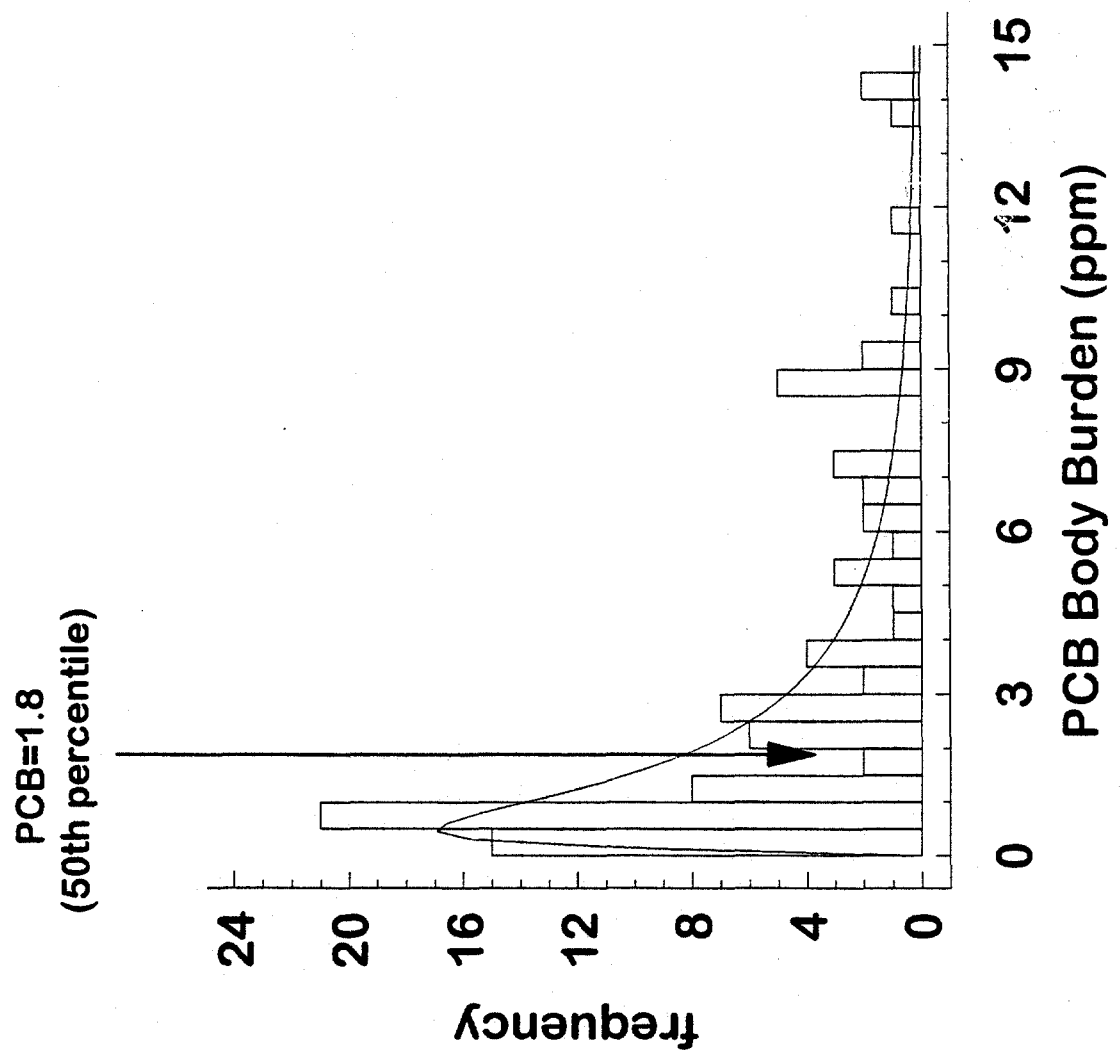


Figure 1. Total wet PCBs (ppm) in examined sample of Hudson River striped bass. Modeled log normal distribution is presented by curve.

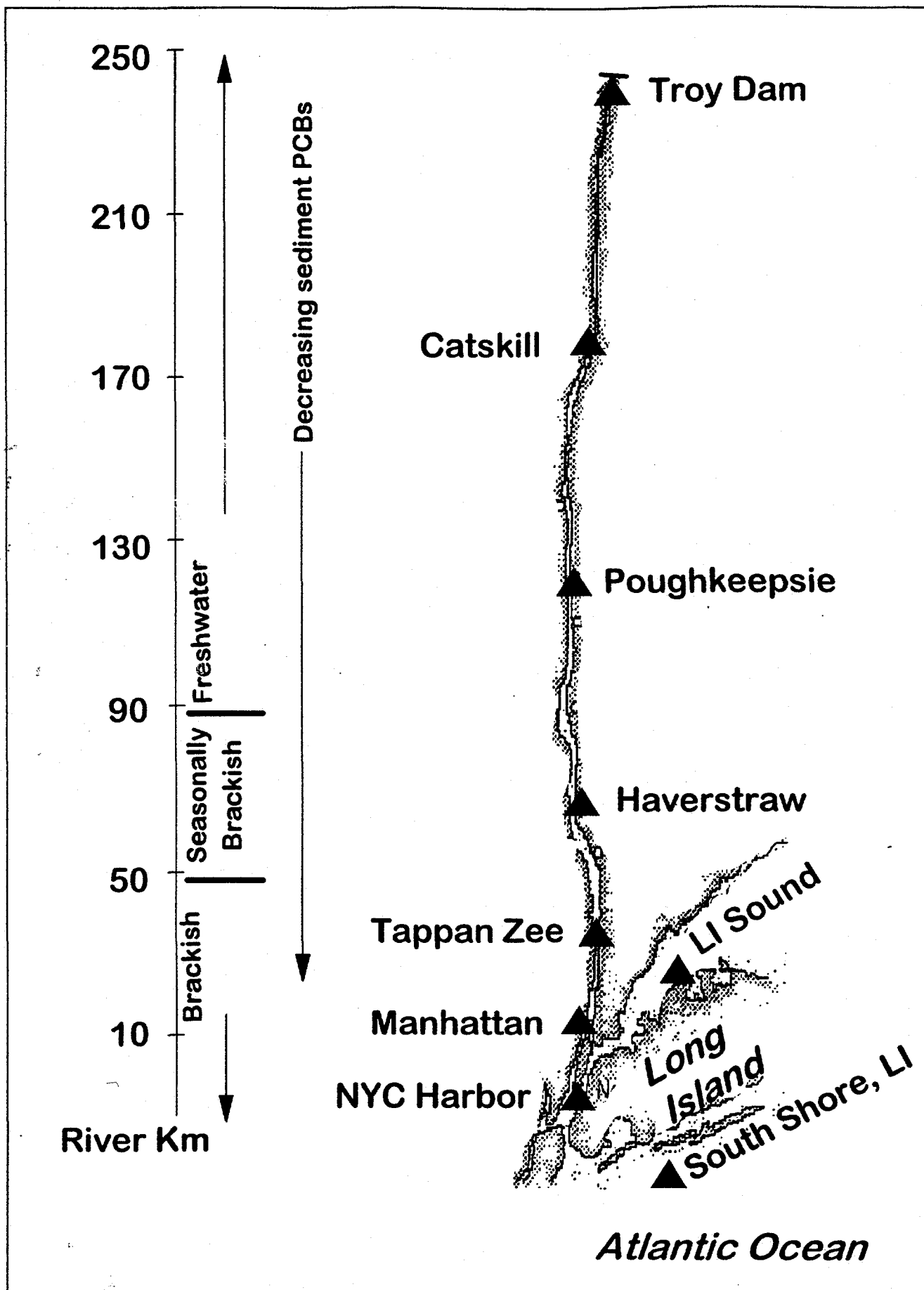


Figure 2. Map of the Hudson River Estuary. Collection sites are shown by triangles.

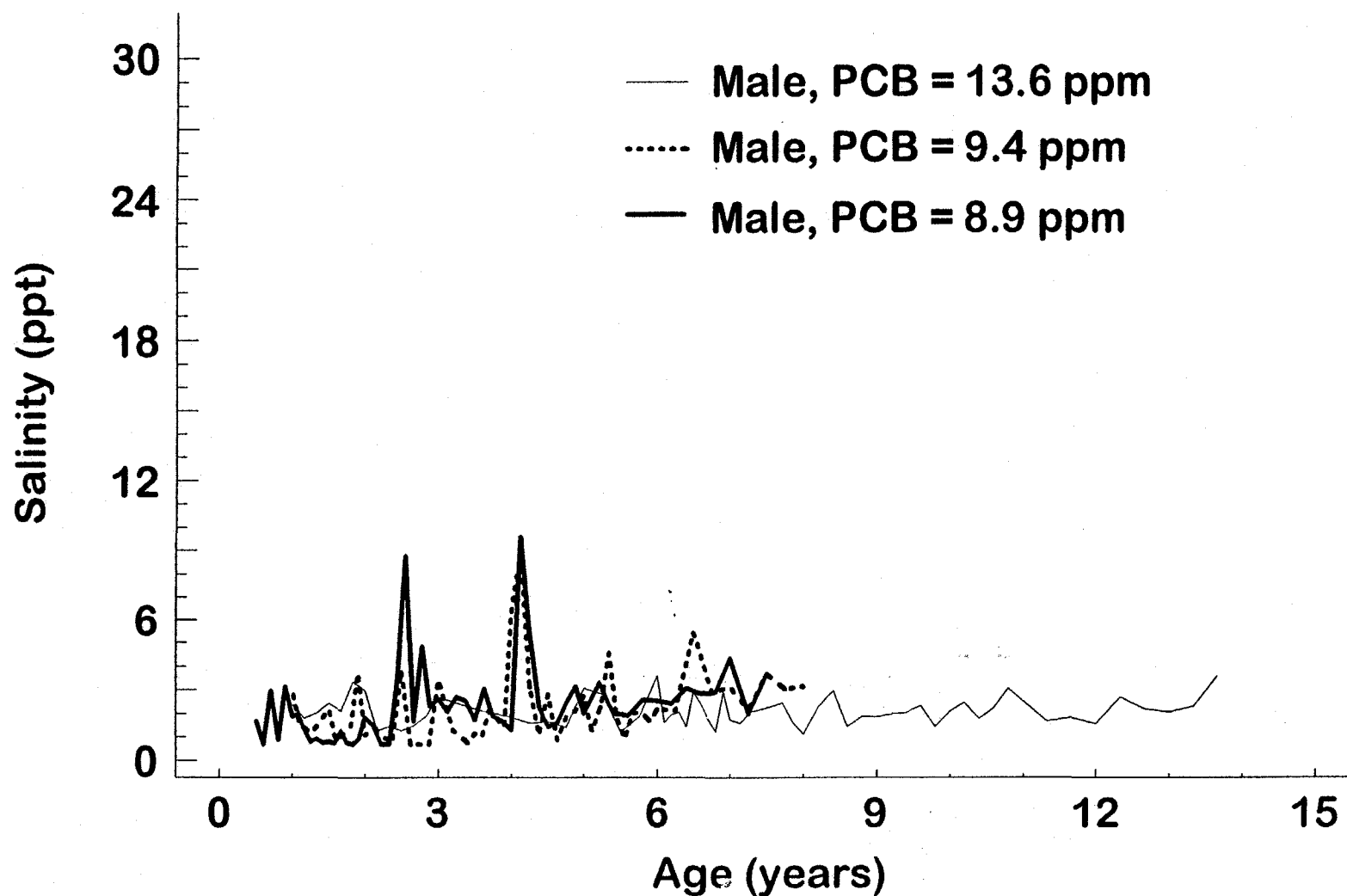


Figure 3. Representative time series of salinity habitation for resident striped bass. Salinity habitation was determined based upon microanalysis of Sr:Ca ratios. Total PCB body burdens (wet weight based) are indicated. Total PCB body burden was determined through the aroclor method on a single fillet with skin on and scales removed (muscle tissue).

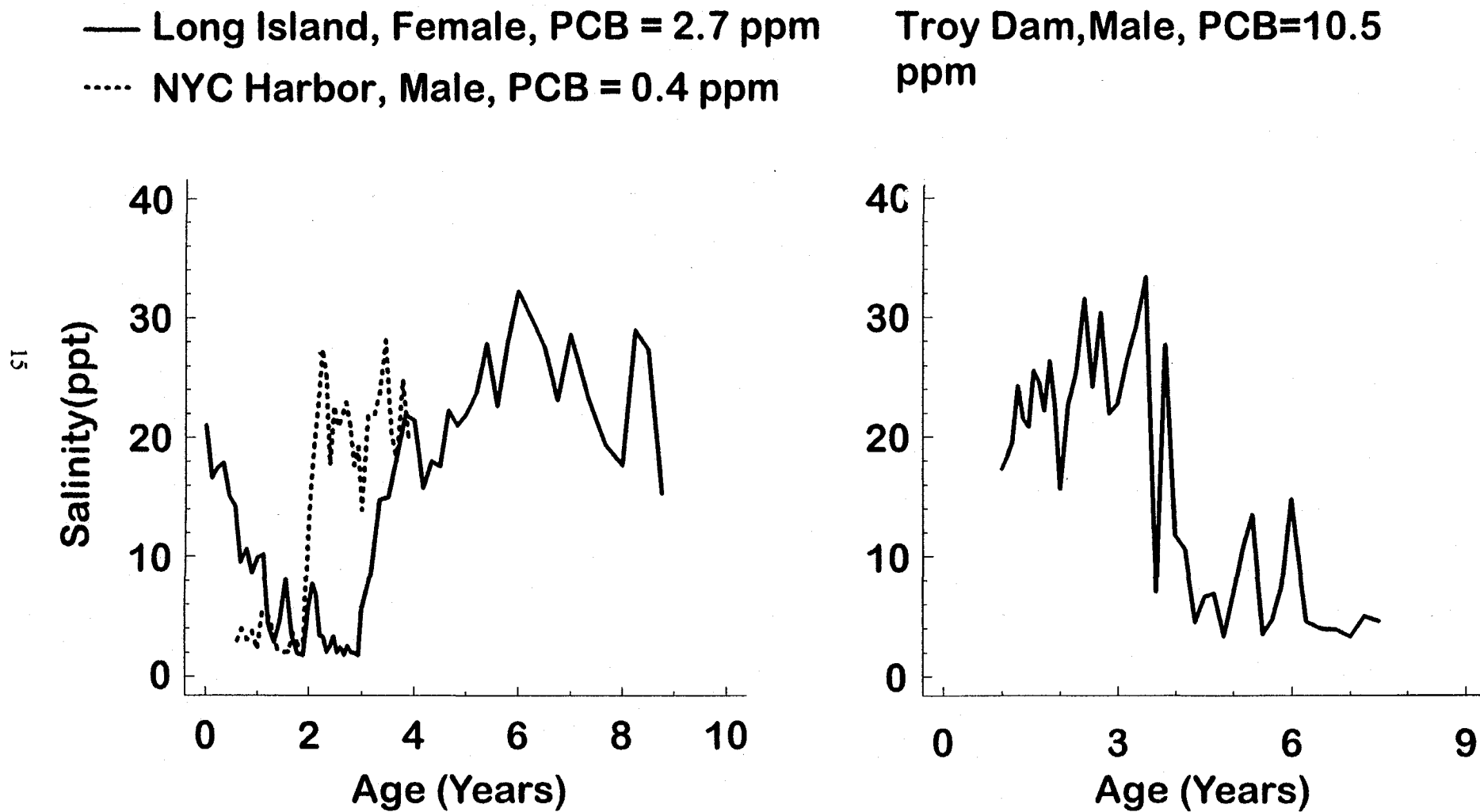


Figure 4. Representative time series of salinity habitation of striped bass, showing habitat shifts. Salinity habitation was determined based upon microanalysis of Sr:Ca ratios. Total PCB body burdens (wet weight based) are indicated.

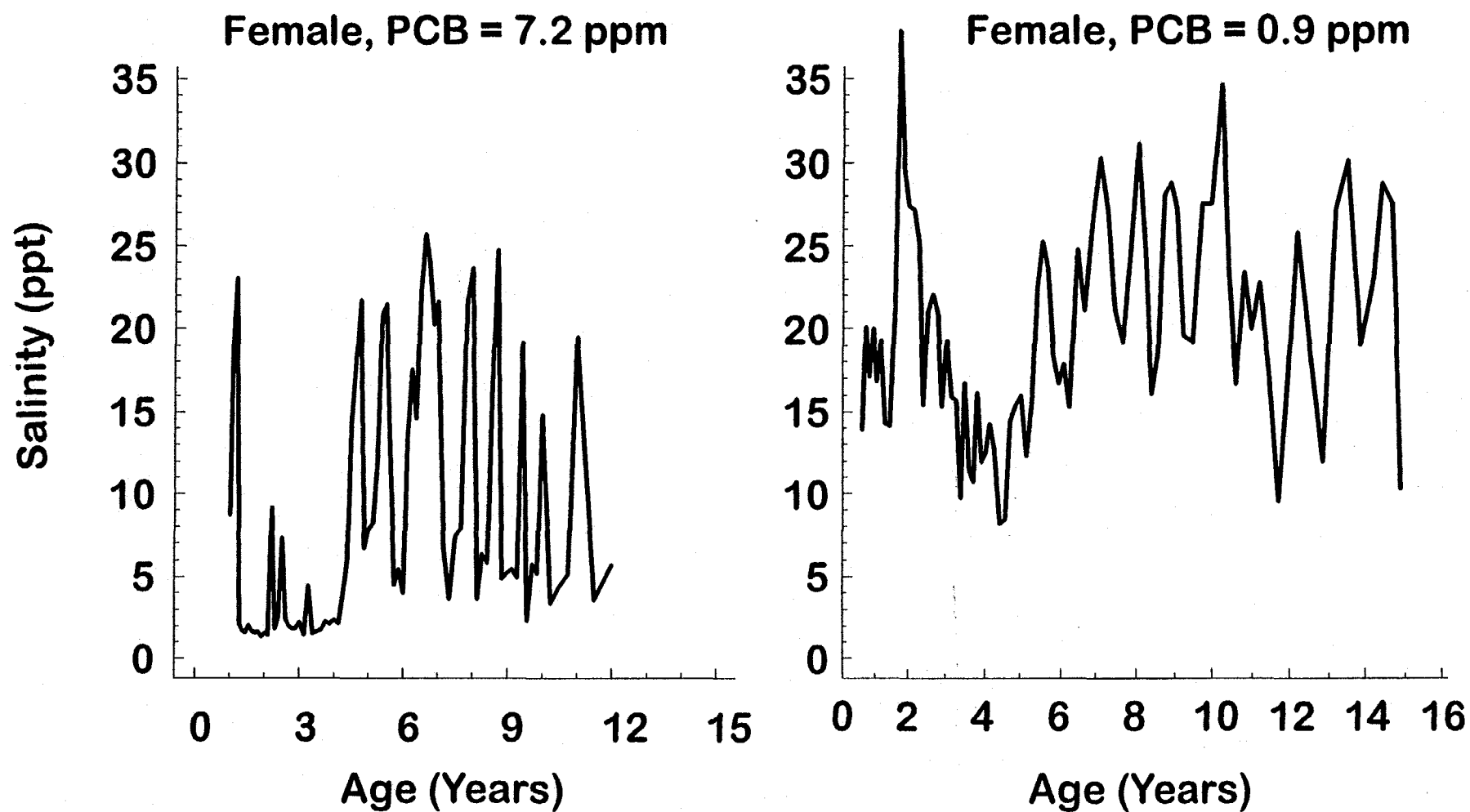


Figure 5. Representative time series of salinity habitation of female striped bass, showing anadromous migratory behavior. Salinity habitation was determined based upon microanalysis of Sr:Ca ratios. Total PCB body burdens (wet weight based) are indicated.

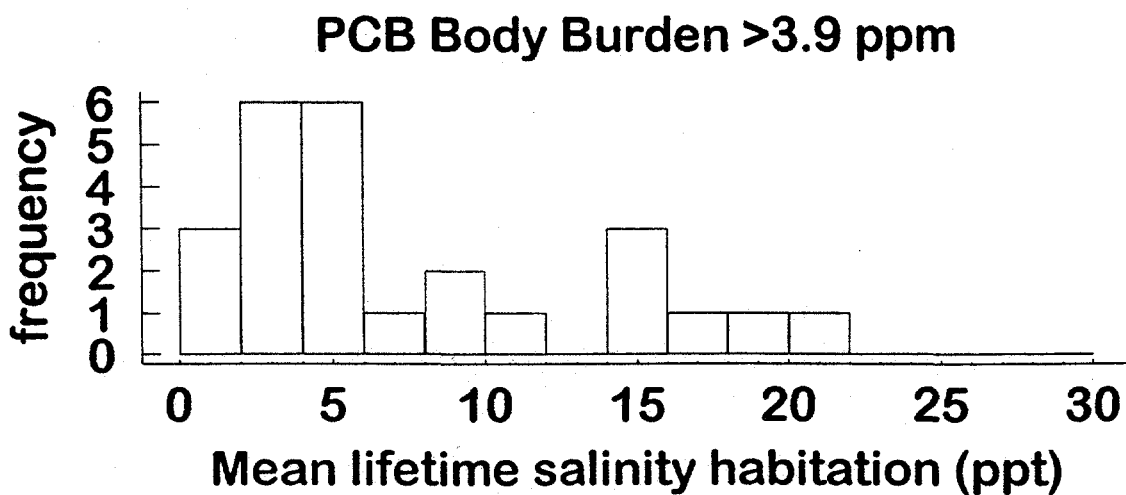
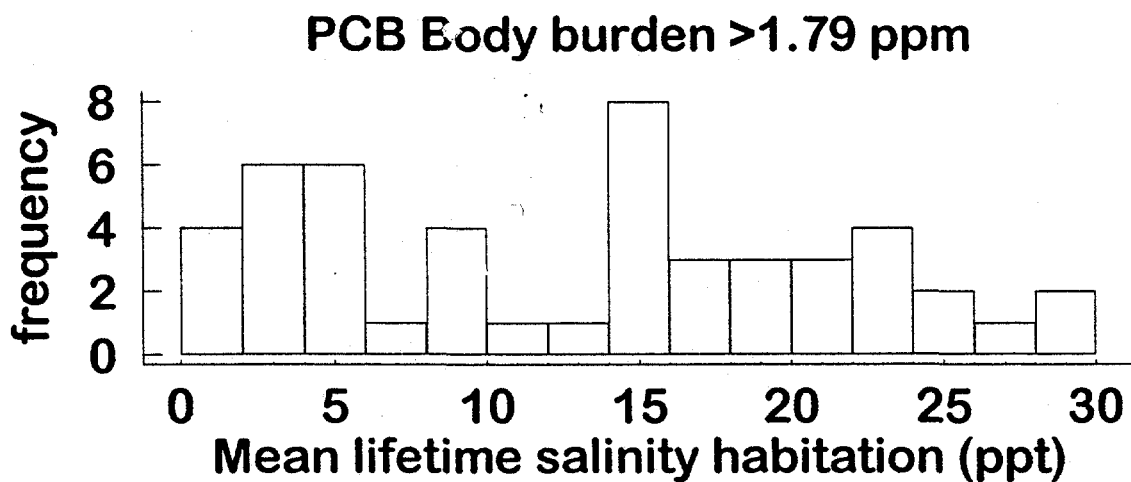
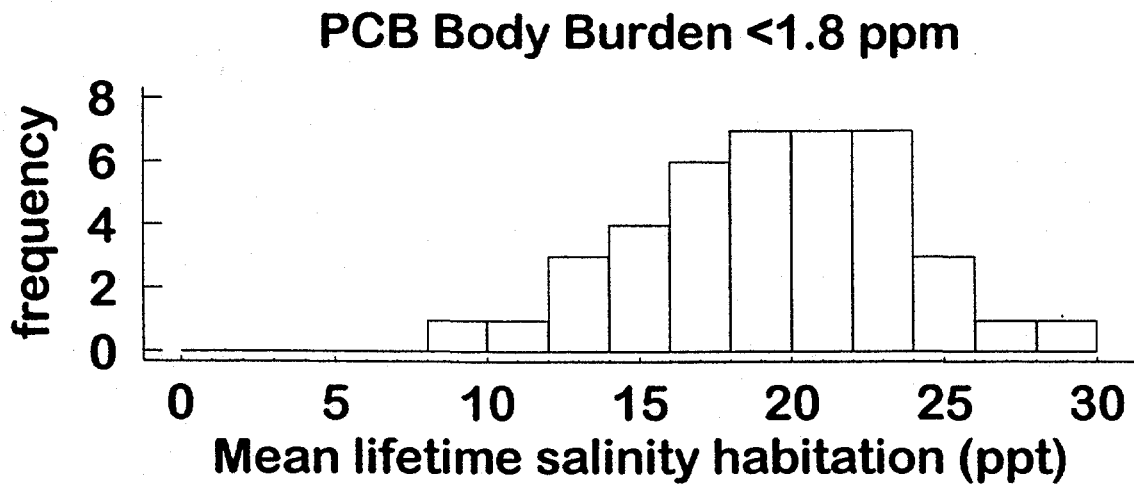


Figure 6. Frequency histogram of lifetime salinity habitation for “cold” (<1.8 ppm PCBs), “hot” (≥1.8 ppm PCBs), and highly contaminated (≥4 ppm PCBs) Hudson River striped bass.

$$\text{TPCB} = 21.04 (\text{recent salinity history})^{-0.92}; r^2 = 0.51; n = 90$$

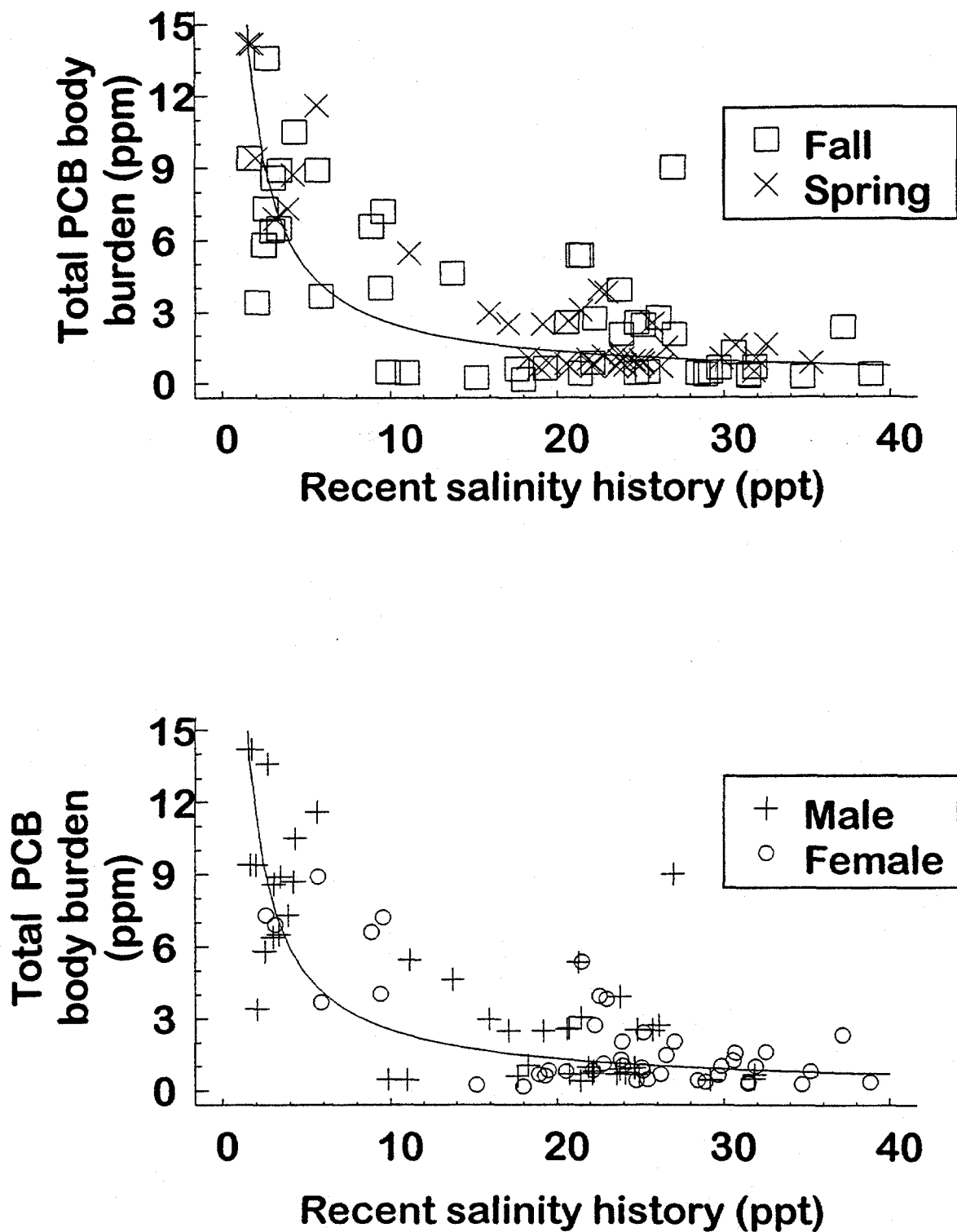


Figure 7. Mean salinity history of the most recent growth season versus total PCB body burden by season (a) and sex (b). Coefficient of determination for a power function is indicated.

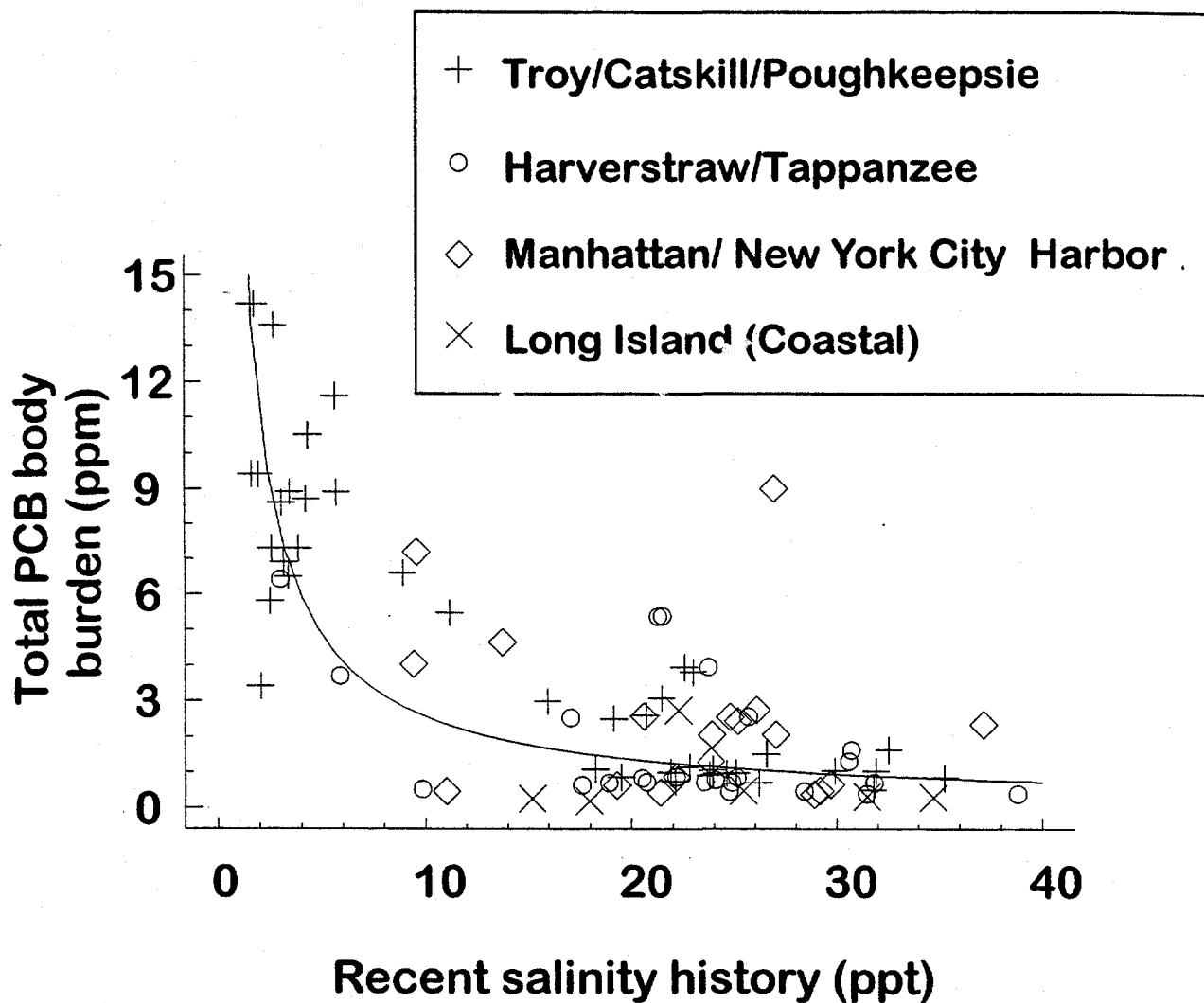


Figure 8. Mean salinity history of the most recent growth season versus total PCB body burden by collection site.

CHAPTER 2. Linking Habitat Use of Hudson River Striped Bass to Accumulation of Polychlorinated Biphenyl Congeners

Jeffrey T. F. Ashley, David H. Secor, Erik R. Zlokovitz, Joel E. Baker and Samantha Q. Wales

ABSTRACT

Since 1976, the commercial striped bass fishery in the Hudson River (NY) has been closed due to total polychlorinated biphenyls (*t*-PCBs) concentrations in edible tissues exceeding the US Food and Drug Administration's advisory level of 2 µg/g-wet weight. Seventy-one fish collected throughout the Hudson River estuary and Long Island Sound were analyzed for congener specific PCBs and life-time migration behaviors were determined by otolith strontium and calcium microanalysis. Mean salinity encountered during the last growth season prior to capture was inversely correlated to the *t*-PCB body burden. In general, striped bass permanently residing in fresh and oligohaline portions of the estuary adjacent to known PCB sources had higher *t*-PCB levels and congeneric patterns with higher proportions of lower chlorinated congeners (di-, tri-, and tetrachlorobiphenyls). Conversely, those fish spending the majority of their life in more saline waters of the estuary or those migrating frequently throughout the salinity gradient had patterns which were more highly chlorinated than the resident contingent. Although there is evidence supporting additional PCB sources in the Hudson River (e.g., New York Harbor), the limited resolution of otolith analysis in identifying exact locations based on salinity ranges within the lower Hudson River hampers a full evaluation of this issue.

INTRODUCTION

In estuaries and coastal embayments, the distribution of dissolved, particulate and sedimentary hydrophobic organic contaminants (HOCs) such as polychlorinated biphenyls (PCBs) is often spatially heterogeneous (e.g. Chapter 2; Kennicutt et al. 1994). The exposure and subsequent accumulation of these contaminants to aquatic organisms is therefore influenced, in part, by proximity to the contaminant inventories. For resident organisms such as bivalves and non-migratory fishes, the body burdens of PCBs often accurately mirror the contaminant regime of the organisms' habitat (e.g. Lake et al. 1995). However, for migratory species such as the Hudson River striped bass (*Morone saxatilis*), the evaluation of HOC accumulation requires consideration of temporal variability in exposure.

The Hudson River is an estuary that has enormous spatial variability in PCB contamination. From the mid 1940s to the mid 1970s, the Hudson River estuary received over 2.5×10^5 Kg of PCBs largely as a result of industrial discharges above the Troy Dam at Ft. Edward and Hudson Falls (Achman et al. 1996; Armstrong and Sloan, 1988; Bush et al. 1989). Sedimentary PCB inventories reveal a considerable concentration gradient (Figure 2.1) down-estuary due to advective, dispersive and dilution effects (Bush et al. 1994; Bopp et al. 1981). However, as a consequence of the decades of PCB release in the upper estuary and their persistence, the commercial striped bass fishery in the entire Hudson River was closed and consumption advisories for recreational anglers were issued in

1976. Although concentrations in edible portions of striped bass declined significantly after the termination of direct discharge in the upper estuary in 1978, annual averages still exceed the 2 µg/g (ppm) action limit promulgated by the US Food and Drug Administration (FDA) (Sloan et al. 1995).

Hudson River striped bass are anadromous, migrating annually to fresh waters to spawn in the spring, returning to coastal and marine environments thereafter. The migration behavior of these and other anadromous fishes has recently been evaluated using otolith microanalysis (Kalish 1990; Secor 1992; Secor and Piccoli 1996). In this technique, an electron microprobe measures the molar concentrations of Ca and Sr in a series of points within the otolith of the fish (the calcium carbonate 'ear stone' responsible for hearing and equilibrium). In estuarine environments, Sr is a very reliable tracer for salinity (Ingram and Sloan 1995). Abundant in seawater, Sr is diluted in estuarine environments by freshwater input. Calcium concentration remains relatively invariant throughout the otolith. A fish's age-and season-specific habitat (salinity) history may be elucidated by relating the ratio of Sr to Ca (Sr:Ca) to seasonal bands (annuli) within the otolith's microstructure (Secor et al. 1995).

Thomann et al. (1991) modeled PCB contamination in the Hudson River striped bass by assuming that the entire population of fish began emigrating into coastal environments following sexual maturity. However, Secor and Piccoli (1996) concluded that Hudson River striped bass migratory behavior is highly variable. To investigate the effect of habitat use on PCB body burden, Zlokovitz and Secor (in press) evaluated the lifetime salinity histories of a sample of striped bass collected along the Hudson River estuary and Long Island Sound during the Fall and Spring of 1994/95 and related them to individual total PCB (*t*-PCB) body burdens reported by the New York Department of Environmental Conservation (NYDEC). They found *t*-PCB body burdens were inversely correlated with recent habitat use as measured by the mean salinity encountered during the last growth season prior to capture. In general, those fish residing in fresh to oligohaline regions near the source had the highest contaminant body burdens while those inhabiting largely meso- to euhaline waters had significantly lower *t*-PCB concentrations. The observed relationship between recent habitat use and body burden was independent of effects due to season, sex, or fish size.

Congener specific PCB profiles in surficial sediments collected along the estuarine gradient (Figure 2.2) reveal a shift from higher chlorinated patterns in areas of higher salinity to a more "unweathered" profile having more lower chlorinated congeners (Kevin Farley; unpublished data). Resident fish species utilizing the upper estuary would be expected to have congeneric PCB patterns reflecting the latter profile. Supporting this, Bush et al. (1989) analyzed congener specific PCBs in striped bass and suggested that the presence of lower chlorinated congeners, specifically 2,2'- and 2,6-dichlorobiphenyl, indicated a recent exposure to upper Hudson River PCB source. However, they also observed a sub-set of striped bass PCB patterns which were depleted in those congeners suggesting that a contingent was not exposed to the Hudson River source or if so, had depurated those less chlorinated congeners indicative of near-source between the time of exposure and collection (Fisk et al. 1998).

The objectives of this study were three-fold. First, this study was performed to further support the evidence presented by Zlokovitz and Secor (in press) that habitat use is a major determinant of *t*-PCB accumulation in Hudson River and Long Island Sound striped bass and accounts for the highly variable contaminant body burdens seen within the population. Secondly, through congener specific PCB analysis, pattern similarities/differences and their relation to habitat use was evaluated. We

hypothesized that Hudson River striped bass permanently residing in fresh to oligohaline waters would have a higher proportion of lower chlorinated congeners. For those fish not utilizing the upper contaminated portions of the estuary, or those spending only a portion of their life there, we hypothesized a more highly chlorinated congener pattern resulting from depuration of lower chlorinated congeners. However, other significant sources of PCBs may exist within the estuary. Lastly, through principal component analysis, additional sources having unique congeneric patterns, if present, may be discerned. In addition to the three primary objectives, this study also represents one of the few (Bush et al. 1989) to present congeneric patterns for Hudson River and Long Island Sound striped bass.

METHODS AND MATERIALS

Sample Collection

Since 1976, the New York State Department of Environmental Conservation (NYDEC) has routinely monitored PCB concentrations in the Hudson River, south shore of Long Island, and Long Island Sound to document spatial and temporal contaminant patterns for purposes of establishing consumption advisories and to assist in the management and regulation of a contaminated fishery. In this study, a sub-set of fish collected from the fall of 1994 and spring of 1995 were analyzed. The majority of fish were collected by beach haul seine. Angling provided a small portion of the total catch. Fish selected for PCB analysis were filleted (consisting of one side of the fish with skin intact but scales removed) and frozen until subsequent analysis.

Of the hundreds of Hudson River striped bass captured by NYDEC in the Fall 94/Spring 95 collection effort and analyzed for *t*-PCBs by Hazleton Environmental Services (Madison, WI, USA), we sub-sampled seventy-one for subsequent otolith and congener-specific PCB analyses. The samples (33 males; 37 females; 1 unidentified) were chosen to include fish from five zones within the Hudson River (Troy, Catskill, Poughkeepsie, Haverstraw Bay, New York Harbor) and one zone incorporating sites from Long Island Sound (Figure 2.3). Within each zone, sub-sampled fish represented sex, catch season (fall and spring) and *t*-PCB level as homogeneously as possible.

Sample Extraction and Clean-up

A portion of the frozen filets (20 g) were homogenized and Soxhlet-extracted for 16 hours with dichloromethane (DCM) by Hazleton Environmental Services (Madison, WI, USA). Lipid content was determined by gravimetric analysis and expressed as a percentage of the total wet weight of fish. Sample extracts of the subset of Hudson River and Long Island Sound striped bass were obtained from Hazleton Environmental Services. Lipid was removed by gel permeation chromatography (GPC) on subsamples (500 μ L) of each extract. The collected lipid-free fractions were solvent reduced using rotoevaporation, exchanged with hexane, and further concentrated under a purified N₂ stream. Liquid-solid chromatography using Florisil as the stationary phase was used as a clean-up step prior to congeneric analysis (Ashley and Baker, in press). Eluted fractions were solvent reduced using rotoevaporation, exchanged with hexane, and further concentrated under a purified N₂ stream to ca. 1 mL prior to instrumental analysis.

Instrumental Analysis

Congener specific PCBs were analyzed using a Hewlett Packard 5890 gas chromatograph equipped with a ^{63}Ni electron capture detector and a 5% phenylmethyl silicon capillary column. The column was 60 m long and had a 0.25 mm internal diameter with 0.25 μm stationary phase film thickness (DB-5, J&W Scientific). Nitrogen and hydrogen were used as the carrier and make-up gases, respectively (flow rates = 30 mL/min), and the inlet pressure was 100 kPa. The temperature program was as follows: 100°C for 2 minutes, 100-170°C at 4°C/min, 170-280°C at 3°C/min, and 5 minutes at 280°C. The injector and detector temperatures were 225°C and 285°C respectively. An auto sampler (HP 7673) was used to inject a 2 μL sample in the splitless injection-mode. Data were acquired using both an HP3393A integrator and Chemstation software (Hewlett Packard). The identification and quantification of PCB congeners followed the method of Mullin (1985) in which the identities and concentrations of each congener in a mixed Aroclor standard (25:18:18 mixture of Aroclors 1232, 1248 and 1262) were determined by calibration with individual PCB congener standards. Congener identities in the sample extracts were based on their chromatographic retention times relative to the internal standards added. In cases where two or more congeners could not be chromatographically resolved, the combined concentrations were reported. Internal standards, 2,3,6-trichlorobiphenyl (PCB#30) and 2,2',3,4,4',5,6,6'-octachlorobiphenyl (PCB#204), were added to all the samples and calibration standards prior to instrumental analysis. Total PCBs (*t*-PCBs) were calculated by summing those congeners detected above the detection limit.

Analytical Quality Assurance

To assess precision of the PCB analysis, two sample replicates were taken from each sample extraction test tube of seven randomly selected samples. The average percent difference between duplicate samples for total PCB concentrations was ca. 7%. Recoveries were assessed by the addition of surrogate PCB congeners 14, 65 and 166 prior to lipid extraction by GPC and were $76 \pm 24\%$, $71 \pm 18\%$ and $87 \pm 26\%$, respectively. Laboratory blanks were generated to monitor possible laboratory contamination. Matrix blanks consisting of approximately 30 g of clean Na_2SO_4 were analyzed using the same procedures as the fish extracts obtained from Hazelton Environmental Services, Inc. The masses of most PCB congeners in samples were well above those found in the blanks. Masses of PCBs quantified in fish samples were not adjusted for the contribution by the blank. In the quantification of each PCB congener, the method detection limit was estimated as three times the peak areas on the chromatogram of the matrix blanks. The blank based detection limits for total PCBs was 27.0 ng/sample. For the vast majority of PCB congeners, sample concentrations were well above detectable levels. A standard reference material (Organics in Mussel Tissue) was obtained from the National Institute of Standards and Technology (NIST) and was used to evaluate extraction efficiency. The values for select PCB congeners were within an average of 15% of the certified values.

Otolith Analysis

Sagittal otoliths were removed from striped bass carcasses. Otoliths were cleaned (10% bleach), embedded in Spurr low-viscosity resin, and sectioned transversely (1mm) through the otolith cores (Zokovitz and Secor, in press). Sections were polished to minimize artifacts in microprobe analysis (Kalish 1990). Because annuli in striped bass otoliths form at an annual rate, age was determined to >95% precision (Secor et al. 1994) by counting each annulus (comprised of an opaque zone and a

translucent zone). Each annulus comprised a narrow opaque and a wide translucent zone when viewed under transmitted light microscopy. Ages of all fish were individually determined by counting annuli under light microscopy (magnification 60x or 150x) by a single reader. To determine salinity histories of each fish, electron probe otolith microanalysis of strontium and calcium was performed by X-ray wavelength dispersive spectrometry using a JEOL JXA-840A microprobe (Center for Microanalysis, University of Maryland, College Park, MD, USA). Time series of Sr:Ca ratios were compiled for each striped bass. To convert Sr:Ca values to salinity, the logistic relationship developed by Secor et al. (1995) was used:

$$\text{Salinity Habitation (ppt)} = 40.302 (1 + 56.337e^{-1523.310(\text{Sr/Ca})})^{-1}; r^2 = 0.94; n = 54$$

Salinity habitation estimated the salinity inhabited by the fish for the period of time represented by each Sr:Ca datum. Based on residuals from the relationship, Sr:Ca typically predicted salinity habitation with a precision error less than 6 ppt.

Chemometrics

Principal component analysis (PCA) was performed on the concentrations of individual congeners to mathematically aid in discrimination of congeneric pattern differences/similarities. Our assumption underlying the use of this technique is that fish samples of common habitat use will tend to have similar patterns of PCB congeners, even though absolute concentrations may vary widely due to such factors as age, lipid content and diet. To remove the effect of absolute concentration on the first principal component, individual PCB congener concentrations were normalized to *t*-PCB (Schwartz et al. 1991; Wenning et al. 1992). In some samples where several congener concentrations were below the instrumental detection limit, the detection limit was substituted such that those congeners could be used in the PCA (Meglan 1992). The first two principal component scores of a PCA were used to detect relationships (differences/similarities) among individual PCB congener patterns. The resulting coefficients in the principal component equation (the eigenvectors) were used to identify those specific congeners which varied the most between habitat types. Using those select congeners, additional uni-variate statistical treatments (e.g., regressions, ANOVA) were performed to test if observed differences in PCB congener patterns between fish utilizing different salinity ranges were statistically significant.

In addition to the uni- and multi-variate techniques above, scatter plots comparing populations of the end members of both the habitat use and *t*-PCB spectra were used to discern differences in PCB congener patterns. A scatter plot clearly depicts the relative similarities/differences of two individual or averaged congeneric patterns. If the patterns are similar, a 1:1 relationship will be observed with a corresponding high linear correlation coefficient (*r*) value. Conversely, patterns which are not similar will deviate from the ideal case and yield a lower *r* value. Congeners not falling on the 1:1 line indicate either enrichment or depletion of a congener(s) in one of the samples compared to the other.

RESULTS

Salinity (Migration) Profiles

Using electron microanalysis of otolith Sr and Ca, a time series of salinity habitation (migration behavior) for each fish's lifetime was generated. Four distinct migratory patterns were discerned (Figure 2.4a-d). The first pattern represents resident behavior at salinities less than 5 ppt and was found for all fish captured at Troy (Figure 2.4a). Individuals having this pattern had the highest average *t*-PCBs body burdens ($3,500 \pm 900$ ng/g wet wgt) due to constant exposure to the highly contaminated upper fresh water portion of the estuary (Zlokovitz and Secor, in press). The second and third patterns involved habitat shifts from either high to low (Figure 2.4b) or from low to high salinities (Figure 2.4c). Habitat shifts from saline waters to fresh waters often resulted in *t*-PCB concentrations which were higher than the mean value for all fish throughout the estuary and Long Island ($1,300 \pm 1,200$ ng/g wet wgt). Conversely, shifts from low to high salinity often resulted in lower *t*-PCB body burdens. However, anomalies were observed. For example, a female captured at Haverstraw (river km 70) and having relatively high *t*-PCB concentrations (3,000 ng/g wet wgt) spent its early life in freshwater near the known source but inhabited meso- to polyhaline regions for most of the remainder of its lifetime. The final pattern determined through otolith chemistry was one incorporating annual migrations from fresh water/oligohaline to marine habitats (Figure 2.4d), indicating possible spawning migrations (Secor and Piccoli 1996).

Mean salinity during the last year of a fish's life has been used as an index of recent habitat use for Hudson River striped bass (Zlokovitz and Secor, in press). Although all fish captured at Troy (river km 250) displayed resident behavior (mean salinities <5 ppt), fish caught at the other locations generally had widely varying habitat uses (Table 2.1). For example, fish caught approximately 85 km down-estuary of Troy at Catskill (river km 175) had mean salinity values ranging from 3.4 - 34.5 ppt. Similarly, those fish captured at Haverstraw (river km 70) ranged in habitat use from 2.7 to 30.4 ppt. The wide ranges of habitat use arise from the fact that collections were made both in the Fall and the Spring. In Fall, fish collected up-estuary tended to be resident; in Spring, fish were better mixed up-estuary because these are spawning grounds. With the exception of three fish having mean salinity values >11 ppt and one having >35 ppt usage, those fish collected in the New York Harbor ($n = 17$) used habitats within the relatively small range of 19.5 - 28.9 ppt.

Using *t*-PCBs as determined by the "Aroclor Method" (Hazleton Laboratories), Zlokovitz and Secor (in press) found contaminant body burdens were strongly and inversely related to mean salinity of the last growth year ($r = -0.71$; $p < 0.001$). Using the sum of all quantified congeners in this study, *t*-PCB concentrations (expressed as mass/mass wet wgt) were similarly well correlated to habitat use as expressed by mean salinity of the last growth season (Figure 2.5; $r = -0.75$; $p < 0.001$). However, by eliminating the sub-population of resident, near-source fish, the strong negative correlation significantly diminished ($r = -0.30$; $p < 0.001$). Other factors such as lipid content, length, age, sex and weight were poorly correlated to *t*-PCB concentrations ($r < 0.2$; $p < 0.001$) suggesting habitat use as the major determinant of the magnitude of contaminant body burdens. Despite this, there was considerable scatter in data points reflecting the large variability in migration behavior of the sampled striped bass as well as in *t*-PCB body burdens (Figure 2.5).

PCB Congener Patterns

Four representative congener patterns corresponding to the individual fish with varying habitat use from Figure 2.4 are shown in Figure 2.6. All other patterns are compiled with their respective lifetime salinity profile in Appendix C. The majority (>95%) of analyzed congeners were detected in the fish samples. Those congeners chromatographically eluting before congeners 12+13 (1, 4+10, 7+9, 6, 8+5, and 19) were often below the instrumental detection limit. However, coeluting congeners 4+10 (2,2'- and 2,6-dichlorobiphenyl) were often present in larger relative proportions in those samples displaying resident behavior (e.g., Figure 2.6a vs. 2.6b-d). These congeners have been reported to be elevated in sediment and prey fish samples from the upper estuary suggesting a recent exposure to unweathered, near-source PCBs (Bush *et al.*, 1989). Congeners 31+28, 66+95, 153+132+105, 163+138, and 180 consistently represented the largest contributing peaks in the congener patterns. Those resident fish exclusively using habitats of mean salinity <5 ppt (e.g., Figure 2.4a) often, but not exclusively, had PCB congener patterns having a higher proportion of lower chlorinated congeners (di-, tri-, and tetrachlorobiphenyls) (Figure 2.6a) compared to those patterns (Figure 2.6b-d) obtained from fish exhibiting the three other migration behaviors (Figure 2.4b-d). In comparison, the majority of fish using habitats of mean salinity (during the last growth year) of >5 ppt had congeneric profiles having a larger proportion of higher chlorinated congeners. However, there were several individuals having a 'source-like' PCB congener pattern and, as observed through lifetime salinity chronologies, had not utilized the fresh or oligohaline portions of the Hudson River either recently (within three years of time of collection) or ever.

Principal Component Analysis of PCB Congener Patterns

The first two principal components (PC1 and PC2) described 41% and 10% of the variability among the PCB congener patterns of all fish, respectively. Distinct separation of fish samples was not observed from a PCA crossplot (Figure 2.7). Based on mean salinity of the last growth year, each fish was denoted by one of the following salinity ranges: 'fresh to oligohaline' (<5 ppt), 'oligo- to mesohaline' (5-18 ppt), 'meso- to polyhaline' (18-25 ppt), or 'poly- to euhaline' (>25 ppt) (Figure 2.7). As the distance between denoted salinity groups increases, the normalized congener patterns become more different between those groups. For example, the individual patterns observed for those resident fish utilizing fresh to oligohaline waters most greatly differed from those using habitats of mean salinities greater than 25 ppt as indicated by the largest separation of these two groups on the PCA crossplot (Figure 2.7). On average, as PC1 scores increase, the more saline the water the fish utilized during the last growth year. For PC1, coefficient (eigenvectors) weightings were by far highest for the coeluting congeners 31+28 and 153+132+105. As expected, PC1 and the ratio of the concentrations of the two coeluting congeners ([31+28] to [153+132+105]) were highly correlated ($r = 0.88$; $p < 0.001$). Coupling the information gained by the PCA crossplot and the coefficients, the ratio also was negatively well correlated to the mean salinity of the last growth year (Figure 2.8; $r = -0.50$; $p < 0.001$).

Statistical Verification of PCB Congener Pattern Differences

To further facilitate recognition of differences/similarities in PCB congener patterns based on habitat use and to verify those differences statistically, individual fish were grouped according to the mean salinity (at 5 ppt intervals; Table 2.1) and were denoted as either 'hot' (those having *t*-PCBs

$\geq 1,000$ ng/g wet wgt) or 'cold' (those having *t*-PCBs $< 1,000$ ng/g wet wgt) (Table 2.1). Average normalized concentrations and associated standard deviations (when $n > 2$) for the two congener groups ([31+28] to [153+132+105]) were calculated for each salinity range within the hot and cold classifications. By using the two coeluting congener groups ([31+28] to [153+132+105]), the likelihood of detecting statistically significant differences among patterns increases. In general, the patterns of hot fish became increasingly dominated by the lower chlorinated coeluting congeners 31+28 with increasing use of fresh water while the higher chlorinated coeluting congeners 153+132+105 decreased in normalized concentration from marine to fresh waters. Using a pairwise multiple comparison (Fisher LSD Method), statistically significant differences in normalized concentrations of both coeluting groups of congeners were observed between those fish in the 0-10 ppt mean salinity range and those using waters greater than 20 ppt ($p < 0.05$). For cold fish, the mean values of normalized concentrations of both congener groups between salinity ranges were not great enough to exclude the possibility of differences arising from random variability (ANOVA; $p = 0.20$). However, it is important to note only two cold fish having mean salinities below 15 ppt were analyzed. Therefore, statistically there were no significant differences among the patterns of cold fish throughout mean salinities of 15 ppt and greater.

Lastly, to compare congeneric patterns of fish using the same habitat but having different *t*-PCB body burdens, average normalized congener concentrations of hot fish from 20-25 ppt mean salinity range were compared to those cold fish from the same habitat range using a scatter plot (Figure 2.9a). There is little difference in the congener patterns between these sub-populations having varying *t*-PCBs ($r = 0.98$; $p < 0.001$). The average normalized concentration patterns for the sub-population of 'hot' fish permanently residing in the fresh to oligohaline waters of the upper estuary (< 5 ppt) near the source and those 'cold' fish residing and migrating in predominantly coastal/marine waters (> 30 ppt) were compared using a scatter plot (Figure 2.9b; $r = 0.89$; $p < 0.001$). Those lower chlorinated congeners such as the di- through tetrachlorobiphenyls (including the coeluting congeners 31+28) were enriched in those fish exclusively utilizing the fresh and oligohaline waters of the upper estuary. Conversely, the more highly chlorinated congeners dominated the pattern of those fish residing in marine waters farther from the major upper Hudson River source.

DISCUSSION

The majority of Hudson River striped bass utilize the estuary only for portions of their lives. Age and sex greatly affect habitat choice. Typically, young of the year and yearlings reside in the estuary while many older fish return to portions of the estuary only to overwinter and/or spawn. Salinity chronologies determined for the 1994/95 Fall and Spring collected striped bass affirm recent findings (Secor and Piccoli 1996; Zlokovitz and Secor, in press) of tremendous variability in habitat use (as expressed by mean salinity of the last growth year) within the Hudson River population (Figure 2.4). Similarly, as others have reported (e.g., Armstrong and Sloan, 1988; Sloan et al. 1995; Bush et al. 1989), *t*-PCB body burdens of Hudson River and Long Island Sound striped bass vary widely as well (Table 2.1). Variability in PCB concentrations within a fish population not associated with the fishes' characteristics (% lipid, length, etc.) have also been observed in the lake trout of Lake Michigan. Using an individual-based model approach, Madenjian et al. (1993) found that the variation in contaminant concentrations among individual fish could be explained by subjecting subsets of the population to different PCB concentrations in prey fish. In the Hudson River however, the variation in *t*-PCB body burdens is largely driven by the widely varying patterns of habitat use (Figure 2.5) in

an estuary which is known to be dominated by a significant and localized source of contamination (Figure 2.1).

Differences among congener patterns of Hudson River striped bass collected throughout the estuary and Long Island were detectable but not pronounced (Figure 2.6). Most notable was the higher proportion of lower chlorinated congeners in those patterns of many striped bass permanently residing in the fresh to oligohaline waters (e.g., Figure 2.6a) compared to those utilizing other portions of the estuary (e.g., Figure 2.6b-d). However, as revealed by the ratio of coeluting congeners (31+28) to (153+132+105) (Figure 2.8b), considerable variability in the patterns exist within a population of fish using similar salinity ranges. For example, the population of fish residing permanently in the fresh to oligohaline waters (0-5 ppt) of the upper estuary had patterns that exemplified both near-source (lower chlorinated) and further from known source (higher chlorinated) profiles. Of the 12 fish utilizing fresh to oligohaline waters (0-5 ppt) and displaying resident lifetime behaviors (e.g., Figure 2.4a), all but two were caught in the Troy Dam region (Figure 2.8b). The Troy-caught fish may be considered truly resident. The two fish within this denoted salinity range having mean salinity ratios of 3.0 and 3.9 ppt and coeluting congener ratios of 0.30 and 0.15 (indicating patterns that were dominated by higher chlorinated PCB congeners; Figure 2.8b) were caught at Catskill (river km 175) and Haverstraw (river km 70). Unlike the those caught at Troy, these two fish migrated to these areas down-estuary and may have depurated lower chlorinated congeners between the time of exposure to the unweathered source around the Troy Dam and their capture location. Similarly, a fish with mean salinity of 5.9 ppt and an equally low ratio of 0.23 was caught down-estuary at Haverstraw. These individual cases suggest that the resolution of habitat use determination through otolith chemistry may be limited.

On average, fish utilizing the 0 to 5 ppt salinity range had congener patterns that were statistically different from those utilizing down-estuary salinity ranges. Patterns dominated by lower chlorinated congeners were indicative of lifetime exposure to unweathered PCBs in the fresh to oligohaline waters of the upper estuary (Troy Dam) while patterns shifted to more higher chlorinated congeners down-estuary. Bush et al. (1989) observed similar pattern differences when comparing individuals captured from the Hudson River to those captured from the Long Island Sound area. They speculated that most of the fish from Long Island Sound were either not exposed to the Hudson River estuary or had been absent from the estuary for an extended time such that the less chlorinated congeners had a chance to depurate. According to tagging studies by Clark (1968), most Long Island Sound striped bass do not utilize the Hudson River estuary or New York Harbor for growth. The salinity profiles of the fish utilizing salinities >30 ppt and having low *t*-PCBs body burdens indicate little growth or PCB bioaccumulation occurring in fresh waters. The resulting average congeneric pattern from those fish can therefore be confidently labeled as representative of the 'background' contingent of bass having little to no interactions with the known source at in the Troy Dam area (Figure 2.10b), even though some of these patterns were source-like (e.g., those having low ratios of coeluting congeners 31+28 to 153+132+105; Figure 2.8b). Conversely, the average congeneric pattern from the resident, near-source contingent (with the exception of those caught in locations other than Troy) represents that expected under constant exposure from the upper estuary source (Figure 2.10a).

In the salinity range from 20 to 25 ppt there was considerable variability in the concentration of *t*-PCBs possibly suggesting that a sub population from this area may have been exposed to a large regional source of PCBs (e.g., New York Harbor). Moreover, within this salinity range, there were

several fish that displayed source-like patterns as indicated by the ratio of coeluting congeners 31+28 to 153+132+105 (Figure 2.6b), even though their individual lifetime salinity chronologies suggested that they had not been in fresh to oligohaline (0 to 5 ppt) waters for the recent (i.e., the last three years) or all of their lives. To discriminate potential unique PCB signals from this area, average PCB congener patterns of hot and cold fish from this salinity range were compared using a scatter plot (Figure 2.9a). The resulting strong linear correlation suggests little difference in PCB congener patterns of the two groups. There are two plausible explanations for these pattern similarities. One is that as the 'hot' population has been exposed to the upper estuary source but has had some time to depurate the lower chlorinated congeners. Those highly chlorinated congeners having slower depuration rates, would be retained for longer times. On the other hand, the patterns of the 'hot' contingent with mean salinities of 20-25 ppt may be reflective of a local source, one having more chlorinated congeners than the up-estuary PCB source profile. It has been widely accepted that the upper Hudson River is a major source of PCB contamination to the lower estuary (Feng et al. 1988), however elevated concentrations of PCBs in sediments from New York Harbor have been reported (Bopp et al. 1981). Recently, Durrel and Lizotte (1998) estimated that 88 Kg of PCB is annually discharged from New York and New Jersey wastewater treatment plants. Whether these inputs are significantly contributing to the inventories of PCBs in the sediment, water and biota and are providing a unique congener pattern in fish utilizing the Harbor as primary habitat, remains unclear. This is partly due to the limited resolution in pinpointing the usage of suspected contaminated areas such as New York Harbor using the salinity profiles derived from otolith analysis. Moreover, Madenjian et al. (1993) suggested that fish that occupy the upper trophic levels in large lakes (e.g., salmonids) are probably poor indicators of the source pattern to the lake because of changes to the congener distribution pattern as PCBs are transported through the food web. Source pattern recognition is most likely equally marred by trophic transfer in Hudson River striped bass.

CONCLUSIONS

Contamination of PCBs in the upper Hudson River not only resulted in elevated body burdens of those striped bass permanently residing in the area but also imparted a characteristic congeneric pattern to the contingent, one that was dominated by lower chlorinated PCB congeners. Based on the congener patterns of sampled Hudson River and Long Island Sound striped bass, there was evidence to suggest other important sources within the estuary. However, due to the limited resolution in pinpointing exact locations with respect to mean salinities within the Hudson River, the source of these PCBs is unknown but likely to be of urban origin (NY Harbor). Other more accurate techniques for evaluating lifetime habitat use such as biotelemetry (Secor, pers. comm.) should be investigated. This study demonstrates the need to adopt an individual-based approach when modeling both the magnitude and pattern of PCB accumulation in Hudson River striped bass such that consideration of the variability in habitat use may be incorporated. Although habitat use was observed to be a determinant of PCB exposure and accumulation in the Hudson River, other factors such as dietary differences down the estuarine gradient of the river and Long Island Sound (e.g. Clark 1968), metabolic elimination (e.g., Brown 1992) and depuration kinetics for PCBs (e.g., Fisk et al. 1998; Thomann et al. 1991) in striped bass may be important in the heterogeneously contaminated Hudson River.

Table 2.1. Classification of Hudson River striped bass samples according to habitat use (mean salinity range encountered during the past year of life) and contaminant body burden. Fish having $t\text{-PCB} \geq 1,000$ ng/g were classified as 'hot'; all others were denoted as 'cold'.

Mean Salinity Range	tag #:	Sex	Season Captured	River Km	Location Caught	Age (years)	Weight (g)	Length (mm)	% Lipids	Mean Salinity, ppt	t-PCBs ng/g wet wt	Hot or Cold Classification
Mean Salinities of 0 to 5 ppt (freshwater/resident):												
	127427	M	Fall	250	Troy	6	1800	570	6.64	1.63	4937	hot
	127449	M	Fall	250	Troy	6	1310	502	1.11	2.05	1771	hot
	127438	M	Fall	250	Troy	8	1300	528	1.52	2.49	3374	hot
	127429	F	Fall	250	Troy	14	8890	950	4.75	2.58	4025	hot
	127442	M	Fall	250	Troy	13	3780	685	4.24	2.65	4374	hot
	127452	M	Fall	70	Haver	10	1570	534	3.01	2.98	2553	hot
	127448	M	Fall	250	Troy	8	1440	541	1.00	3.05	3820	hot
	127674	F	spring	250	Troy	8	4280	763	7.35	3.13	3689	hot
	127446	M	Fall	250	Troy	7	2180	620	2.63	3.35	3348	hot
	127428	M	Fall	250	Troy	6	2220	619	4.37	3.42	4730	hot
	127749	M	spring	175	Catskill	16	2900	600	5.90	3.87	2072	hot
	127432	M	Fall	250	Troy	7	2720	641	5.73	4.29	3300	hot
					average:	9	2866	629	4	3	3499	
					std dev:	3	2036	120	2	1	947	
Mean Salinities of 5 to 10 ppt (oligohaline):												
	127688	F	spring	250	Troy	14	7920	898	3.35	5.67	3396	hot
	127548	F	Fall	70	Haver	6	4350	745	5.76	5.87	1695	hot
	127684	F	spring	250	Troy	9	5620	770	6.84	8.88	2379	hot
	128929	F	Fall	5	NY Harb	5	2250	580	7.00	9.42	2362	hot
	128671	F	Fall	5	NY Harb	12	6800	867	6.56	9.56	3011	hot
					average:	9	5388	772	6	8	2369	
					std dev:	3	1969	112	1	2	587	
	127520	M	Fall	70	Haver	4	2400	609	5.95	9.86	245	cold
Mean Salinities of 10 to 15 ppt (oligohaline):												
	127724	M	spring	120	Pough	9	2800	610	6.71	11.17	1753	hot
	128662	M	Fall	5	NY Harb	4	950	457	4.37	11.01	270	cold
Mean Salinities of 15 to 20 ppt (mesohaline):												
	127728	M	spring	120	Pough	5	2900	626	14.40	15.95	1076	hot
	128872	F	Fall		Long Isle	4	1500	535	1.79	15.20	186	cold
	127528	M	Fall	70	Haver	5	2500	611	5.99	17.63	134	cold
	128762	F	Fall		Long Isle	5	3440	723	2.23	17.98	803	cold
	127748	M	spring	175	Catskill	4	1320	510	3.55	18.26	619	cold
	127727	M	spring	120	Pough	5	2290	592	6.54	19.16	876	cold
	128687	F	Fall	5	NY Harb	4	1280	359	5.58	19.30	387	cold
	127750	F	spring	175	Catskill	7	4940	755	4.85	19.52	353	cold
					average:	5	2467	612	4	18	480	
					std dev:	1	1240	86	2	1	270	
Mean Salinities of 20 to 25 ppt (mesohaline):												
	128656	M	Fall	5	NY Harb	6	2800	631	9.07	20.60	1460	hot
	127729	M	spring	120	Pough	5	2800	607	8.10	20.70	1326	hot
	127730	M	spring	120	Pough	7	3180	660	7.29	21.47	1426	hot
	127510	F	Fall	70	Haver	5	2250	590	4.97	21.51	2979	hot
	128967	F	Fall		Long Isle	8	7210	870	8.37	22.28	1183	hot
	127747	F	spring	175	Catskill	6	3500	670	6.56	22.57	1631	hot
	128637	M	Fall	5	NY Harb	7	2710	660	4.00	24.80	1309	hot
					average:	6	3493	670	7	22	1616	
					std dev:	1	1560	86	2	1	571	
	127638	F	spring	70	Haver	5	2420	613	9.57	20.54	549	cold
	127649	M	spring	70	Haver	5	2600	595	9.02	20.75	747	cold
	128802	M	Fall	5	NY Harb	3	1170	474	4.55	21.41	234	cold
	127734	M	spring	120	Pough	4	2040	574	3.68	22.12	383	cold
	128701	F	Fall	5	NY Harb	15	9190	1007	2.34	22.18	508	cold
	127616	M	spring	70	Haver	5	2100	596	4.35	22.21	409	cold
	127637	M	spring	70	Haver	4	1900	561	5.60	23.60	417	cold
	127736	M	spring	120	Pough	5	3380	672	6.60	23.79	504	cold
	127591	F	spring	70	Haver	6	2920	645	3.94	23.86	440	cold
	128674	F	Fall	5	NY Harb	8	3440	696	3.50	23.91	956	cold
	127739	F	spring	175	Catskill	7	4480	740	4.77	23.97	542	cold
	127707	?	spring	120	Pough	8	4420	753	6.40	24.64	340	cold
	127542	F	Fall	70	Haver	7	3050	669	3.39	24.77	304	cold
					average:	6	3316	661	5	23	487	
					std dev:	3	1929	124	2	1	184	
Mean Salinities of 25 to 30 ppt (euhaline):												
	127462	M	Fall	70	Haver	11	6550	763	3.74	25.16	2120	hot
	128847	F	Fall	5	NY Harb	5	1750	533	3.50	25.18	1078	hot
	128635	M	Fall	5	NY Harb	7	3870	718	5.29	26.08	1458	hot
	128634	M	Fall	5	NY Harb	10	7500	858	13.80	26.97	4380	hot
	128668	F	Fall	5	NY Harb	13	5950	840	2.89	27.05	1332	hot
					average:	9	5124	742	6	26	2074	
					std dev:	3	2065	116	4	1	1203	
	127622	F	spring	70	Haver	5	2010	575	3.73	25.16	511	cold
	127656	F	spring	175	Catskill	10	8300	845	5.35	25.10	494	cold
	127740	F	spring	175	Catskill	7	5902	805	4.89	26.22	356	cold
	127746	F	spring	175	Catskill	5	3330	682	6.38	26.56	681	cold
	128664	M	Fall	5	NY Harb	5	1650	502	6.19	29.17	215	cold
	128665	F	Fall	5	NY Harb	3	1300	463	8.01	29.70	357	cold
	128681	F	Fall		Long Isle	3	1340	492	6.17	25.49	264	cold
	128801	F	Fall	5	NY Harb	4	1080	470	4.58	28.91	247	cold
					average:	5	3114	604	6	27	391	
					std dev:	2	2466	144	1	2	150	
Mean Salinities > 30 ppt (euhaline):												
	128667	F	Fall	5	NY Harb	10	3250	686	3.49	37.16	1328	hot
	127830	F	spring	70	Haver	8	3300	680	2.34	30.60	595	cold
	127569	F	spring	70	Haver	12	11464	980	5.00	30.70	638	cold
	128680	F	Fall		Long Isle	4	1860	559	4.31	31.47	233	cold
	127513	F	Fall	70	Haver	5	2660	661	2.83	31.49	211	cold
	127741	M	spring	175	Catskill	8	4000	681	7.41	31.79	679	cold
	127546	M	Fall	70	Haver	5	5100	717	7.86	31.84	531	cold
	127654	F	spring	175	Catskill	8	6360	801	2.24	31.92	448	cold
	127743	F	spring	175	Catskill	7	3820	696	3.33	32.55	795	cold
	127657	F	spring	175	Catskill	12	9307	920	3.83	35.27	316	cold
					average:	8	5319	744	4	32	494	
					std dev:	3	3017	126	2	1	194	

Table 2.1, page 2

Mean Salinity Range	Tag #	Sex	Season Captured	River Km	Location Caught	Age (years)	Weight (g)	Length (mm)	% Lipids	Mean Salinity, ppt	C-PCBs ng/g wet wt	Hot or Cold Classification
Mean Salinities of 0 to 5 ppt (freshwater/resident):												
	127427	M	Fall	250	Troy	6	1800	570	6.64	1.63	4937	hot
	127449	M	Fall	250	Troy	6	1310	502	1.11	2.05	1771	hot
	127438	M	Fall	250	Troy	8	1300	528	1.52	2.49	3374	hot
	127429	F	Fall	250	Troy	14	8890	950	4.75	2.58	4025	hot
	127442	M	Fall	250	Troy	13	3780	685	4.24	2.65	4374	hot
	127452	M	Fall	70	Haver	10	1570	534	3.01	2.98	2553	hot
	127448	M	Fall	250	Troy	8	1440	541	1.00	3.05	3820	hot
	127674	F	spring	250	Troy	8	4280	763	7.35	3.13	3689	hot
	127446	M	Fall	250	Troy	7	2180	620	2.63	3.33	3348	hot
	127428	M	Fall	250	Troy	6	2220	619	4.37	3.42	4730	hot
	127749	M	spring	175	Catskill	16	2900	600	3.90	3.87	2072	hot
	127432	M	Fall	250	Troy	7	2720	641	5.73	4.29	3300	hot
					average:	9	2866	629	4	3	3499	
					std dev:	3	2036	120	2	1	947	
Mean Salinities of 5 to 10 ppt (oligohaline):												
	127688	F	spring	250	Troy	14	7920	898	3.35	5.67	3396	hot
	127548	F	Fall	70	Haver	6	4350	745	5.76	5.87	1693	hot
	127684	F	spring	250	Troy	9	5620	770	6.84	8.88	2379	hot
	128929	F	Fall	5	NY Harb	5	2250	580	7.00	9.42	2362	hot
	128671	F	Fall	5	NY Harb	12	6800	867	6.56	9.56	3011	hot
					average:	9	3388	772	6	8	2569	
					std dev:	3	1969	112	1	2	587	
	127520	M	Fall	70	Haver	4	2400	609	5.95	9.86	245	cold
Mean Salinities of 10 to 15 ppt (oligohaline):												
	127724	M	spring	120	Pough	9	2800	610	6.71	11.17	1753	hot
	128662	M	Fall	5	NY Harb	4	950	27	4.37	11.01	270	cold
Mean Salinities of 15 to 20 ppt (mesohaline):												
	127728	M	spring	120	Pough	5	2900	605	14.40	15.95	1076	hot
	128872	F	Fall		Long Isle	4	1500	535	1.79	15.20	186	cold
	127528	M	Fall	70	Haver	5	2500	611	5.99	17.63	134	cold
	128762	F	Fall		Long Isle	5	3440	723	2.23	17.98	803	cold
	127748	M	spring	175	Catskill	4	1320	516	3.55	18.26	619	cold
	127727	M	spring	120	Pough	5	2290	590	6.54	19.16	876	cold
	128687	F	Fall	5	NY Harb	4	1280	559	5.58	19.30	387	cold
	127750	F	spring	175	Catskill	7	4940	755	4.85	19.52	353	cold
					average:	5	2467	612	4	18	480	
					std dev:	1	1240	86	2	1	270	
Mean Salinities of 20 to 25 ppt (mesohaline):												
	128636	M	Fall	5	NY Harb	6	2800	631	9.07	20.60	1460	hot
	127729	M	spring	120	Pough	5	2800	607	8.10	20.70	1326	hot
	127730	M	spring	120	Pough	7	3180	660	7.29	21.47	1426	hot
	127510	F	Fall	70	Haver	5	2250	590	4.97	21.51	2979	hot
	128967	F	Fall		Long Isle	8	7210	870	8.37	22.28	1183	hot
	127747	F	spring	175	Catskill	6	3500	670	6.56	22.57	1631	hot
	128637	M	Fall	5	NY Harb	7	2710	660	4.00	24.80	1309	hot
					average:	6	3493	670	7	22	1616	
					std dev:	1	1560	86	2	1	571	
	127638	F	spring	70	Haver	5	2420	613	9.57	20.54	549	cold
	127649	M	spring	70	Haver	5	2600	595	9.02	20.75	747	cold
	128802	M	Fall	5	NY Harb	3	1170	474	4.55	21.41	234	cold
	127734	M	spring	120	Pough	4	2040	574	3.68	22.12	383	cold
	128701	F	Fall	5	NY Harb	15	9190	1007	2.34	22.18	508	cold
	127616	M	spring	70	Haver	5	2100	596	4.35	22.21	409	cold
	127637	M	spring	70	Haver	4	1900	561	5.60	23.60	417	cold
	127736	M	spring	120	Pough	5	3380	672	6.60	23.79	504	cold
	127591	F	spring	70	Haver	6	2920	645	3.94	23.86	440	cold
	128674	F	Fall	5	NY Harb	8	3440	696	3.50	23.91	956	cold
	127739	F	spring	175	Catskill	7	4480	740	4.77	23.97	542	cold
	127707	?	spring	120	Pough	8	4420	753	6.40	24.64	340	cold
	127542	F	Fall	70	Haver	7	3050	669	3.39	24.77	304	cold
					average:	6	3316	661	5	23	487	
					std dev:	3	1929	124	2	1	184	
Mean Salinities of 25 to 30 ppt (euhaline):												
	127462	M	Fall	70	Haver	11	6550	763	3.74	25.16	2120	hot
	128847	F	Fall	5	NY Harb	5	1750	533	3.50	25.18	1078	hot
	128635	M	Fall	5	NY Harb	7	3870	718	5.29	26.08	1458	hot
	128634	M	Fall	5	NY Harb	10	7500	858	13.80	26.97	4380	hot
	128668	F	Fall	5	NY Harb	13	5950	840	2.89	27.05	1332	hot
					average:	9	5124	742	6	26	2074	
					std dev:	3	2065	116	4	1	1203	
	127622	F	spring	70	Haver	5	2010	575	3.73	25.16	511	cold
	127656	F	spring	175	Catskill	10	8300	845	5.35	25.10	494	cold
	127740	F	spring	175	Catskill	7	5902	805	4.89	26.22	356	cold
	127746	F	spring	175	Catskill	5	3330	682	6.38	26.56	681	cold
	128664	M	Fall	5	NY Harb	5	1650	502	6.19	29.17	215	cold
	128665	F	Fall	5	NY Harb	3	1300	463	8.01	29.70	357	cold
	128681	F	Fall	5	Long Isle	3	1340	492	6.17	25.49	264	cold
	128801	F	Fall	5	NY Harb	4	1080	470	4.58	28.91	247	cold
					average:	5	3114	604	6	27	391	
					std dev:	2	2466	144	1	2	150	
Mean Salinities > 30 ppt (euhaline):												
	128667	F	Fall	5	NY Harb	10	3250	686	3.49	37.16	1328	hot
	127830	F	spring	70	Haver	8	3300	680	2.34	30.60	595	cold
	127569	F	spring	70	Haver	12	11464	980	5.00	30.70	638	cold
	128680	F	Fall		Long Isle	4	1860	559	4.31	31.47	233	cold
	127513	F	Fall	70	Haver	5	2660	661	2.83	31.49	211	cold
	127741	M	spring	175	Catskill	8	4000	681	7.41	31.79	679	cold
	127546	M	Fall	70	Haver	5	5100	717	7.86	31.84	531	cold
	127654	F	spring	175	Catskill	8	6360	801	2.24	31.92	448	cold
	127743	F	spring	175	Catskill	7	3820	696	3.33	32.55	795	cold
	127657	F	spring	175	Catskill	12	9307	920	3.83	35.27	316	cold
					average:	8	5319	744	4	32	494	
					std dev:	3	3017	126	2	1	194	

Table 2.1, page 3

Mean Salinity Range	Tag #	Sex	Season Captured	River Km	Location Caught	Age (years)	Weight (g)	Length (mm)	% Lipid	Mean Salinity, ppt	L-POLs mg/g wet wt.	Hot or Cold	Classification
<i>Mean Salinities of 0 to 5 ppt (freshwater/estuarine):</i>													
	127427	M	Fall	230	Troy	6	1800	570	6.64	1.63	4937	hot	
	127449	M	Fall	230	Troy	6	1310	502	1.11	2.05	1771	hot	
	127438	M	Fall	230	Troy	8	1300	528	1.52	2.49	3374	hot	
	127429	F	Fall	230	Troy	14	8890	950	4.75	2.58	4025	hot	
	127442	M	Fall	230	Troy	13	3780	685	4.24	2.65	4374	hot	
	127452	M	Fall	70	Harver	10	1570	534	3.01	2.98	2553	hot	
	127448	M	Fall	230	Troy	8	1440	541	1.00	3.05	3020	hot	
	127674	F	spring	230	Troy	8	4280	783	7.35	3.15	3689	hot	
	127646	M	Fall	230	Troy	7	2180	620	2.63	3.35	3348	hot	
	127428	M	Fall	230	Troy	6	2220	619	4.37	3.42	4710	hot	
	127749	M	spring	175	Cadkill	16	2900	600	3.90	3.87	2072	hot	
	127432	M	Fall	230	Troy	7	2720	641	5.73	4.29	3300	hot	
			average:		std dev:	9	2666	629	4	3	3499		
						3	2636	120	2	1	947		
<i>Mean Salinities of 5 to 10 ppt (saltwater):</i>													
	127088	F	spring	230	Troy	14	7920	898	3.35	5.67	3396	hot	
	127548	F	Fall	70	Harver	6	4330	745	5.76	5.87	1695	hot	
	127684	F	spring	230	Troy	9	5620	770	6.84	8.88	2379	hot	
	128929	F	Fall	5	NY Harb	5	2250	580	7.00	9.42	2362	hot	
	128671	F	Fall	5	NY Harb	12	6800	867	6.56	9.56	3011	hot	
			average:		std dev:	9	5348	772	6	8	2569		
						3	1969	112	1	3	587		
	127520	M	Fall	70	Harver	4	2400	609	5.95	9.86	245	cold	
<i>Mean Salinities of 10 to 15 ppt (saltwater):</i>													
	127724	M	spring	120	Pough	9	2800	610	6.71	11.17	1753	hot	
	128662	M	Fall	5	NY Harb	4	950	457	4.37	11.01	270	cold	
<i>Mean Salinities of 15 to 20 ppt (nearshore):</i>													
	127728	M	spring	120	Pough	5	2900	626	14.40	15.95	1076	hot	
	128872	F	Fall	70	Long Isle	4	1500	535	1.79	15.20	186	cold	
	127558	M	Fall	70	Harver	5	2500	611	5.99	17.63	134	cold	
	128762	F	Fall	175	Cadkill	5	3440	723	2.23	17.98	803	cold	
	127748	M	spring	120	Pough	5	1320	510	3.55	18.26	619	cold	
	127727	M	spring	120	Pough	5	2290	592	6.54	19.16	876	cold	
	128687	F	Fall	5	NY Harb	4	1280	559	5.58	19.30	387	cold	
	127730	F	spring	175	Cadkill	7	4940	755	4.85	19.52	353	cold	
			average:		std dev:	7	2467	612	4	18	480		
						1	1240	86	2	1	270		
<i>Mean Salinities of 20 to 25 ppt (nearshore):</i>													
	128636	M	Fall	5	NY Harb	6	2800	631	9.07	20.60	1460	hot	
	127759	M	spring	120	Pough	5	2800	607	8.10	20.70	1326	hot	
	127730	M	spring	120	Pough	7	2180	660	7.29	21.47	1426	hot	
	127510	F	Fall	70	Harver	5	2250	590	4.97	21.51	2979	hot	
	128957	F	Fall	175	Long Isle	8	7210	870	8.37	22.28	1183	hot	
	127517	F	spring	175	Cadkill	6	3500	670	6.56	22.57	1631	hot	
	128637	M	Fall	5	NY Harb	7	2710	660	4.00	24.80	1309	hot	
			average:		std dev:	6	3493	679	7	22	1616		
						1	1540	86	2	1	571		
	127638	F	spring	70	Harver	5	2420	613	9.57	20.54	549	cold	
	127649	M	spring	70	Harver	5	2600	595	9.02	20.75	747	cold	
	128802	M	Fall	5	NY Harb	3	1170	474	4.55	21.41	234	cold	
	127754	M	spring	120	Pough	4	2040	574	3.68	22.12	383	cold	
	128701	F	Fall	5	NY Harb	15	9190	1007	2.34	22.18	508	cold	
	127616	M	spring	70	Harver	5	2100	596	4.35	22.21	409	cold	
	127637	M	spring	70	Harver	5	1900	561	5.60	23.60	417	cold	
	127736	M	spring	120	Pough	4	3380	672	6.60	23.79	504	cold	
	127591	F	spring	70	Harver	6	2920	645	3.94	23.86	440	cold	
	128874	F	spring	70	Harver	8	3440	696	3.50	23.91	956	cold	
	127739	F	spring	175	Cadkill	7	4480	740	4.77	23.97	542	cold	
	127707	?	spring	120	Pough	8	4420	733	6.40	24.64	340	cold	
	127542	F	Fall	70	Harver	7	3050	669	3.39	24.77	304	cold	
			average:		std dev:	6	3216	647	5	23	487		
						3	1929	124	2	1	184		
<i>Mean Salinities of 25 to 30 ppt (saltwater):</i>													
	127462	M	Fall	70	Harver	11	6550	763	3.74	25.16	2120	hot	
	128417	F	Fall	5	NY Harb	5	1750	533	3.50	25.18	1078	hot	
	128635	M	Fall	5	NY Harb	7	3870	718	5.29	26.08	1458	hot	
	128634	M	Fall	5	NY Harb	10	7500	858	13.80	26.97	4380	hot	
	128668	F	Fall	5	NY Harb	13	5950	840	2.89	27.05	1332	hot	
			average:		std dev:	9	5124	742	26	26	2074		
						3	2065	116	4	1	1203		
	127622	F	spring	70	Harver	5	2010	575	3.73	25.16	511	cold	
	127656	F	spring	175	Cadkill	10	8300	845	5.35	25.10	494	cold	
	127740	F	spring	175	Cadkill	7	5902	805	4.89	26.22	356	cold	
	127746	F	spring	175	Cadkill	5	3330	682	6.38	26.56	681	cold	
	128664	M	Fall	5	NY Harb	5	1650	502	6.19	29.17	215	cold	
	128665	F	Fall	5	NY Harb	3	1300	463	8.01	29.70	357	cold	
	128681	F	Fall	5	Long Isle	3	3100	177	7.86	31.84	531	cold	
	128801	F	Fall	5	NY Harb	9	6560	801	2.24	31.92	448	cold	
			average:		std dev:	7	3820	696	3.33	32.55	795		
						12	9307	920	3.83	35.27	316	cold	
						8	3319	744	4	32	494		
						3	3017	124	2	1	194		
<i>Mean Salinities > 30 ppt (saltwater):</i>													
	128657	F	Fall	5	NY Harb	10	3250	686	3.49	37.16	1328	hot	
	127830	F	spring	70	Harver	8	3300	680	2.34	30.60	595	cold	
	127569	F	spring	70	Harver	12	11464	980	5.00	30.70	638	cold	
	128680	F	Fall	70	Long Isle	4	1860	559	4.31	31.47	233	cold	
	127513	F	Fall	70	Harver	5	2680	661	2.83	31.49	211	cold	
	127741	M	spring	175	Cadkill	8	4000	981	7.41	31.79	679	cold	
	127546	M	spring	175	Cadkill	5	3100	177	7.86	31.84	531	cold	
	127654	F	spring	175	Cadkill	9	6560	801	2.24	31.92	448	cold	
	127743	F	spring	175	Cadkill	7	3820	696	3.33	32.55	795	cold	
	127657	F	spring	175	Cadkill	12	9307	920	3.83	35.27	316	cold	
			average:		std dev:	8	3319	744	4	32	494		
						3	3017	124	2	1	194		

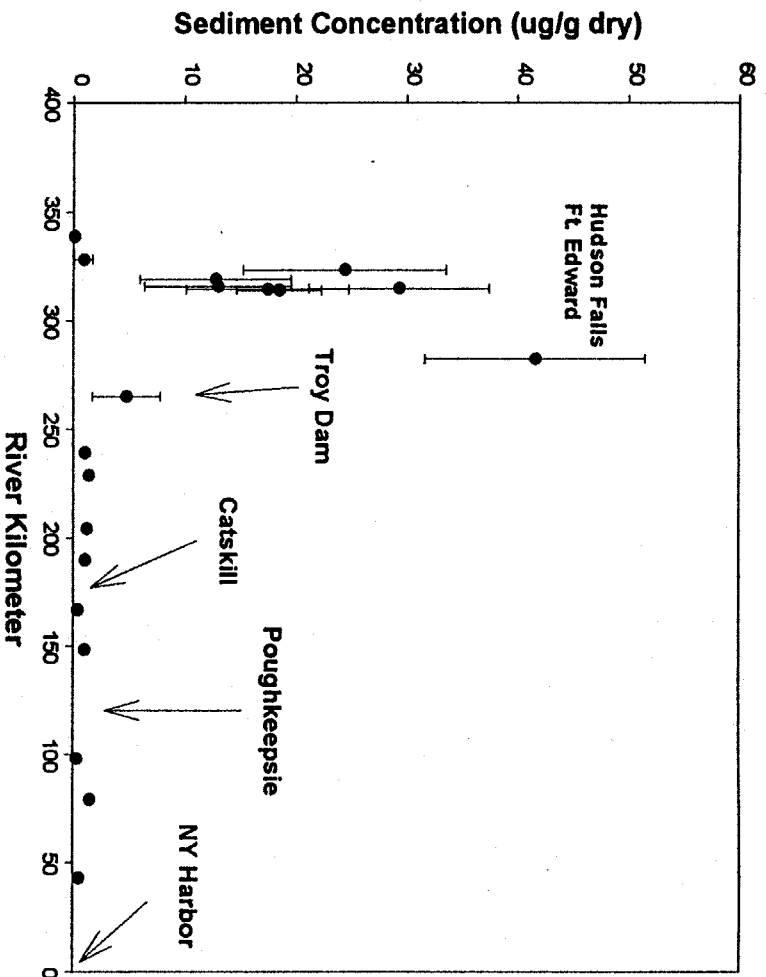


Figure 2.1. Sedimentary total PCB (*l*-PCBs) concentrations as a function of river mile (TAMS Consulting 1997, unpublished data).

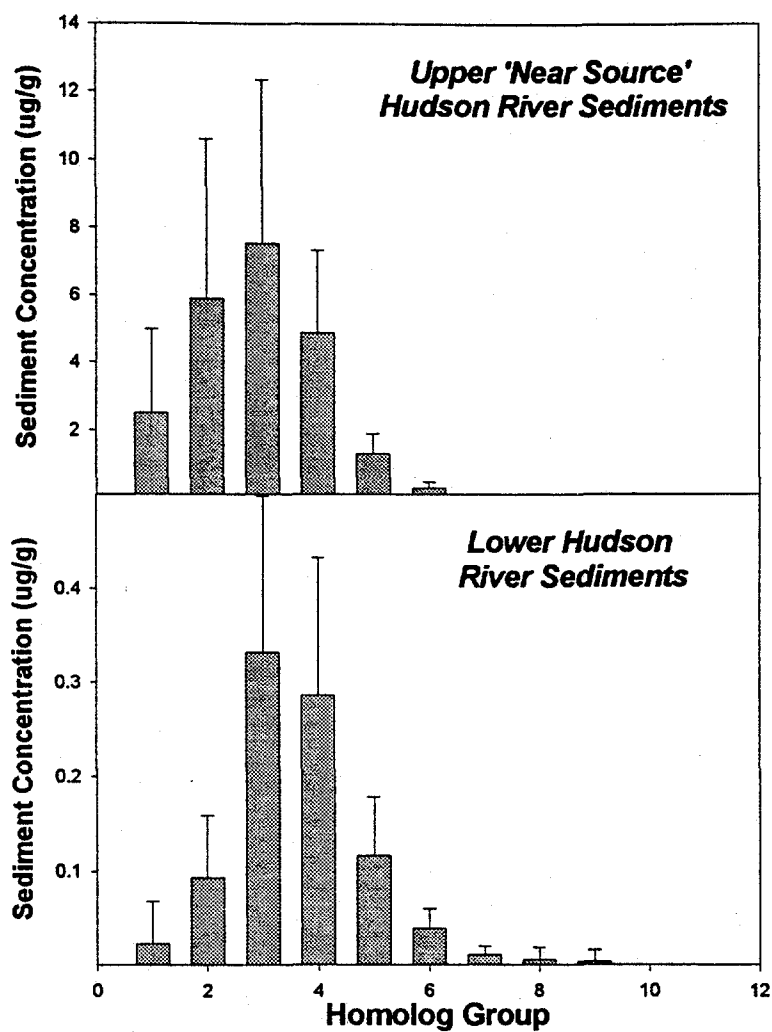


Figure 2.2. PCB homolog pattern for upper Hudson River (Troy) and for lower Hudson River (Haverstraw) (TAMS Consulting 1997, unpublished data).

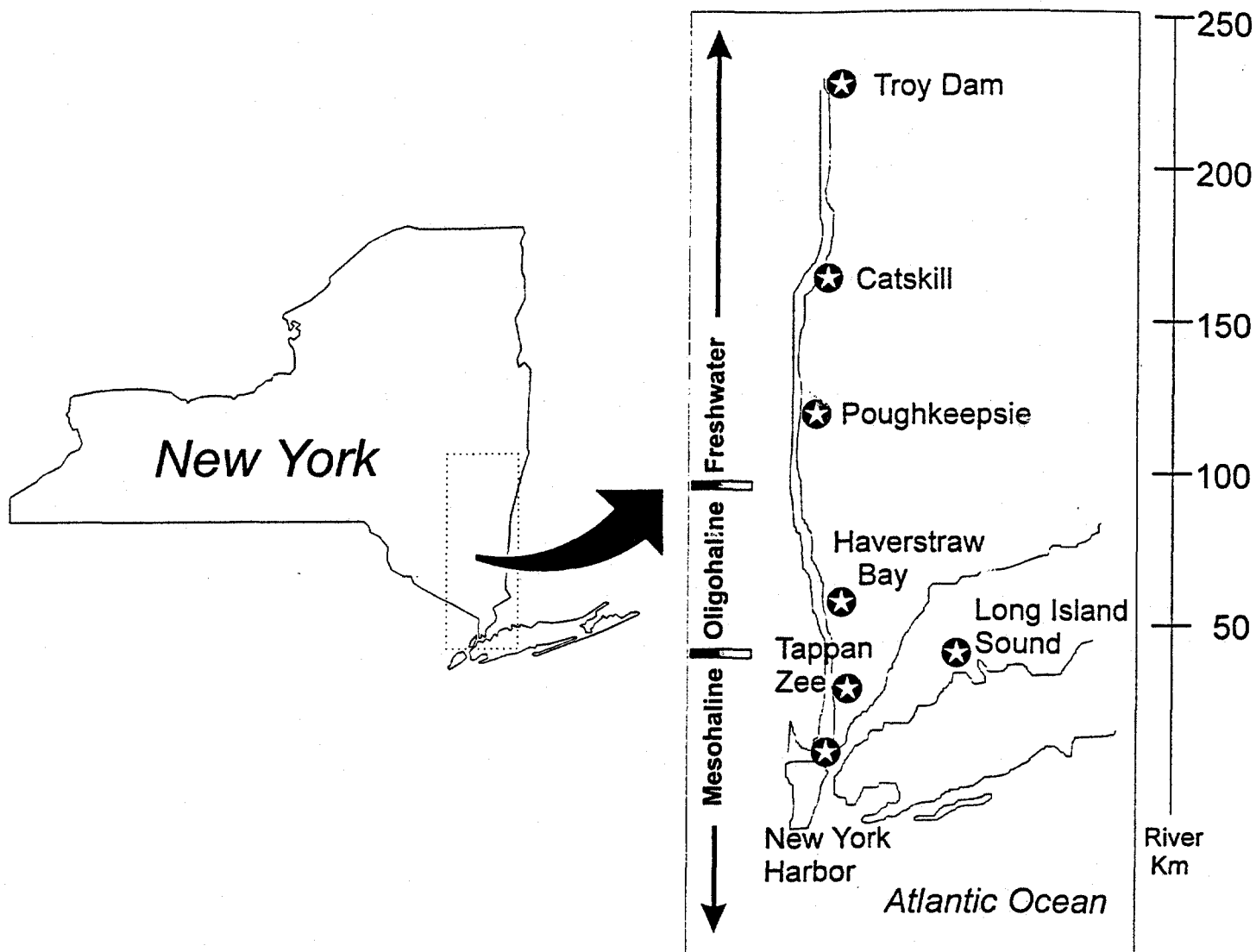


Figure 2.3. Map of the Hudson River Estuary and Long Island Sound showing zones of capture for those fish used in this study.

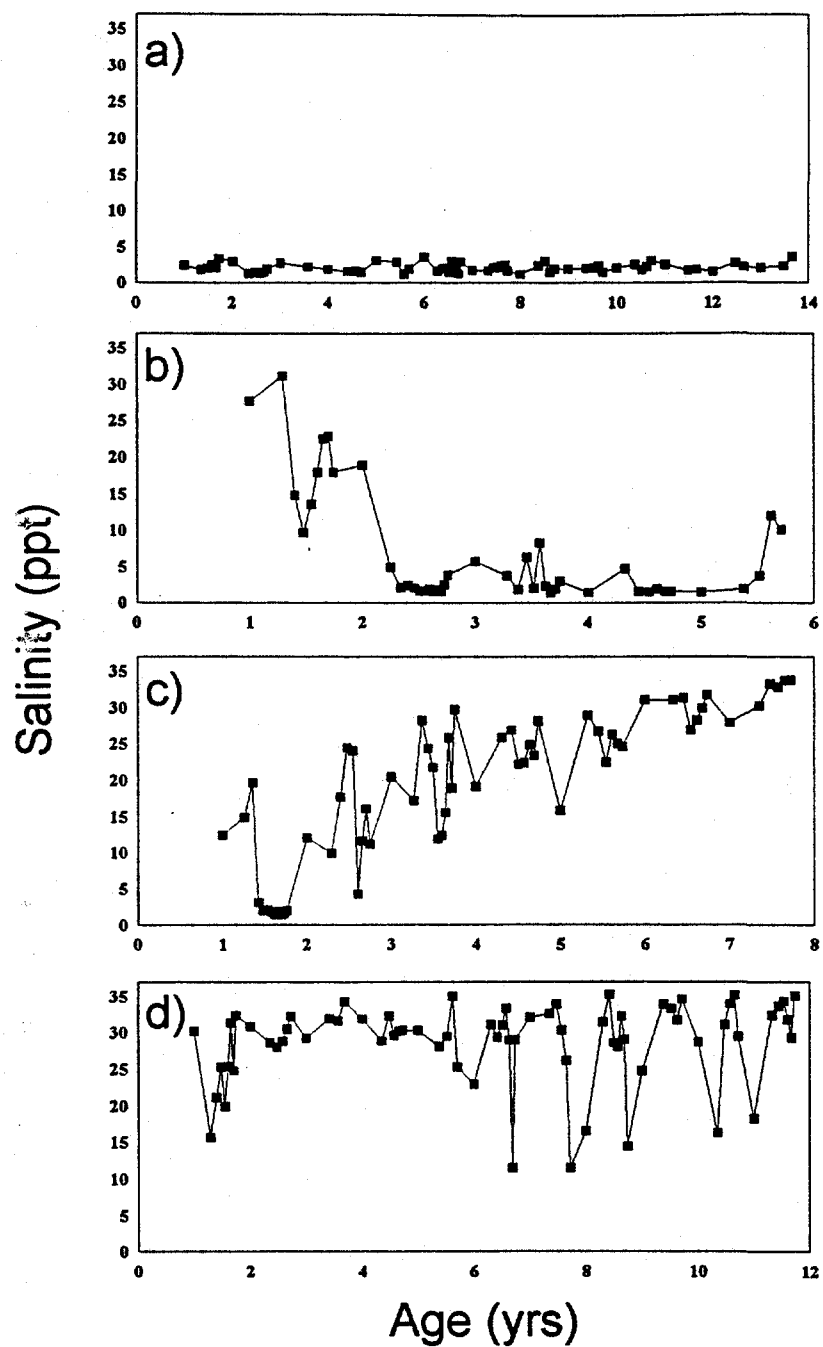


Figure 2.4. Representative time series of salinity habitation for individual fish displaying a) resident behavior (tag #127442), b) a shift from high to low salinity (tag #127548), c) a shift from low salinity to high salinity (tag #127654), and d) resident behavior in saline waters with annual migrations to fresher waters (tag #127569).

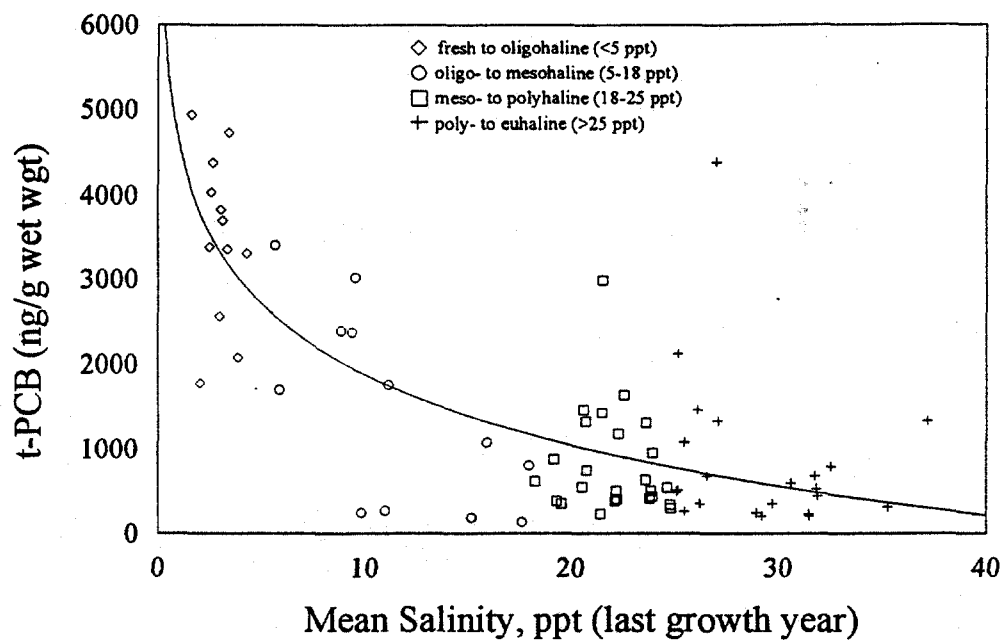


Figure 2.5. Mean salinity of last growth year versus *t*-PCB concentrations as determined by congener specific analysis.

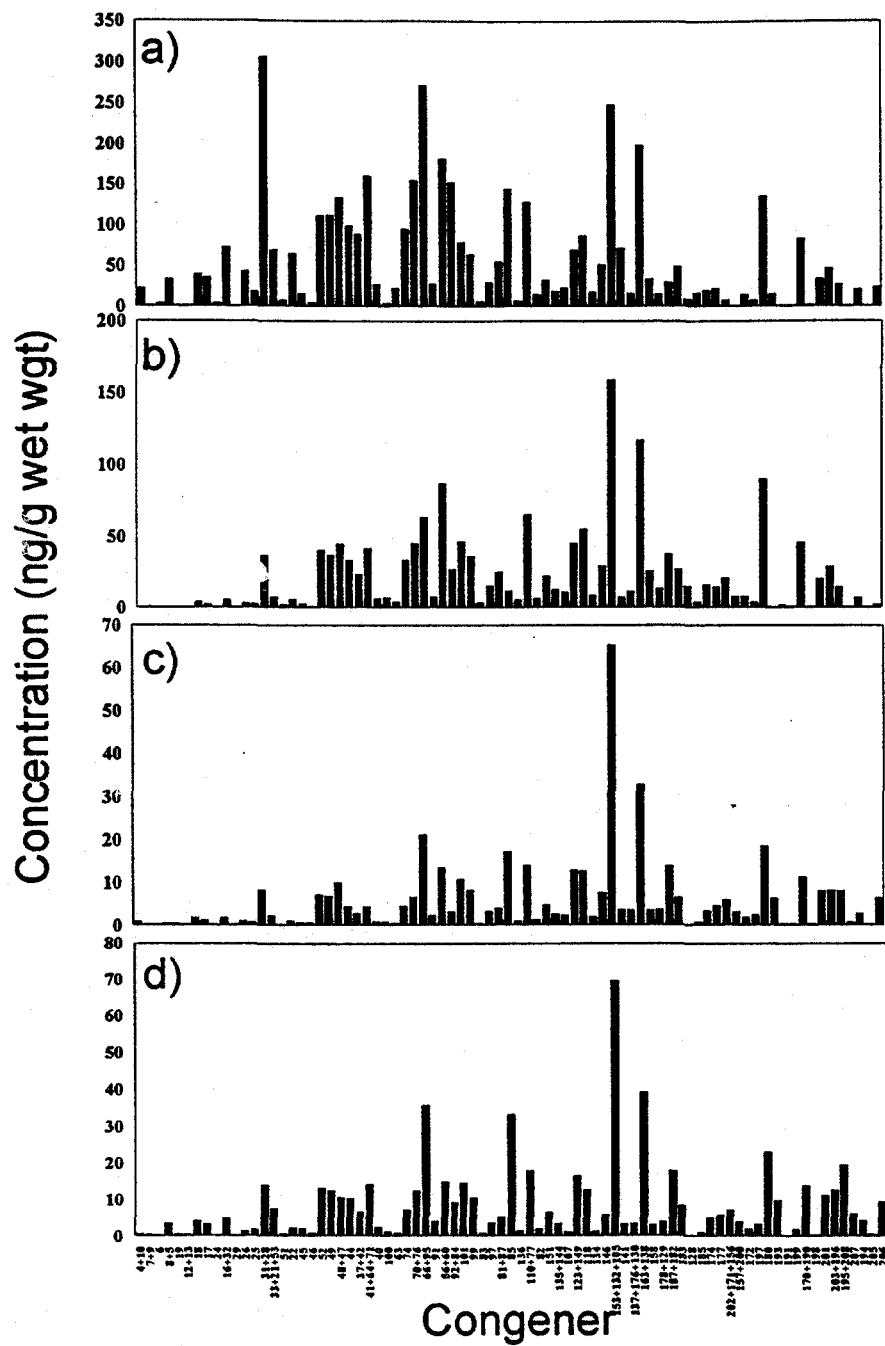


Figure 2.6. Representative PCB congener concentrations displayed in chromatographic elution order for those individual fish having corresponding time series of salinity habitation of Figure 2.1.

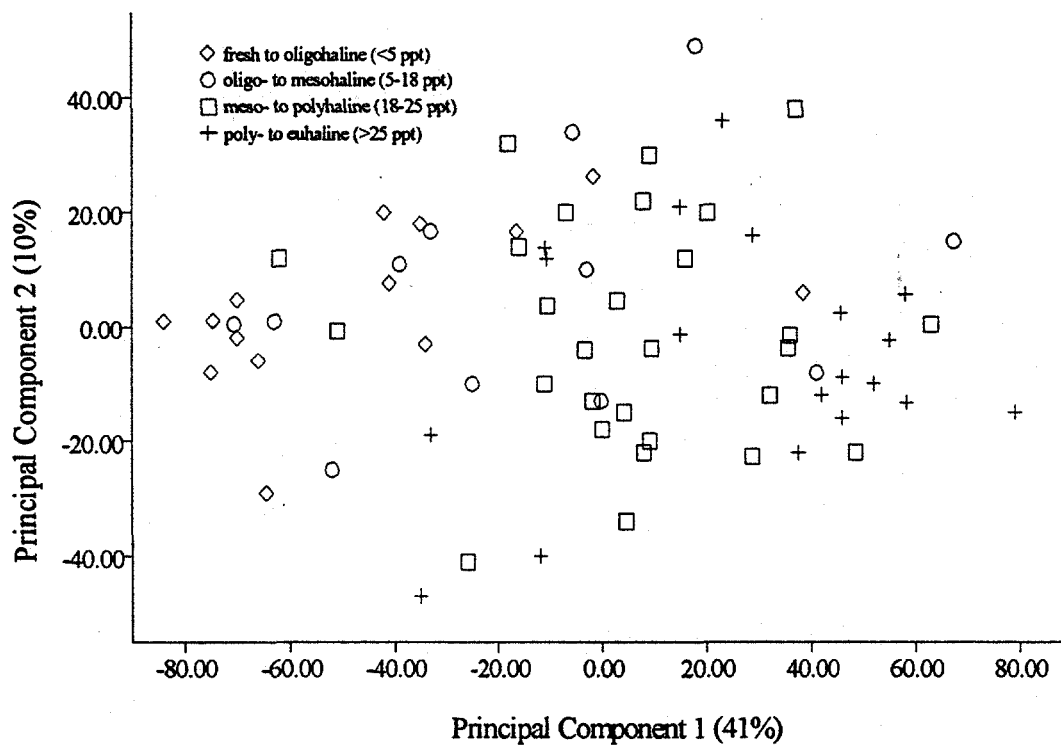


Figure 2.7. Principal component analysis crossplot of principal components 1 and 2. Individual fish are grouped according to mean salinity range of last growth year.

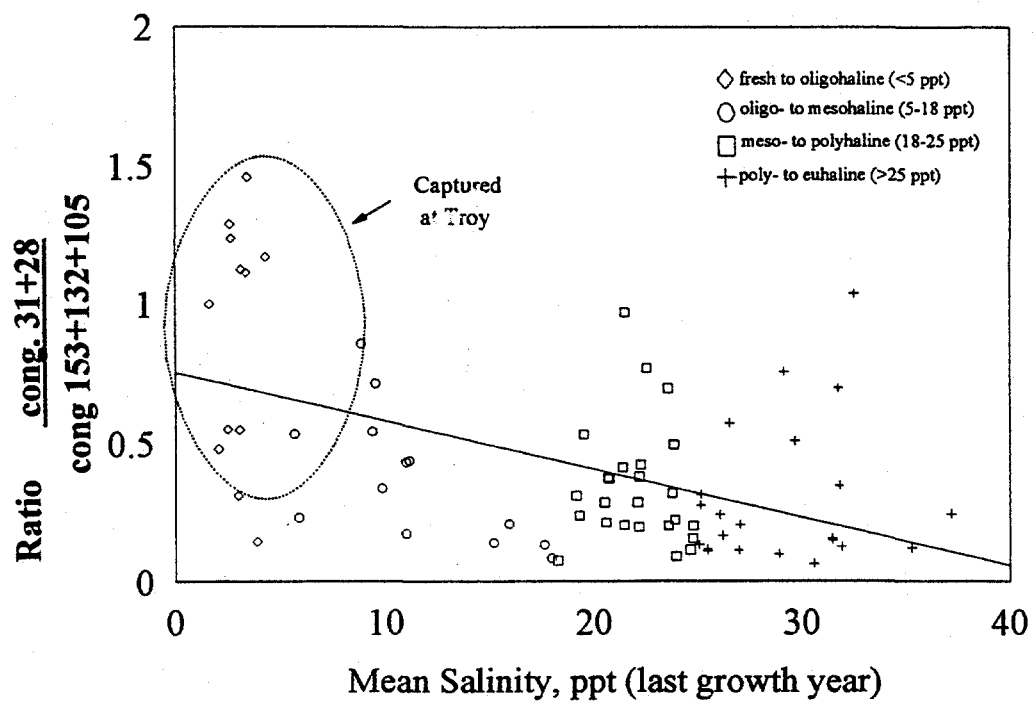


Figure 2.8. The ratio of the concentrations of coeluting congeners 31+28 and 153+132+105 versus mean salinity range for last growth year.

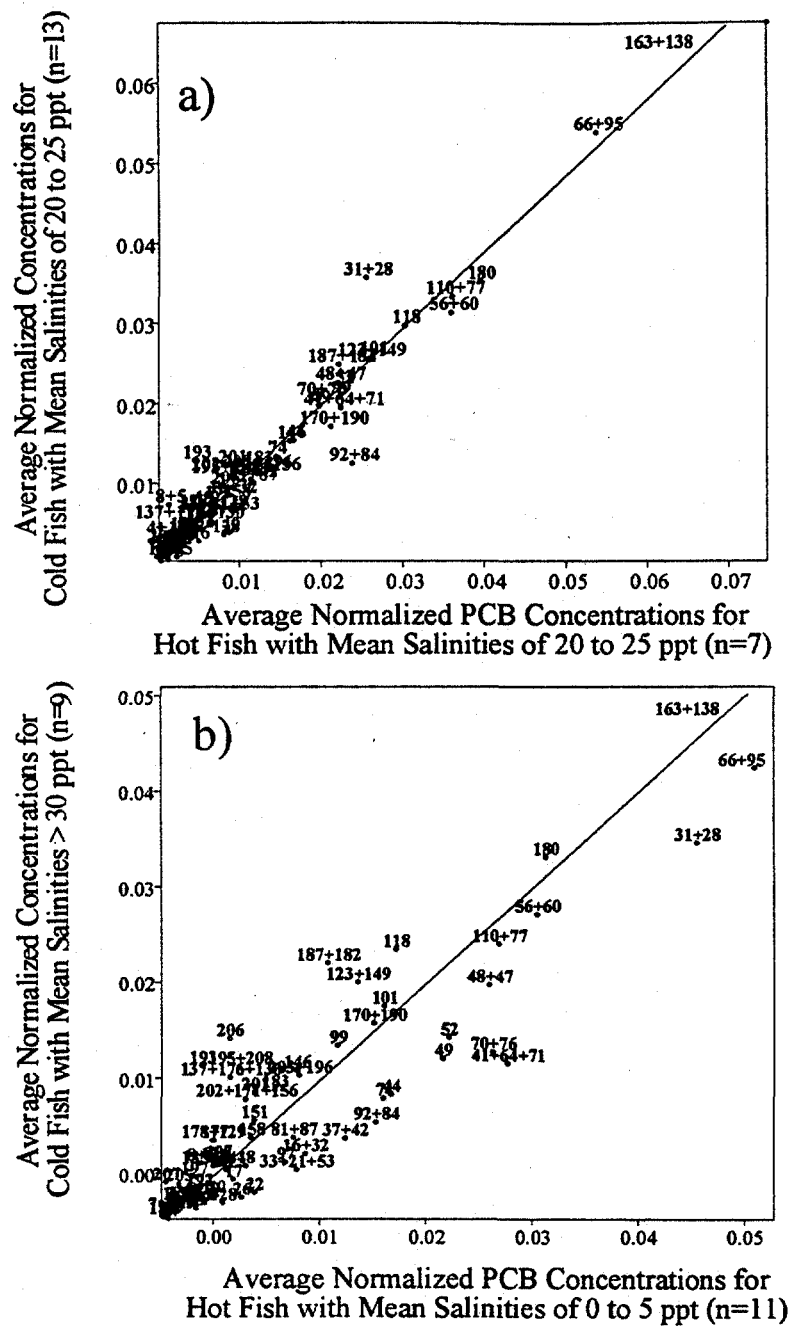


Figure 2.9 Scatter plots of the average normalized congener concentrations of a) 'hot' versus 'cold' contingents having mean salinity ranges of 20-25 ppt, and b) 'hot' resident contingents of 0-5 ppt mean salinity versus 'cold' contingents of mean salinities >30 ppt. Line indicates ideal case under which patterns would be the same.

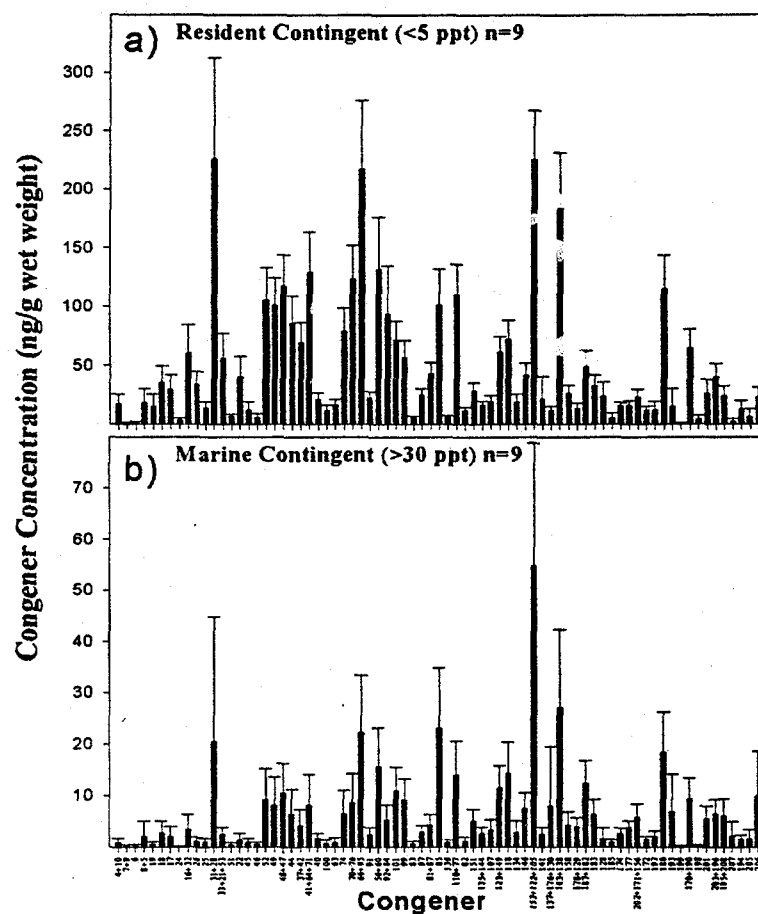


Figure 2.10 Average congener patterns showing absolute concentrations for a) an 'exposed' contingent residing near the known source in the upper Hudson River, and b) a 'background' or marine contingent residing in waters >30 ppt. Error bars represent the standard deviations of the means.

C

HAPTER 3. Identification of Riverine, Estuarine, and Coastal Contingents of Hudson River Striped Bass Based Upon Otolith Elemental Fingerprints

D. H. Secor, J. R. Rooker, E. R. Zlokovitz and V. S. Zdanowicz

ABSTRACT

Elemental fingerprints of otoliths from Hudson River striped bass (*Morone saxatilis*) were used to define resident, estuarine, and coastal migratory contingents which had previously been determined by otolith microprobe of Sr:Ca. Using solution-based inductively coupled plasma mass spectrometry, 14 metals were quantified in whole otoliths. Discriminant analysis of elements other than Sr (deliberately excluded) showed a high degree of separation among the three migratory contingents. Co, Ba, and Rb were higher in otoliths from the freshwater resident group, while Sr was lower. Identification of contingents by the bulk chemistry method indicated divergent lifetime migratory patterns for Hudson River striped bass. We speculate that at the population level, resiliency to exploitation and environmental change is conferred by the maintenance of divergent life cycle pathways by sub-population contingents.

INTRODUCTION

Patterns of migrations in coastal and estuarine fishes are known to be variable at individual and sub-population levels (Leggett 1984; Wroblewski et al. 1994). Migrations within populations are affected by changes in population abundance, climate, flow regimes, and degradation of migration corridors (Leggett 1977). Variable migrations result in differential vulnerability to exploitation and habitat degradation (Kohlenstein 1981; Rose and Leggett 1991; Limburg and Schmidt 1990; Frank 1992; Fogarty 1998; Zlokovitz and Secor, in press). Measuring migration variability within populations is complex because methodologies (e.g. tag-recapture, telemetry, hydroacoustics, biochemical markers) are usually applied at the population level and are rarely applied at the temporal and spatial scales necessary to evaluate variability in seasonal and lifetime migrations (Secor 1997).

The striped bass (*Morone saxatilis*) is a relatively long-lived teleost (ca. 30 years; Secor et al. 1995b) with populations historically ranging between the St. Lawrence River and Gulf of Mexico in North America. The Hudson River population of striped bass is one of two principal populations contributing to coastal fisheries in the U.S. (Wirgin et al. 1993). The population is facultatively anadromous, showing high variability in the degree to which individuals will undertake coastal migrations. Based upon early tagging studies, Clark (1968) proposed the existence of migratory "contingents" of sub-population aggregates which share common migratory histories. This explanation for seasonal and spatial variations in tag-recaptures was criticized because tagged striped bass could not be confidently differentiated from Chesapeake Bay striped bass, the other major

contributor to coastal stocks (Waldman et al. 1990). Also, biases in sampling intensity occurred over spatial and temporal scales, compromising interpretations. More recent population-level explanations of Hudson River striped bass migratory patterns specify size- and sex-specific rates of coastal emigration applied to the entire population (McLaren et al. 1981; Waldman et al. 1990; Dorazio et al. 1994; Secor and Piccoli 1996).

Clark's contingent hypothesis was revisited by Zlokovitz and Secor (in press) who used microprobe of otolith Sr to explore ontogenetic patterns of migration and habitat use. Otolith Sr serves as a tracer of salinity encountered by striped bass (Secor et al. 1995), and thus microprobe of Sr across annuli within the microstructure of otoliths can be used to reconstruct lifetime history of habitat use along a salinity gradient (Secor 1992; Secor and Piccoli 1996). Otolith Sr/Ca analysis revealed three migratory groups for Hudson River striped bass (Figure 1): 1) a resident group, inhabiting freshwater and oligohaline regions of the Hudson River; 2) a lower estuary "mesohaline" group, inhabiting mesohaline and polyhaline regions (New York City Harbor region and Long Island Sound); and 3) a coastal migratory group, which periodically inhabited marine regions.

While otolith Sr is an important scalar of variable migrations by Hudson River striped bass (Secor and Piccoli 1996), otoliths contain other elements which might record more subtle environmental gradients (Thorrold et al. 1997), and thereby more precisely define migratory contingents. Elemental fingerprints have been used as a means to identify natal source and evaluate migration patterns for several coastal and oceanic species (Edmonds et al. 1989, 1991, 1992, Campana et al. 1994, 1995; Thresher et al. 1994; Secor and Zdanowicz 1998). The purpose of this paper is to use otolith elemental fingerprints to examine migratory groups of Hudson River striped bass. Corroboration between approaches is first addressed by comparing otolith Sr measured by microprobe (X-ray wave-length dispersive spectrometry [WDS]) and bulk chemistry (solution-based inductively coupled plasma mass spectrometry [ICPMS] and atomic absorption (AA)). Then, otolith composition is contrasted among contingents to evaluate which elements, other than Sr, are useful indicators of freshwater, estuarine and coastal habitation.

METHODS

Collections

Striped bass were collected during August-December 1994 using a beach-haul seine (100-m long X 3-m deep); some fish from coastal sites were also provided by recreational anglers. Adult females (n = 7) and males (n = 14) were sampled from the Troy Dam region (river km 246), Catskill (river km 162), Poughkeepsie (river km 125), Haverstraw Bay (river km 60), Tappan Zee (river km 40), New York Harbor, and Long Island Sound (Table 1; Figure 2). According to laboratory protocols for ageing fish, sagittal otoliths were removed, cleaned with 10% bleach solution, dried and stored (Secor et al. 1995b). Right otoliths were later prepared for WDS analysis (see Secor and Piccoli 1996 for methods), left otoliths were retained for ICPMS analysis.

WDS Classification of Contingents

Otolith microprobe of Sr and Ca was performed by X-ray WDS using a JEOL JXA-840A microprobe (Center for Microanalysis, University of Maryland, College Park, Maryland). Measurement of Sr and Ca was calibrated using Strontianite (SrCO_3) and calcite (CaCO_3) standards (Secor 1992). The detection limit was 300 ppm for Sr. A series of point measurements of Sr and Ca were taken across similar transects of the otolith microstructure. Each point was approximately $5\mu\text{m}$ in diameter and approximately $1\mu\text{m}$ deep. Intervals between points ranged between 13 and $25\mu\text{m}$. To minimize effects of instrumental variability between runs, Sr was expressed as a ratio (Sr:Ca). Point measurements were related to the annulus or interannular material they sampled. Chronologies based upon Sr:Ca were compiled for each specimen using a logistic relationship between salinity and otolith Sr:Ca based upon laboratory and field experiments (Secor et al. 1995a).

$$\text{Salinity habitation (ppt)} = 40.3 (1 + 56.3e^{-1523(\text{Sr/Ca})})^{-1} \quad (1)$$

This model was used to convert Sr:Ca ratios to salinity habitation. Salinity chronologies were then constructed for each individual (Figure 1). Contingents of striped bass were initially classified on the basis of visual inspection of salinity chronologies (Zlokovitz and Secor, in press). Mean lifetime salinity (the mean of all salinity records from transect points for an individual) corroborated these classifications (Table 1).

Lifetime Sr means computed from WDS measures were compared with Sr levels obtained from whole otolith analysis of Sr by ICPMS. Because lifetime Sr means integrate over entire life histories, it was assumed they represent a similar temporal scale to that represented by the bulk composition of the whole otolith obtained by ICPMS analysis.

ICPMS Analysis of Whole Otoliths

In the laboratory, left otoliths were carefully decontaminated. All reagents were ultrapure grade and all implements and containers were cleaned with dilute nitric acid and rinsed with 18 megohm doubly deionized water (DDIH_2O). Otoliths were soaked in 1% nitric acid for 5 minutes to remove surface contamination and then flooded for 5 min with 3 liters DDIH_2O to rinse the acid. Around 4% of otolith mass was lost due to the decontamination procedure. Comparison of two sets of paired otoliths, one rinsed in acid, the other untreated, showed less than 5% difference in concentrations of Na, Mg, Ca, Co, Ni, Sr, and Ba. Otoliths were then dried under a laminar flow hood and stored in plastic vials.

In preparation for instrumental analysis, each otolith was weighed to the nearest 0.01 mg and placed in a plastic tube. Otoliths were digested in concentrated nitric acid and brought to volume with DDIH_2O . Internal standards were used to compensate for variations in instrumental sensitivity. Trace element (Mg, Mn, Co, Ni, Cu, Zn, Rb, Ag, Cd and Ba) levels were quantified using the method of standard additions. Ca and Sr concentrations were quantified using external calibration standards after further dilution of the digests. Na and K were measured using atomic absorption spectrophotometry (AAS). Procedural blanks and a standard reference material (SRM) were concurrently digested and analyzed following the same procedures. The reference material was SRM

915a (Calcium Carbonate Clinical Standard), obtained through the National Institute of Standards and Technology. This SRM is not certified for verification of trace metal concentrations, so only non-certified values are available for a few elements. Relevant values are (on a dry weight basis): Ca = 40.0%; Mg = 1.0 µg/g; Cu = 0.95 µg/g; and Mn = 0.6 µg/g. Our results ranged from 38.5 to 40.5% for Ca, 0.9 to 1.1 µg/g for Mg, 0.9 to 1.0 µg/g for Cu, and 0.60 to 0.65 µg/g for Mn. Samples were randomized during instrumental analysis to minimize possible bias due to a sequence effect (Campana et al. 1995). For each run blanks were run first, last and interspersed throughout the instrument run.

Element concentrations were used in a discriminant analysis employing the WDS designated groupings as a factor. Because otolith mass did not vary significantly among migratory groups ($p = 0.23$), no corrections were made for mass effects on elemental concentrations. Discriminant analysis tested for multivariate differences among the three migratory classifications. Relative importance of individual elements in discriminating among groups was assessed by using F statistics estimated by the discriminant analysis procedure. Cross-correlation of individual elements was evaluated using Tolerance (Wilkinson 1996), which is inversely related to the correlation of the individual element to others in the multivariate analysis. Thus, a high tolerance indicates independence in the contribution of that element to the model. Principal component analysis was used to evaluate affinity among elements. Individual element concentrations were contrasted among migratory groups using analysis of variance (ANOVA). To meet assumptions of normality, natural logarithms of elemental concentrations were used in univariate contrasts.

RESULTS

WDS measures of lifetime Sr were positively and strongly correlated between ICPMS and WDS methods: $\text{WDS Sr:Ca} = -0.150 + 1.051 \text{ ICPMS Sr:Ca}$ ($r^2 = 0.95$; $n = 21$) (Figure 3). The slope of WDS on ICPMS Sr (1.05) was not significantly different than the expected slope of unity ($p > 0.05$).

Discriminant analysis using Na, Mg, K, Ca, Mn, Co, Ni, Cu, Zn, Rb, Ag, Cd, and Ba showed clear separation of resident, mesohaline, and coastal contingents (Figure 4). Canonical variate one (x-axis) differentiated the resident group from the others; canonical variate 2 (y axis) discriminated between mesohaline and coastal groups. Largest contributing elements to the multivariate analysis (F statistic; Table 2) were Na, Ca, Co, Zn and Rb; Cu and Ba contributed little to the model. Tolerance statistics indicated that Cu, Ag, and Ba showed the highest degree of independence in their individual contributions to the multivariate analysis. Group membership was correctly assigned (100%) by a classification matrix. A jack knifed classification matrix (group assignment excluded case being classified) performed poorly due to low sample sizes: 89%, 38%, and 0% of the resident, mesohaline, and coastal groups were classified correctly. Of the seven mesohaline group fish, three were misclassified as coastal fish and one was misclassified as a resident fish. All coastal group fish were misclassified as mesohaline members by the jackknife procedure.

Variance in principal component scores was mostly explained by the first two principal components (PCA 1 = 32%; PCA 2 = 20%). The plot of score weights by element (Figure 5) shows that PCA1 is positively weighted by physiologically important elements (Ca, K, Na, Mn, Mg), while

PCA2 is positively weighted by elements associated with the physical environment (Co, Cu, Ba, Ni, Ag, Rb).

Univariate analyses showed that significant differences occurred among migratory groups for Co, Sr, Rb, and Ba. Co, Rb, and Ba were significantly (Tukey Multiple Comparison; $p < 0.05$) higher in resident fish while (not included in the multivariate analyses) was significantly lower in resident fish (Figure 6).

DISCUSSION

Contingent Identification

Elemental fingerprints determined by bulk chemical analysis correctly identified contingents of striped bass previously classified through otolith microprobe analysis of Sr:Ca by WDS. Discriminant function analysis showed no misclassifications among contingents. A more robust approach, the jack knifed classification procedure, resulted in a higher degree of misclassification of mesohaline and coastal classes. Therefore, definitive discriminant functions for the three contingents should be based upon a larger sample containing more individuals classified by WDS as mesohaline and coastal.

Corroboration between the WDS and ICPMS methods clearly demonstrates that groups of Hudson River striped bass have unique lifetime patterns of habitat use. Each method has attendant strengths and limitations. WDS analysis has superb spatial resolution with which to estimate temporal patterns of habitat use. However, the number of elements which can be measured is limited to those which occur at concentrations greater than ca. 100 ppm (Campana et al. 1997). Alternatively, ICPMS analysis of otoliths has much greater sensitivity (< 1 ppm); however, solution-based ICPMS analysis of the bulk composition of whole otoliths cannot resolve seasonal or ontogenetic patterns of habitat use and migration.

Consistency between ICPMS and WDS measurements was directly compared for Sr. A higher level of agreement (95%) occurred for paired measures of Sr than reported in the inter-laboratory comparison exercise conducted by Campana et al. (1997). In that study, concentrations of Sr in Atlantic croaker (*Micropogonias undulatus*) otoliths showed much lower correlation (8 - 28%) between WDS and ICPMS methods. In a separate test, a measurement of enhanced concentrations of Sr in artificial beads composed of homogenized Atlantic croaker otoliths showed good agreement between Sr determinations by ICPMS and WDS otolith microprobe methods. Because WDS is sensitive to spatial heterogeneity of Sr in the specimen while ICPMS bulk analysis is not, comparisons between the methods is expected to show reduced correspondence due to nonhomogeneous distribution of Sr in the otolith's microstructure.

The rationale and empirical evidence for the use of Sr as a salinity tracer is well documented (Casselman et al. 1982; Radtke et al. 1988; Kalish 1990; Secor 1992; Rieman et al. 1994; Fowler et al. 1995; Limburg 1995; Mugiya and Tanaka 1995; Secor et al. 1995; Farrell and Campana 1996; Thorrold et al. 1997). Associations between other elements in otoliths and ambient exposure remain poorly investigated. Fowler et al. (1995) found that Atlantic croaker reared at 26 psu salinity

contained significantly less otolith Rb than those reared at 35 psu; Ca and Sr were slightly lower at 26 psu than at 35 psu. Based upon laser-ablation ICPMS analyses of juvenile Atlantic croaker otoliths; Thorrold et al. (1997) speculated that patterns in Mg, Ca, and Ba were related to ingress. They concluded that Mg and Ca were positively, and Ba negatively, related to salinity.

In our study, Co, Rb, and Ba concentrations were higher in otoliths of resident specimens, while Sr levels were lower in resident fish. For the other 10 elements, no statistically significant differences were found between groups. One might expect to find positive correlations between salinity and Na, Mg, K, Ca, Rb, and Sr, since concentrations of those elements are much higher in seawater than freshwater, and, indeed, Sr levels were higher in specimens which utilized mesohaline and coastal (high salinity) habitats than in resident (low salinity) fish. However, Na, Mg, K, and Ca levels showed no differences between groups, while Rb levels were higher in resident fish. In addition, since the Hudson-Raritan estuary is known to be contaminated with a wide range of chemical compounds, it would not be surprising to observe higher concentrations of commonly encountered contaminant metals, such as Cr, Cu, Ni, and Zn, in finfish tissues; including otoliths, from inner estuary sites. However, no such elevated levels were observed. Similarly, simple correlations were not observed between habitat metal concentrations and otolith metal concentrations in a recent study of the elemental composition of otoliths of Atlantic croaker collected along an estuarine pollution gradient (Hanson and Zdanowicz, in press). It is well known that metals are metabolically regulated by fish, and that exposure to elevated levels of contaminants does not insure elevated levels of metals in finfish tissues (Hanson 1997). Thus, the relationship between otolith composition and environmental conditions is complex and appears to be governed by numerous biological and geochemical factors. Much experimental work is needed to elucidate the pathways of incorporation of elements into otoliths and the effects of habitat conditions on those pathways.

Contingents

Identification of contingents by the ICPMS bulk chemistry method indicated that lifetime migratory patterns exist for Hudson River striped bass. Although the sample size was low and individual migratory behaviors within groups were divergent, we were still capable of resolving discrete migratory modes.

Resident behaviors shown by otolith microprobe analysis were most often attributed to males (Table 1; Secor and Piccoli 1996). Sex-specific patterns of resident behavior are common to salmonids, where resident males typically show patterns of more rapid development and maturation than migratory males (Jonsson and Jonsson 1993). Striped bass male residents do not show the dwarf phenotype common to salmonids (Zlokovitz and Secor in press). In addition, several resident females have been observed. Divergent patterns of resident and migratory behaviors are documented for other anadromous and coastal fishes (Jonsson and Jonsson 1993). For Atlantic cod (*Gadus morhua*), Wroblewski et al. (1994) observed a resident "contingent" which overwintered in Trinity Bay (Newfoundland) while most other cod of the associated northern stock migrated offshore. Moreover, Beamish and McFarlane (1988) observed resident versus migratory behaviors for groups of adult sablefish (*Anoplopoma fimbria*) off the west coast of Canada.

Results for striped bass and documentation of migratory modes for other anadromous and coastal fishes (Beamish and McFarlane 1988; Jonnson and Jonnson 1993; Wroblewski et al. 1994) lead us to speculate that alternate migratory behaviors may be accomplished by contingents with proclivities towards discrete migratory modes. The idea that populations are structured as spatial contingents is compatible with recent considerations on metapopulation stock structures (Pulliam 1988; Frank and Leggett 1996). However, rather than specifying that multiple reproductively isolated populations or sub-populations contribute to the dynamics of an overall metapopulation, we believe that at the population level, resiliency to exploitation and environmental change may be conferred by the maintenance of divergent life cycle pathways (Kaitala et al. 1993).

Future studies employing otolith elemental analyses will provide a unique opportunity to examine variability in migratory behaviors. Previous studies on resident and migrant salmonids have relied on phenotypic differences between these forms (Jonnson and Jonnson 1993). For other families, phenotypic (or genotypic) differences between resident and more migratory contingents may be subtle or absent. Otolith elemental fingerprinting should permit identification of resident and migratory contingents of striped bass and other fishes so that alternate life cycle pathways within populations can be more rigorously investigated.

ACKNOWLEDGMENTS

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REFERENCES

- Beamish, R. J. and G. A. McFarlane. 1988. Resident and dispersal behavior of adult sable fish (*Anoplopoma fimbria*) in the slope waters off Canada's west coast. *Can. J. Fish. Aquat. Sci.* 45:152-164.
- Campana, S. E., S. R. Thorrold, S. R., Jones, C. M., Gunther, D. Tubrett, M. Longerich, H. Jackson, S. Halden, J. M. Kalish, P. M. Piccoli, P. DePontual, H. Troadec, H. Panfili, D. H. Secor, K. P. Severin, S. H. Sie, R. Thresher, W. J. Teesdale and J. L. Cambell. 1997. Comparison of accuracy, precision and sensitivity in elemental assays of fish otoliths using the electron microprobe, PIXE and laser ablation ICPMS. *Can. J. Fish. Aquat. Sci.* 54:2068-2079.
- Campana, S. E., J. A. Gagne and J. W. McLaren. 1995. Elemental fingerprinting of fish otoliths using IDICPMS. *Mar. Ecol. Prog. Ser.* 122:115-120.
- Campana, S. E., A. J. Fowler and C.M. Jones. 1994. Otolith elemental fingerprinting for stock identification of Atlantic cod (*Gadus morhua*) using laser ablation ICPMS. *Can. J. Fish Aquat. Sci.* 51:1942-1950.
- Casselman, J. M. 1982. Chemical analyses of the optically different zones in eel otoliths. *Proc 1980 N Amer Eel Conf* : 74-82.

- Clark, J. 1968. Seasonal movements of striped bass contingents of Long Island Sound and the New York Bight. *Trans. Am. Fish. Soc.* 97:320-343.
- Dorazio, R. M., K. A. Hattala, C. B. McCollough and J. E. Skjeveland. 1994. Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. *Trans. Am. Fish. Soc.* 123:950-963.
- Edmonds, J. S., M. J. Moran, N. Caputi and M. Morita. 1989. Trace element analysis of fish sagittae as an aid to stock identification: Pink snapper (*Chrysophrys auratus*) in Western Australian waters. *Can. J. Fish. Aquat. Sci.* 46:50-54.
- Edmonds, J. S., N. Caputi and M. Morita. 1991. Stock discrimination by trace element analysis of otoliths of orange roughy (*Hoplostethus atlanticus*), a deep-water marine teleost. *Aust. J. Mar. Freshw. Res.* 42:383-389.
- Edmonds, J. S., R. C. J. Lenanton, N. Caputi and M. Morita. 1992. Trace elements in the otoliths of yellow-eye mullet (*Aldrichetta forsteri*) as an aid to stock identification. *Fish. Res.* 13:39-51.
- Farrell, J. and S. E. Campana. 1996. Regulation of calcium and strontium deposition on the otoliths of juvenile tilapia, *Oreochromis niloticus*. *Comp. Biochem. Physiol.* 115A:103-109.
- Fogarty, M. J. 1998. Implications of migration and larval interchange in American lobster (*Homarus americanus*) stocks: Spatial structure and resilience. pp. 273-283, In: Jamieson, G. S. and A. Campbell (eds.), *Proc. N. Pacific Symp. Invert. Stock. Assess. Manage. Can. Spec. Publ. Fish. Aquat. Sci.* 125.
- Fowler, A. J., S. E. Campana, C. M. Jones and S. R. Thorrold. 1995. Experimental assessment of the effects of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS. *Can. J. Fish. Aquat. Sci.* 52:1431-1441.
- Frank, K. T. 1992. Demographic consequences of age-specific dispersal in marine fish populations. *Can. J. Fish. Aquat. Sci.* 49:2222-2231.
- Frank, K. T. and W. C. Leggett. 1994. Fisheries ecology in the context of ecological and evolutionary theory. *Ann. Rev. Ecol. Syst.* 25:401-422.
- Hanson, P. J. 1997. Response of hepatic trace element concentrations in fish exposed to elemental and organic contaminants. *Estuaries* 20:659-676.
- Hanson, P. J. and V. S. Zdanowicz. In press. Element composition of otoliths from Atlantic croaker (*Micropogonias undulatus*) along an estuarine pollution gradient. *J. Fish Biol.*
- Jonnson, B. and N. Jonnson. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Rev. Fish. Biol. Fish.* 3:348-365.

- Kalish, J. M. 1990. Use of otolith microchemistry to distinguish progeny of sympatric anadromous and non-anadromous salmonids. *Fish. Bull.* 88:657-666.
- Kaitala, A., V. Kaitala and P. Lundberg. 1993. A theory of partial migration. *Am. Nat.* 142:59-81.
- Leggett, W. C. 1977. The ecology of fish migrations. *Ann. Rev. Ecol. Syst.* 8:285-308.
- Leggett, W. C. 1984. Fish migrations in coastal and estuarine environments: a call for new approaches to the study of an old problem. pp. 159-178, *In*: McCleave, J. D., G. P. Arnold, J. J. Dodson and W. H. Neill (eds.), *Mechanisms of Migration in Fishes*. Plenum Press, NY, NY.
- Limburg, K. E. 1995. Otolith strontium traces environmental history of subyearling American shad *Alosa sapidissima*. *Mar. Ecol. Prog. Ser.* 119:25-35.
- Limburg, K. E. and R. E. Schmidt. 1990. Patterns of fish spawning in Hudson River tributaries: Response to an urban gradient. *Ecology* 71:1238-1245.
- McLaren, J. B., J. C. Cooper, T. B. Hoff and V. Lander. 1981. Movements of Hudson River striped bass. *Trans. Am. Fish. Soc.* 110:158-167.
- Mugiya, Y. and S. Tanaka. 1995. Incorporation of water-borne strontium into otoliths and its turnover in the goldfish *Carassius auratus*: Effects of strontium concentrations, temperature, and 17 B-Estradiol. *Fish. Sci.* 61:29-35.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *Am. Nat.* 132:652-661.
- Rose, G. A. and W. C. Leggett. 1991. Effects of biomass-range interactions on catchability of migratory dispersal fish by mobile fisheries: An example of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 48:843-848.
- Radtke, R., R. A. Kinzie and S. D. Folsom. 1988. Age at recruitment of Hawaiian freshwater gobies. *Environ. Biol. Fishes* 23:205-213.
- Rieman, B. E., D. L. Myers and R. L. Nielson. 1994. Use of otolith microchemistry to discriminant *Oncorhynchus nerka* or resident and anadromous origin. *Can. J. Fish. Aquat. Sci.* 51:68-77.
- Secor, D. H. 1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis*. *Fish. Bull.* 90:798-806.
- Secor, D. H. 1997. Is otolith strontium a useful scalar of life cycles in estuarine fishes? *Int. Counc. Explor. Sea, CM 1997/S:03*, 10 pp.
- Secor, D. H. and V. S. Zdanowicz. 1988. Otolith microconstituent analysis of juvenile bluefin tuna (*Thunnus thynnus*) from the Mediterranean Sea and Pacific Ocean. *Fish. Res.* 36:251-256.

Secor, D. H., A. Henderson-Arzapalo and P. M. Piccoli. 1995a. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? *J. Exp. Mar. Biol. Ecol.* 192:15-33.

Secor, D. H., T. M. Trice and H. T. Hornick. 1995b. Validation of otolith-based ageing and a comparison of otolith and scale-based ageing in mark-recaptured Chesapeake Bay striped bass, *Morone saxatilis*. *Fish. Bull.* 93:186-190.

Secor, D. H. and P. M. Piccoli. 1996. Age- and sex-dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. *Estuaries* 19:778-793.

Thorrold, S. R., C. M. Jones and S. E. Campana. 1997. Response of otolith microchemistry to environmental variations experienced by larval and juvenile Atlantic croaker (*Micropogonias undulatus*). *Limn. Oceanogr.* 42:102-111.

Thresher, R. E., C. H. Proctor, J. S. Gunn and I. R. Horrowfield. 1994. An evaluation of electron-probe microanalysis of otoliths for stock delineation and identification of nursery areas in a southern temperate groundfish, *Nemadactylus macropterus* (Cheilodactylidae). *Fish. Bull.* 92:817-840.

Waldman, J. R., D. J. Dunning, Q. E. Ross and M. T. Mattson. 1990. Range dynamics of Hudson River striped bass along the Atlantic Coast. *Trans. Am. Fish. Soc.* 119:910-919.

Wilkinson, L. 1996. SYSTAT 6.0 for Windows: Statistics, SPSS Inc., Chicago, IL, 751 pp.

Wirgin, I., L. Maceda, J. R. Waldman and R. N. Crittenden. 1993. Use of mitochondrial DNA polymorphisms to estimate the relative contributions of the Hudson River and Chesapeake Bay striped bass to the mixed fishery of the Atlantic coast. *Trans. Am. Fish. Soc.* 122:669-684.

Woblewski, J. S., W. L. Bailey and K. A. Howse. 1994. Observations of adult Atlantic cod (*Gadus morhua*) overwintering in nearshore waters of Trinity Bay, Newfoundland. *Can. J. Fish. Aquat. Sci.* 51:142-150.

Zlokovitz, E. R. and D. H. Secor. In press. Effect of habitat use on PCB body burden in fall-collected, Hudson River striped bass (*Morone saxatilis*). *Can. J. Fish. Aquat. Sci.*

Table 1. Hudson River striped bass sample used for ICPMS analysis. Classification of contingents was based upon inspection of individual salinity chronologies and life-salinity statistics. Sr:Ca ratio and lifetime salinity (\pm s.e) determined as mean of all Sr:Ca or salinity (estimated from equation 1) records for an individual. Means are presented for each classification. For Sr:Ca ratio and lifetime salinity standard errors are reported for group means. TL = total length (mm); F = female; M = male.

Classification	TL (mm)	Sex	Age (yr)	Capture Month (1994)	Capture Site	Sr:Ca Ratio (103)	Lifetime Salinity (ppt)
Coastal	686	F	10	Oct	NY Harbor	3.17	27.84 \pm 9.23
	696	F	8	Oct	NY Harbor	3.00	25.31 \pm 5.76
	840	F	13	Oct	NY Harbor	3.00	25.56 \pm 4.59
	945	F	14	Oct	Long Island	3.03	25.87 \pm 8.28
Mean	792					3.05	26.15 \pm 6.96
Mesohaline	559	F	4	Oct	NY Harbor	2.63	19.88 \pm 4.96
	1007	F	15	Oct	NY Harbor	2.64	20.09 \pm 5.94
	521	M	5	April	Haverstraw Bay	2.32	15.38 \pm 4.10
	574	M	4	April	Poughkeepsie	2.47	17.47 \pm 5.56
	611	M	5	Dec	Haverstraw Bay	2.22	13.89 \pm 7.11
	690	M	6	April	Tappan Zee	2.65	20.15 \pm 6.59
	718	M	7	Oct	NY Harbor	2.39	16.32 \pm 7.39
	772	M	14	Nov	Haverstraw Bay	2.19	13.38 \pm 7.7
Mean	681					2.44	17.07 \pm 6.17
Resident	950	F	14	Aug	Troy	0.99	3.00 \pm 1.85
	502	M	6	Oct	Troy	0.6	1.70 \pm 1.05
	528	M	8	Aug	Troy	0.49	1.46 \pm 1.31
	534	M	10	Nov	Haverstraw Bay	0.82	2.36 \pm 3.77
	538	M	8	June	Troy	0.45	1.37 \pm 0.56
	541	M	8	Oct	Troy	0.66	1.87 \pm 1.56
	570	M	6	Aug	Troy	0.59	1.67 \pm 0.93
	600	M	16	May	Catskill	0.88	2.57 \pm 2.65
	685	M	13	Oct	Troy	0.71	2.00 \pm 0.69
Mean	605					0.69	2.00 \pm 1.60

Table 2. Summary of discriminant analysis of the otolith elemental concentrations among the three striped bass contingents from the Hudson River Estuary. F-statistic indicates the relative importance of the element in model; Tolerance measures the correlation of elements in the model (range:0.0 = high correlation, 1.0 = low correlation).

Element	F-statistic	Tolerance
Na	1.72	0.14
Mg	0.44	0.23
K	0.61	0.28
Ca	1.51	0.07
Mn	0.42	0.20
Co	1.27	0.27
Ni	0.37	0.27
Cu	0.04	0.41
Zn	1.89	0.12
Rb	5.05	0.19
Ag	0.76	0.44
Cd	0.23	0.16
Ba	0.01	0.47

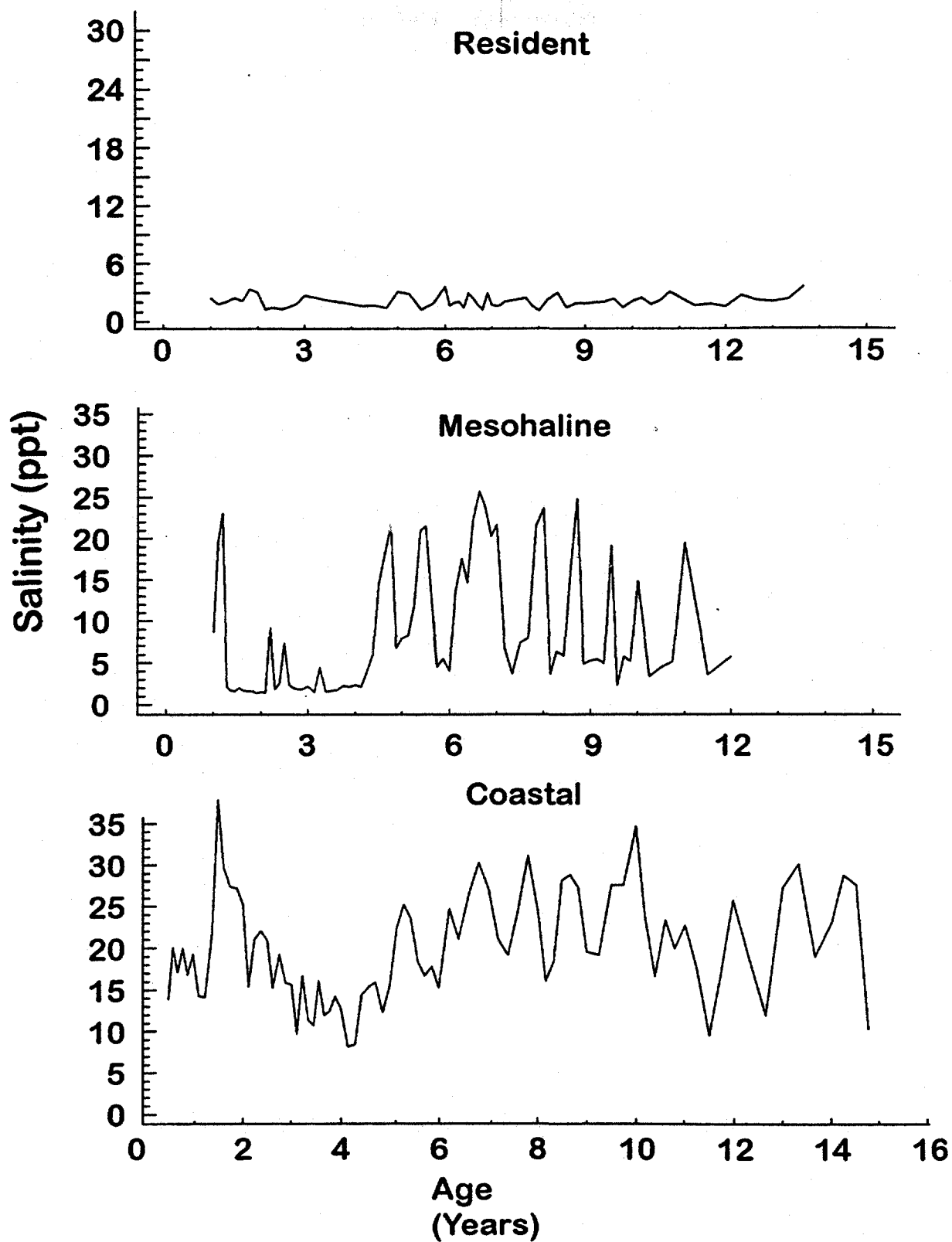


Figure 1. Representative lifetime salinity chronologies for Hudson River striped bass. Chronologies were constructed from WDS otolith microanalysis of Sr:Ca (Secor et al. 1995). Migratory classifications (resident, mesohaline or coastal) are indicated.

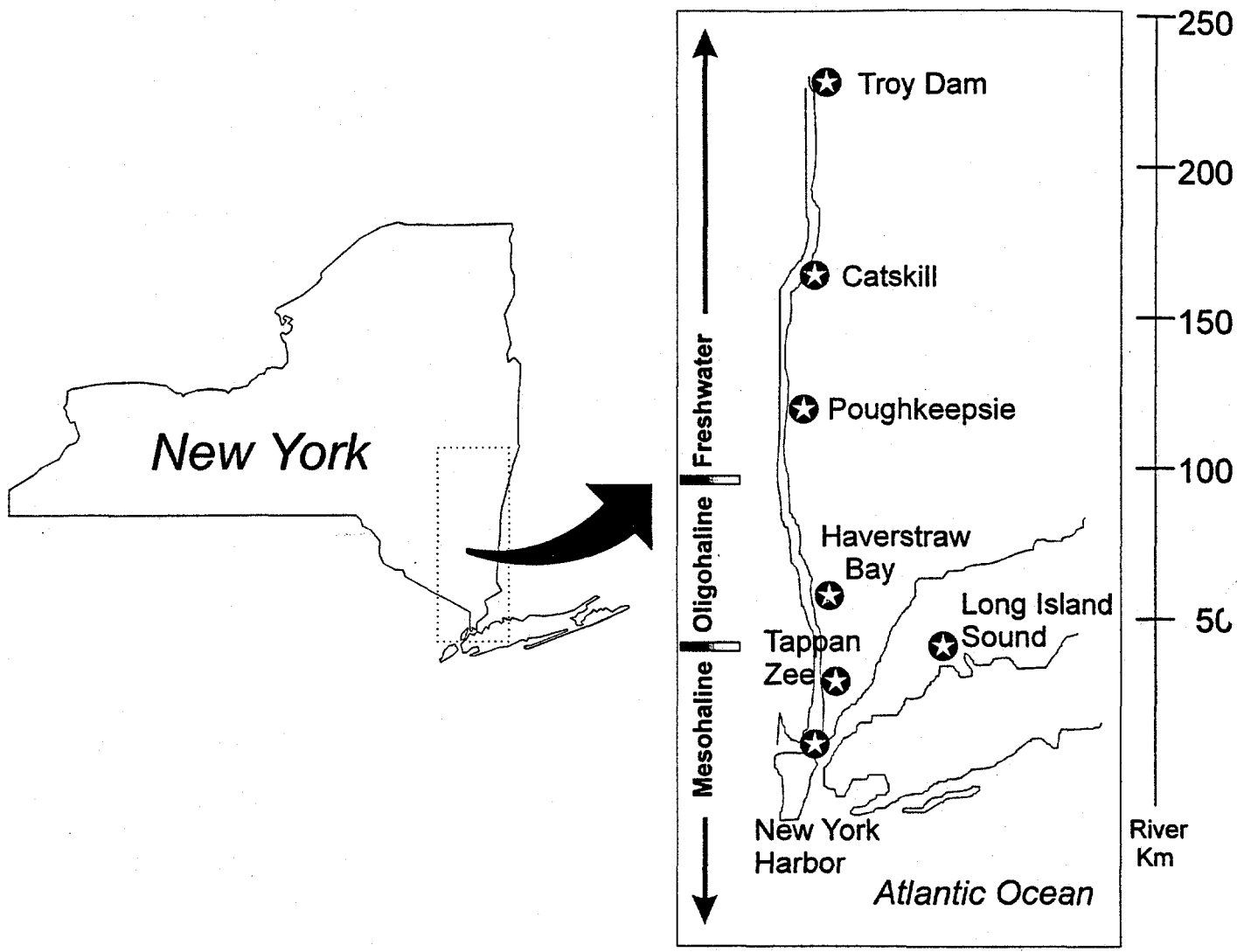


Figure 2. Map of Hudson River Estuary showing locations of striped bass sampling stations.

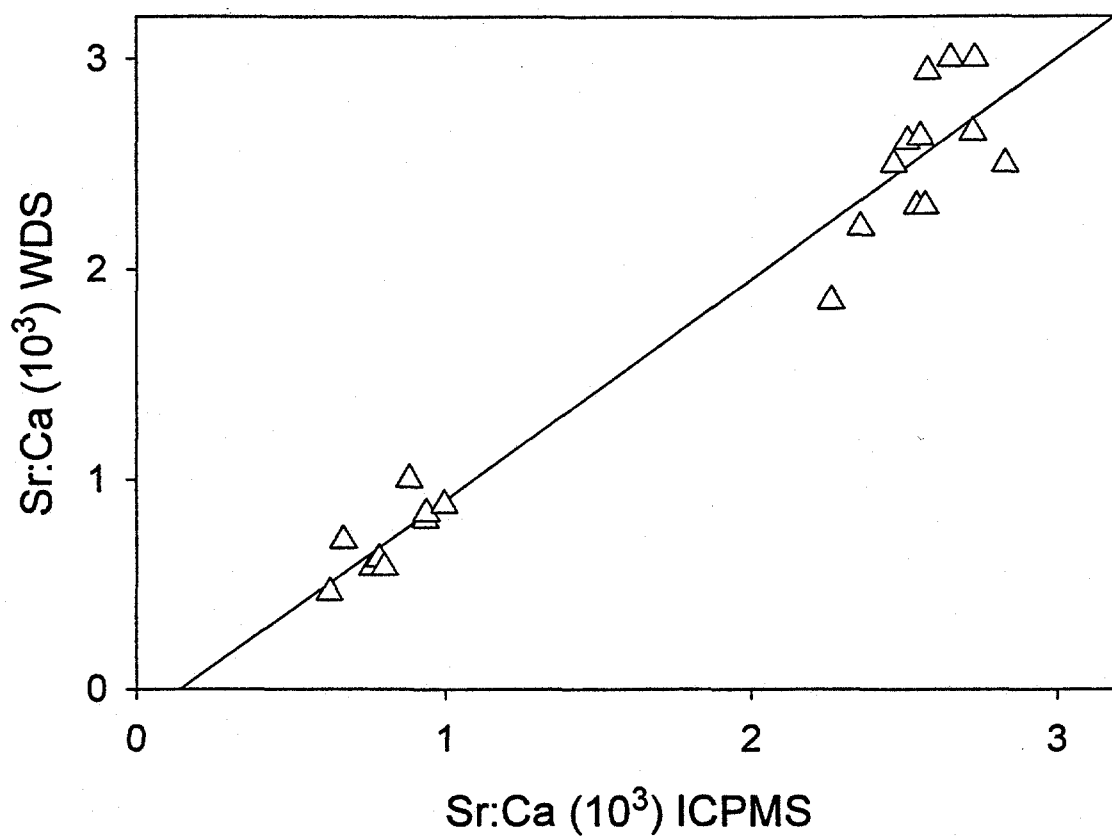


Figure 3. Linear relationship between WDS Sr:Ca ratio (life history transect) and ICPMS Sr:Ca ratio (bulk composition of whole otolith) of individual striped bass. Left and right sagittal otoliths from individual striped bass were used for ICPMS and WDS analyses, respectively.

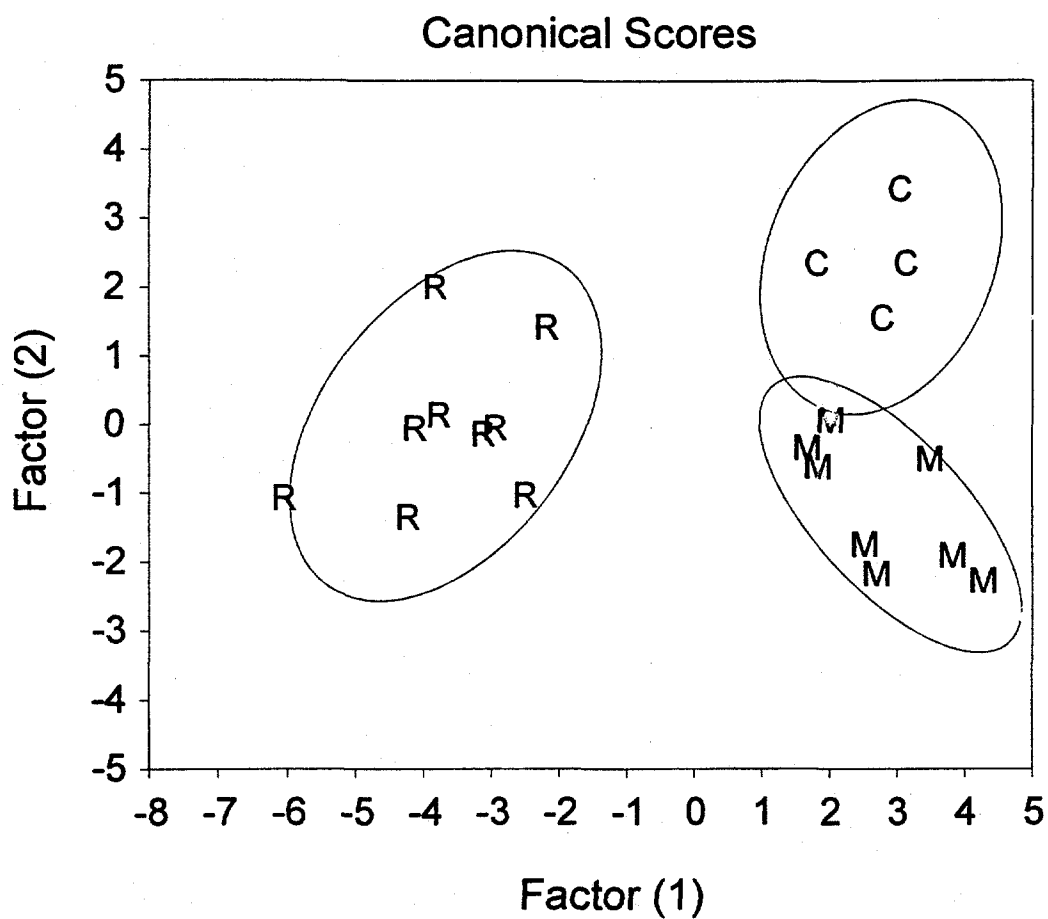


Figure 4. Canonical variable plot of striped bass migratory contingents, R = Resident, M = Mesohaline, C = Coastal from discriminant analysis. 95% confidence ellipses of each group are given.

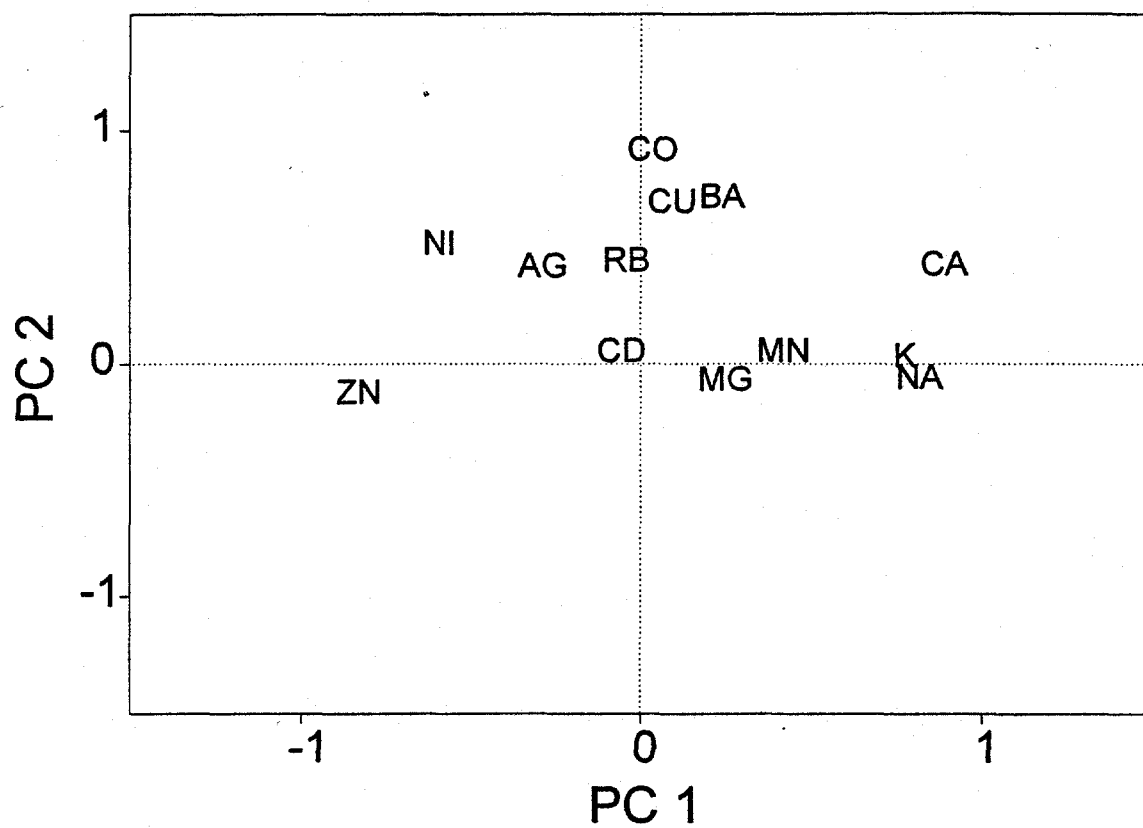


Figure 5. Principal component analysis showing the distribution of standardized variables (elements) along principal component axes 1 and 2. Total variance explained by first 2 components: PCA 1 = 32%, PCA 2 = 20%.

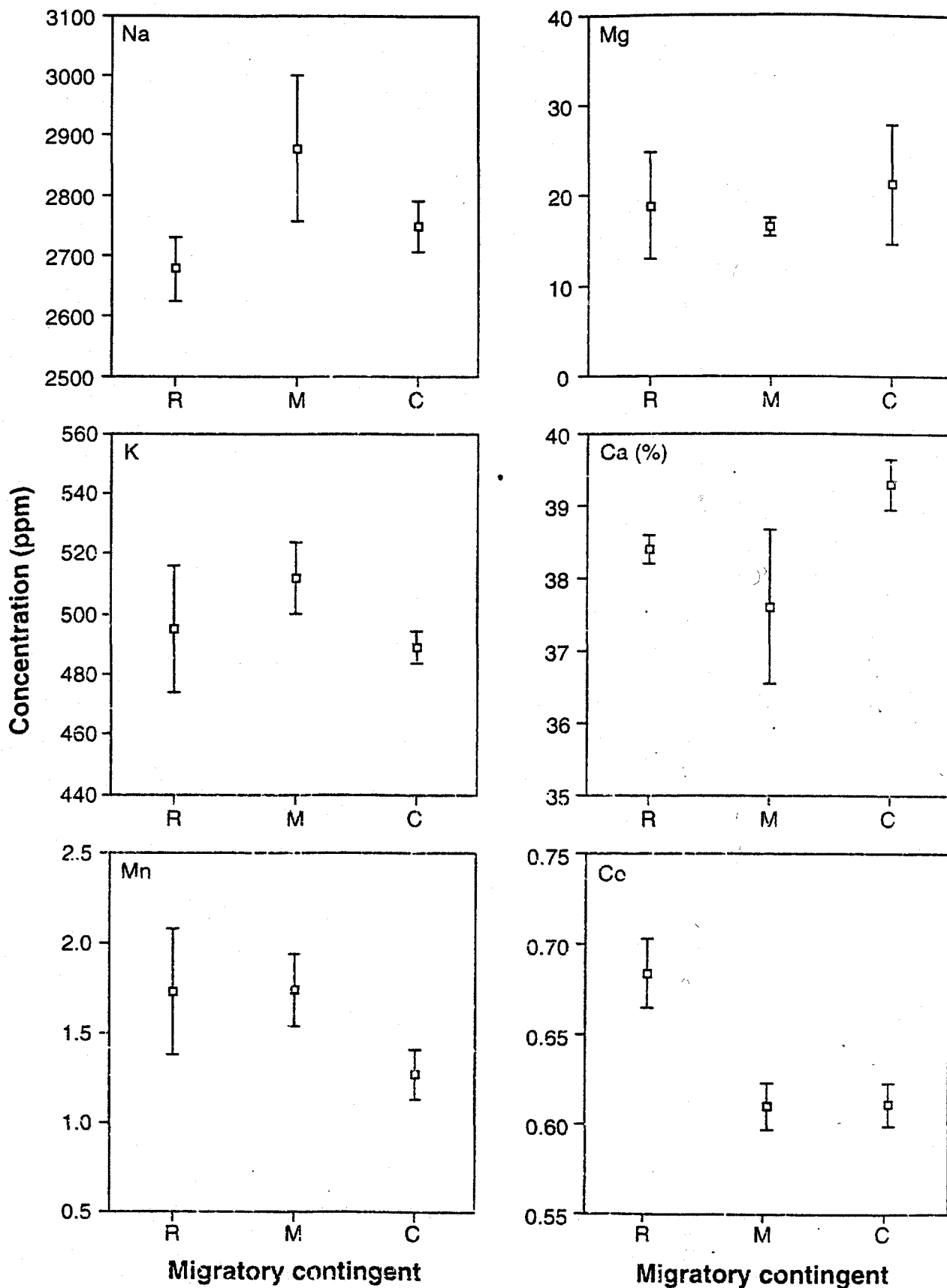
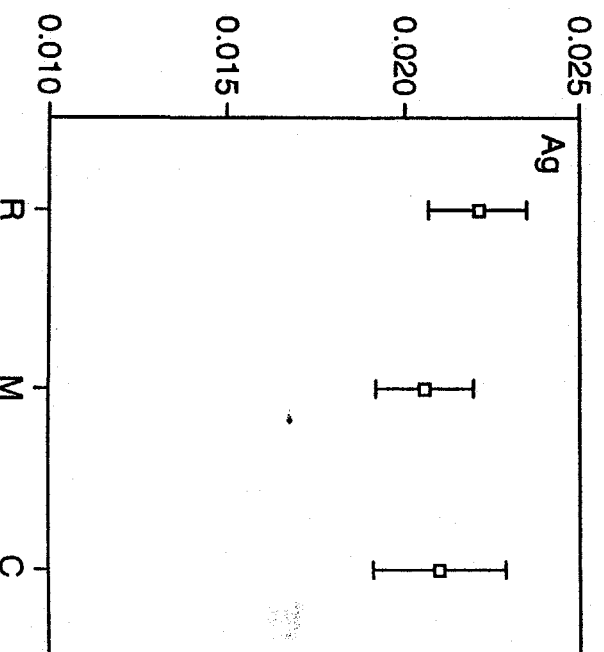
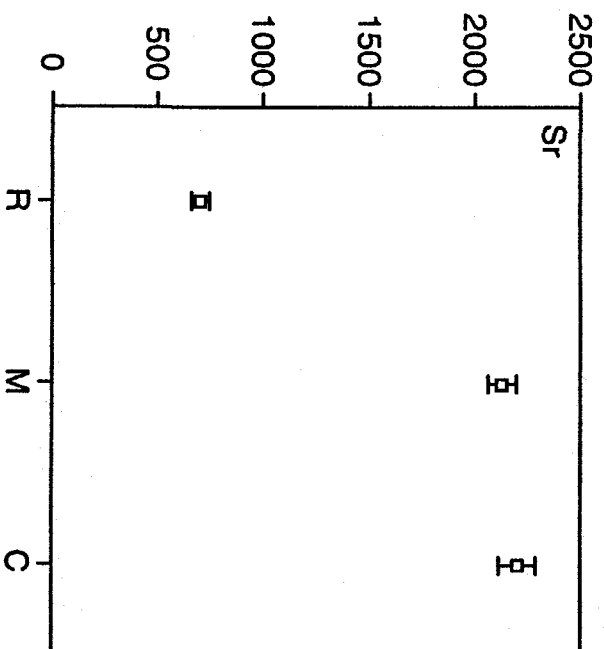
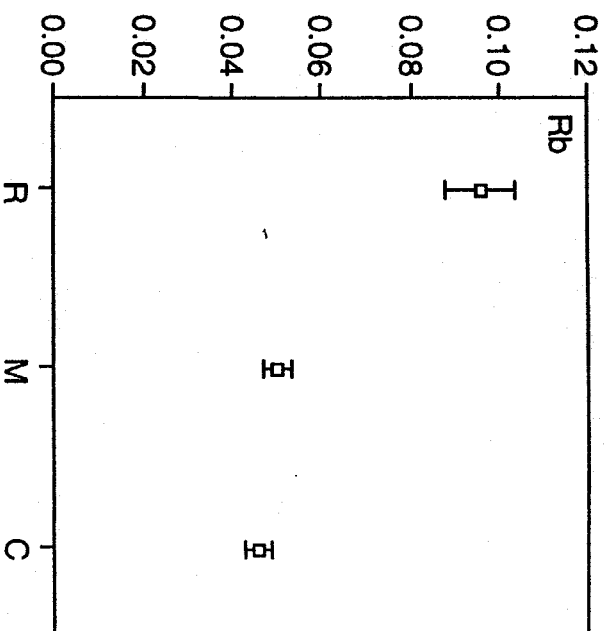
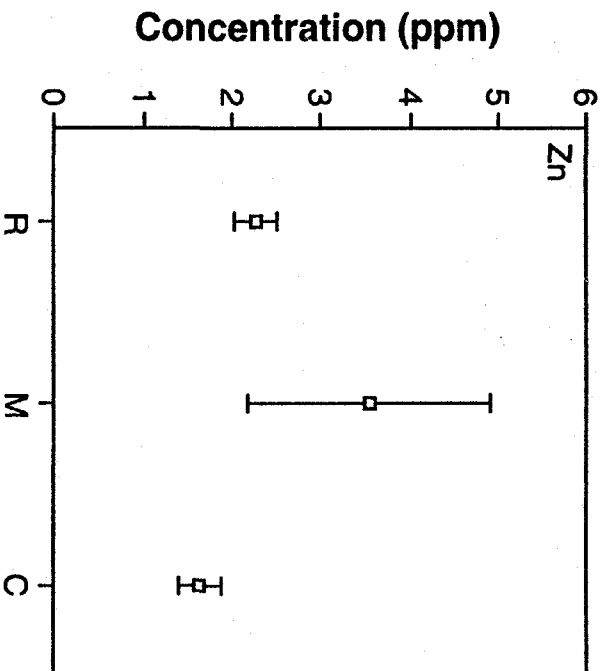
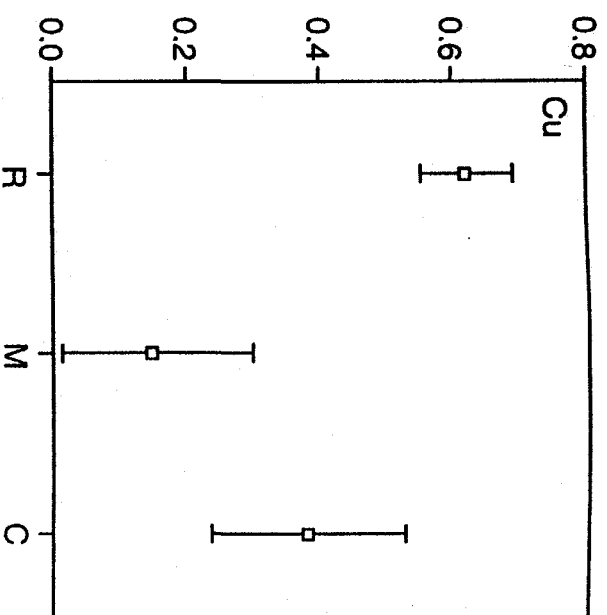
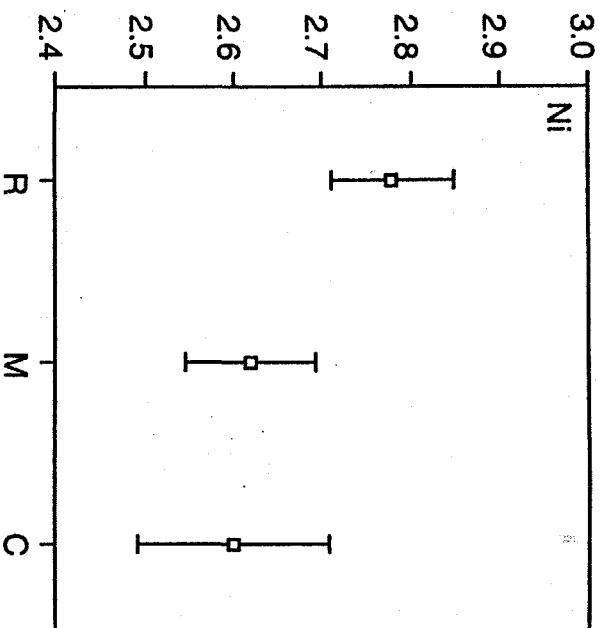


Figure 6. Element concentrations (μg/g dry otolith mass) for striped bass from the three contingents, R = Resident, M = Mesohaline, and C = Coastal. Interquartile range (25th and 75th percentile) is shown by extent of boxes, with normal and boldface horizontal lines within boxes representing median (50th percentile) and mean, respectively. Error bars denote range of 10th and 90th percentile.



Concentration (ppm)

Migratory contingent

Migratory contingent

Figure 6, page 2

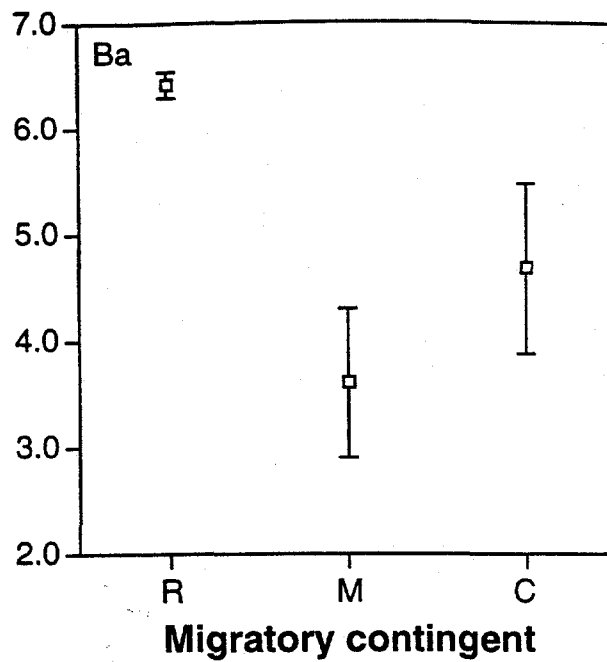
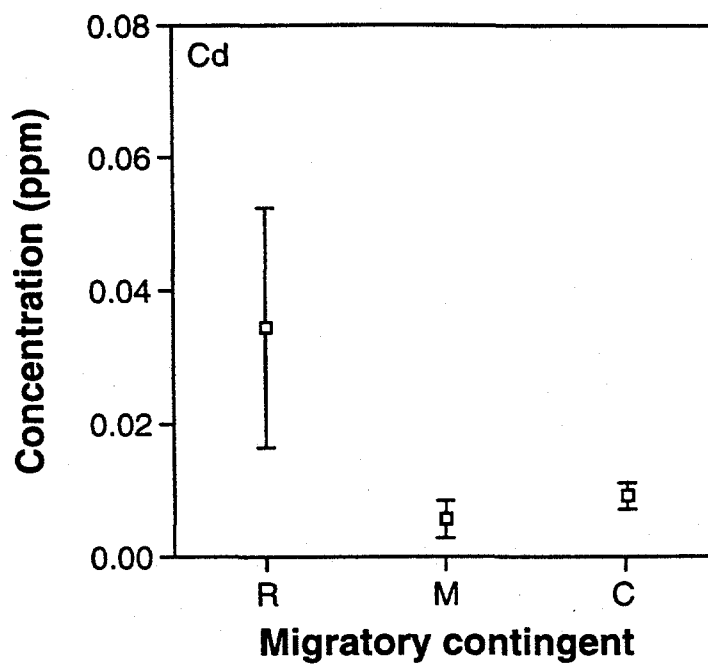


Figure 6, page 3

CHAPTER 4. Specifying Divergent Migration Patterns in the Concept of Stock: The Contingent Hypothesis

David H. Secor

ABSTRACT

The current concept of stock does not sufficiently accommodate the effects of migration behavior on population dynamics. New insight on the prevalence and ecological significance of divergent migrations within stocks has arisen through advancing technologies in tracking fishes. In particular, otolith elemental analysis may provide unique perspective on divergent migrations within stocks. Using otolith elemental fingerprints of Hudson River striped bass (*Morone saxatilis*), I evaluated Clark's (1968) contingent hypothesis of intrapopulation migratory groups. Similar to the results of Clark's earlier tagging study, I observed three spatially discrete cohorts of Hudson River striped bass. An intriguing question is, if such contingents exist, then how are they regulated? Using frameworks for understanding smoltification in salmonids and ontogenetic niche shifts, I hypothesize that early life decisions regarding energy allocation lead to later divergence in habitat shifts (migration). This mechanism results in the maintenance of "retentive" and "exploratory" behaviors and contributes to features of population regulation including persistence, range contraction and expansion, and colonization. Examples of divergent migration tactics exist for a diverse array of taxa. Because the current meaning of stock is synonymous with biological population, factors which affect accessibility to human impacts (i.e. contingent dynamics) remain unspecified. The stock concept should incorporate a hierarchy of biological levels which evaluate both lineage (subpopulation - population - metapopulation - subspecies - species) and accessibility (individual - brood - school/shoal - yearclass - contingent).

INTRODUCTION

The observation of racial differences within species, each race with divergent migration behaviors, may have originated in the early nineteenth century when a Korean naturalist, Yak-Jun Jung, observed that herring (*Clupea pallasii*) found in the Yellow Sea contained fewer vertebrae than those in the Japan/East Sea (Jung 1816). Initial recognition of migratory races in the west rests firmly with F. Heincke (Heincke 1898; Sinclair and Solemdal 1988), who observed that individuals collected from different spawning shoals of North Sea Atlantic herring (*Clupea harengus*) exhibited subtle but demonstrable morphometric differences. By sampling spawning shoals, Heincke recognized that common lineage preserved divergent migratory behaviors among races (populations).

Early emphasis on stocks focused on schools or shoals of fish. Indeed, acceptance of Hjort's year-class paradigm (Hjort and Lea 1914) was not immediately accepted due in part to its implication that population-wide phenomena (year-class dominance) would dominate processes which controlled

fish school abundance and membership. Hjort's most ardent critic, D'Arcy Thompson (1914) argued that Hjort and Lea's strong 1904 year-class of Atlantic herring was an artefact of combining individuals among schools. Hjort's theory of population regulation has played an important role in the conception of fish stock. If schools or shoals were commonly affected by pulsed recruitment events, then would it not be more beneficial for managers to consider aggregates based upon common lineage (i.e. common spawning) rather than those based upon common migration behaviors.

In this prospectus, I advance that a level of fish aggregation based upon divergent migration behaviors or habitat use, termed here as *contingents*, remains a useful unit for stock management and conservation. The term contingent has precedence, initially defined for groups of Hudson River striped bass *Morone saxatilis*, by Clark (1968): "*A contingent is . . . a group of fish . . . [which] once established, . . . appears to maintain its integrity by engaging in a distinct pattern of seasonal migration not shared by fish of other contingents.*" I argue that inclusion of contingent behavior in the concept of stock may be a useful means in evaluating the effects of divergent migrations on stock dynamics.

Increased perspective on the prevalence and ecological significance of divergent migrations has arisen through advancing technologies. Of these, otolith elemental analysis has seen especially rapid development and application over the past five years. In this paper, I preview insights which might be on the horizon by addressing how divergent migrations can be incorporated into the stock concept. What does the emerging method of otolith composition tell us about fish stocks? Based upon otolith elemental fingerprinting, I evaluate Clark's contingent hypothesis for Hudson River striped bass and summarize examples of contingent behaviors for other taxa. An intriguing question is that if contingents exist, how are they regulated? Using frameworks for understanding ontogenetic niche shifts and density dependent habitat selection, I hypothesize that early life decisions regarding energy allocation (Metcalf and Thorpe 1992; Thorpe et al. 1992) vary within populations and lead to life-time divergence in habitat selection (Werner and Gilliam 1984; Thorpe 1989). This mechanism results in the maintenance of "retentive" and "exploratory" behaviors and contributes to features of population regulation including persistence, range contraction and expansion, and colonization. Concluding the review, I suggest that the current concept of stock has become synonymous with biological population. In the future a more useful approach to stock definition may incorporate biological inputs relevant to both lineage and accessibility.

Individual Migratory Behaviors and Closed Populations

Migrations are defined by both local and directed movements related to environmental gradients (MacCall 1990). Over shorter time intervals, migrations are manifest as shoals of fish utilizing common habitat. For this reason, I do not view schools (migratory aggregations) and shoals (habitat-associated aggregations) as necessarily distinct entities as has been stated by Pitcher and Parish (1993). I use the terms "habitat use" or "migration," and "shoal" or "school" interchangeably, dependent upon the degree of resident or dispersive behavior by a fish aggregation.

Current concepts on the role of migration in population dynamics are well exemplified by the two recent publications, *Marine Populations* (Sinclair 1988) and *Dynamic Geography of Marine Populations* (MacCall 1990). In the Member-Vagrant theory, Sinclair (1988) expands on the

fish school abundance and membership. Hjort's most ardent critic, D'Arcy Thompson (1914) argued that Hjort and Lea's strong 1904 year-class of Atlantic herring was an artefact of combining individuals among schools. Hjort's theory of population regulation has played an important role in the conception of fish stock. If schools or shoals were commonly affected by pulsed recruitment events, then would it not be more beneficial for managers to consider aggregates based upon common lineage (i.e. common spawning) rather than those based upon common migration behaviors.

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Harden-Jones migration triangle (Harden Jones 1968) which describes a closed circuit of migration: individuals always return whence they were spawned. Sinclair emphasized that life cycle closure ('membership') is an essential requirement for reproductive isolation in a diffusive environment. That larval or juvenile stage individuals might substantially deviate from the population's trajectory ('vagrancy') would mean they would be lost to the population; they could not re-enter the circuit.

MacCall's "Basin Model" emphasizes the energetic rather than reproductive consequences of variable habitat use. The theory builds on the Fretwell and Lucas ideal free distribution model, whereby dispersion operates to maximize individual fitness (a joint product of lifetime growth, survival, and reproduction probabilities). Individuals densely concentrated into a favorable habitat will share a low marginal fitness, and at some point will move to less crowded, albeit less energetically favorable habitats. Dispersion along habitat gradients cause equilibration of marginal fitness among all individuals, and in general, local abundances should be directly related to habitat values (MacCall 1990). The ability of fish to make choices among local habitats based upon energetic returns has been confirmed in laboratory and field experiments (Werner et al. 1983a, b).

The two view points on fish migration appear at odds with each: Sinclair's migration imperative versus MacCall's habitat choice. These ideas can be reconciled if we assume that ontogenetic migration behaviors subsume habitat choice. In this framework (Figure 1), a migration circuit defines necessary ontogenetic niche shifts: spawning to nursery habitat; nursery habitat to adult feeding/wintering grounds; and adult feeding/winter grounds to spawning habitat. The circuit follows a mean migratory trajectory. The trajectory itself is a path which expands and contracts according to the energetic demands of the population. The ideal free distribution theory would indicate that the mean trajectory should follow areas of highest fish density (most suitable habitat) and that individuals should diffuse in a density dependent manner from the mean trajectory to habitats less favorable. However, if an individual or shoal digresses too far, it will not be able to rejoin the migratory circuit.

In large part, this paper concerns how we come to think of the odd fish at the odd place and time. While current population-level models on migration do not necessarily exclude the possibility of such anomalous occurrences, they rarely seek to explain such behavior or understand its consequences. The consequences of intrapopulation divergence in migrations recently has been addressed for Atlantic cod (*Gadus morhua*) and American lobster (*Homarus americanus*) with models showing the response of resource species to exploitation due to density dependent migrations. Hutchings (1996) proposed that increased aggregation of cod at low densities due to density-dependent habitat selection resulted in increased catchability. Fogarty (1998) demonstrated that offshore lobster spawning may be conferring a high degree of reproductive subsidy to an inshore stock. These exercises provide insight on the Scotian Shelf cod collapse and the resiliency of the New England lobster fishery in novel frameworks which specify unique spatial dynamics within stocks.

Otolith Composition Analysis of Migratory Behaviors and Fish Stocks

Recent advances in otolith microconstituent analysis provide researchers with an empirical means of measuring fish migration and habitat use throughout ontogeny. Otoliths are calcium carbonate concretions in the vestibular organs of fishes which grow by accretion of daily and annual

increments. Otoliths are acellular, >90% inorganic, and less influenced by physiology than other fish hard parts (Mugiya and Watabe 1977). Probe-based measures (e.g. electron, proton, or laser probes) of elements from sectioned otoliths yield both spatial and temporal information on fish dispersal and movement. First, spatial patterns of habitat use are inferred for important environmental scalars (typically salinity or temperature) through measurement of otolith microconstituents (Radtke et al. 1988; 1990; Kalish 1990). Secondly, precise measures are made within and among daily or seasonal (annular) increments to construct a chronology of habitat occurrences which is related to fish age, ontogenetic stage, or season (Townsend et al. 1989; 1992; Secor 1992; Secor and Piccoli 1996). Bulk chemistry methods which fuse the entire otolith, while nonspecific to ontogenetic migrations and habitat use, can none-the-less provide information on lifetime differences in habitat use. So-called otolith "elemental fingerprints" (Campana et al. 1994; see glossary in Secor and Chesney 1997) have been used to identify natal source and evaluate migration patterns for several coastal and oceanic species (Edmonds et al. 1989; 1991; 1992; Campana et al. 1994; 1995).

Although otolith composition studies have been applied to stock discrimination and migration questions for nearly two decades (Casseiman 1982), the approach remains novel and the accuracy with which otoliths record environmental histories is poorly known (Secor et al. 1995). Otoliths are relatively pure products and we should expect differential resolution and biases with among elements (Gunn et al. 1992; Milton and Chenery 1998; Proctor and Thresher 1998). Three assumptions are important: 1) Otolith microconstituents are accurately measured (Gunn et al. 1992; Proctor and Thresher 1998); 2) Otolith microconstituents record chemical or physical attributes of the environment (Townsend et al. 1989; 1992; 1995, Fowler et al. 1995a,b; and Secor et al. 1995); and 3) Temporal changes in environmental conditions are reflected in changes of microconstituents in the otolith's microstructure (Secor et al. 1995; 1998).

The literature contains ample applications of otolith Sr as a tracer for both salinity and temperature. Because salinity is of marine origin and dilutes conservatively with freshwater input (Ingram and Sloan 1992), investigators have assumed that otolith Sr and salinity should be positively related. Dissociation constants for Sr in aragonite (the typical crystalline structure of sagittal otoliths) are temperature dependent, with higher rates of incorporation at low temperatures. Therefore, otolith Sr is expected to be related inversely to temperature. Townsend et al. (1992) proposed a physiologically mediated rate of Sr incorporation, where decreased discrimination against Sr incorporation occurred at low temperatures. Relatively few investigations have tested the reliability with which otolith Sr records temporal and habitat changes in these environmental scalars (Secor and Rooker, in review).

Results of many otolith composition studies to date are encouraging, the field is rapidly expanding in application, and it is timely to consider how the otolith composition approach will address stock issues in the future. Despite the paucity of studies which validate otolith composition approaches, results from numerous studies show definite applications - e.g. differences in elemental fingerprints among fish aggregations, or trends in elemental concentrations across otolith microstructure which are consistent with migration along an environmental scalar. Assuming otolith composition serves as a natural tag, how might precise ontogenetic information on migration and habitat use be used to evaluate stock structure and interactions among stocks?

Revisiting Clark's Contingents

Striped Bass Migrations in the New York Bight

Striped bass is a long-lived (>30 years; Secor et al. 1995b), euryhaline species which supports important commercial fisheries in North America. Several populations exhibit anadromous behaviors and contribute to a mixed coastal stock (Merriman 1941; Raney et al. 1954). Members of this stock are principally drawn from Hudson River and Chesapeake Bay populations (Merriman 1941; Wirgin et al. 1993).

The issue of the natality of the coastal striped bass stock has been addressed by several generations of scientists. Merriman (1941), Raney et al. (1954), and Goodyear (1985) observed that coastal catches of the northern coastal stock (from New Jersey to Massachusetts) were positively correlated with strong recruitments in the Chesapeake Bay. Stock identification methods, applied to populations of striped bass include morphometrics, meristics, protein assays, and biochemical markers (Table 1). These studies have taken samples from New York Bight and, not surprisingly, have assigned high membership by the Hudson River population.

NY Harbor region, Long Island Sound, and the Great South Bay (Figure 2) serve as important habitat for striped bass and have supported important commercial and recreational fisheries throughout this century. This Harbor-LI "System" comprises numerous small and large embayments which provide nursery habitat (McKown and Penski 1994). Seasonally, this system harbors abundant tomcod *Microgadus tomcod*, menhaden *Brevoortia tyrannus* and anchovy *Anchoa mitchilli*, principal prey items for larger striped bass (>1 year old; Gardiner and Hoff 1982). NY Harbor and lower Hudson River Estuary are important overwintering grounds for striped bass (Raney 1954; McLaren et al. 1981; Waldman 1986) and Long Island Sound and coastal regions south of Long Island serve as important migration corridors (Merriman 1941).

Migration behaviors of striped bass within the Harbor-LI System have been investigated using mark-recapture investigations on nearly a continuous basis since 1936 (Table 2). Most tagging studies, including Clark's (1968) have sought to describe seasonal migrations. Typically, studies have tagged small males and immature females (<70 cm TL) over several sites and seasons. Most fish were tagged in Long Island Sound or the New York City Harbor region, and most recaptures occurred from these locations. In some studies, significant recaptures (>10%) occurred in the Chesapeake Bay (Merriman 1941; Clark 1968; Austin and Custer 1977; Boreman and Lewis 1987) supporting Merriman's contention that strong year-classes in the Bay can influence harvests in LI Sound. Several studies noted schooling and shoal behaviors associated with specific seasons in the Harbor-LY System. Raney et al. (1954) for instance, described an overwintering group in the Hudson River estuary as the "Hudson Race." Despite uncertainty in the assumption of stock origin, the young ages of tagged fish and low rate of recaptures outside of the New York Bight suggested that most tagged fish probably originated from the Hudson River.

Clark's Contingent Hypothesis

Clark (1968) showed a strong "clustering effect" of fish in the Harbor - LI System (Boreman and Lewis 1987), where tagging location influenced recapture location. Striped bass tagged in New York Harbor exhibited little dispersal in all seasons, tending to be recaptured in New York Harbor or western Long Island Sound (Figure 2A). Fish tagged in eastern Long Island Sound were more dispersive but tended to be recaptured throughout Long Island Sound and off of Cape Cod (Figure 2B). Clark concluded that these two groups, plus an additional migratory Atlantic group were "contingents," each contingent defined by a unique seasonal migration:

"Variations in migration patterns, shown by differences of seasonal distribution of tag recaptures, suggest that different contingents of striped bass occupied the area of our study during the course of each year. We have attempted to identify these and to describe their migratory characteristics. We do not argue that these contingents are genetically distinct, but that they are separate components of the Atlantic population.¹ They may have formed simply by the accident of being brought together in one nursery area as juveniles. However, a contingent may be formed; once established it appears to maintain its integrity by engaging in a distinct pattern of seasonal migrations not shared by fish of other contingents." (Emphasis added).

Clark's contingent hypothesis was not accepted due in part to limitations in the design of his mark-recapture study (Waldman 1986; Waldman et al. 1990). Because most fish tagged in Clark's study were young males and immature females (<60 cm TL), migration patterns which vary with size and sex could be incorrectly interpreted as contingent behaviors (Chapotan and Sykes 1961; Kohlenstein 1981; Waldman et al. 1990; Dorazio et al. 1994; Secor and Piccoli 1996).

Support of the Contingent Hypothesis through Otolith Composition Studies

We evaluated Clark's contingent hypothesis using otolith Sr microprobe analysis (Secor and Piccoli 1996; Zlokovitz and Secor, in press) and measurement of elemental fingerprints by ICPMS bulk chemistry (Secor et al., in press). Microprobe analysis of Sr across annuli was used to reconstruct ontogenetic patterns of habitat use along a salinity gradient (Secor 1992). Otolith microprobe analysis revealed three migration groups of Hudson River striped bass (Figure 3): 1) a resident group, inhabiting freshwater and oligohaline regions of the Hudson River; 2) a lower estuary "mesohaline" group, inhabiting mesohaline and polyhaline regions (Harbor-LI System); and 3) a coastal migratory group. These patterns reflected three discrete behaviors which persisted throughout the lives of juveniles and adults. Thus, contingent integrity can persist throughout the life of an individual in accordance with Clark's original hypothesis.

While otolith strontium (salinity) served as a useful scalar to describe variable migrations, we investigated other elements which might record more subtle environmental gradients (Secor et al., in press) and thereby more precisely define contingents. For otolith pairs, we measured elemental

¹Clark used 'population' in a different context than the accepted definition of common lineage as "all striped bass that occupy a given area within the range of the species". The three contingents: Hudson River Estuary, Western Long Island, and Hudson-Atlantic contingents were all believed by Clark to have originated in the Hudson River.

fingerprints (left otolith) for individuals which had been classified previously as resident, mesohaline, or coastal based upon otolith Sr microprobe analysis (right otolith). Elemental fingerprints based upon Na, Mg, K, Ca, Mn, Co, Ni, Cu, Zn, Rb, Ag, Cd, and Ba showed clear separation of resident, mesohaline, and coastal contingents (Figure 4). Corroboration among the methods provided a clear demonstration that groups of Hudson River striped bass have unique life-time patterns of habitat use.

How discrete are migration patterns (contingents) within the Hudson River population? This question will require a large and unbiased sample. To initially engage the question, I assembled samples taken from several studies (Secor 1995; Secor and Piccoli 1996; Zlokovitz and Secor, in press) and calculated "life-time salinity habitation" for each fish as the mean of all salinity records. This measure integrates all habitats which contributed to growth over a life-time (seasons and years). Frequency histograms of life-time habitation for Hudson River and Chesapeake Bay striped bass showed wide estuarine distribution (Figure 5), consistent with striped bass's euryhaline nature. Polymodal structure also was observed, particularly for males, which are more likely to exhibit resident behaviors than females. The polymodal structure of life-time habitation supports Clark's early observation of discrete migratory groups at an intrapopulation level.

Based upon recent otolith composition studies, Clark's work cannot be discounted. Indeed, if we examine recapture data (Figure 2), particularly for fish tagged in NY Harbor, explanations other than unique migration behaviors, are difficult to erect. The distribution of recaptures for the Harbor contingent was very unique, particularly when we compare it to an adjacent tagging region, western Long Island Sound. Recaptures indicated a very limited region of dispersal, a retentive behavior of habitat use. The Long Island Sound contingent in contrast showed more dispersive behaviors. Disproportionate recapture effort across the Harbor-LI system can be largely discounted since relative recapture rates varied according to initial tagging locations. Clark did not tag fish in the Hudson River proper, so a freshwater-resident contingent was undescribed prior to our studies. Combining our results with Clark's, there is evidence for contingents centered in the HR, NY Harbor, W. LI, and coastal Atlantic.

The striped bass case study exemplifies how otolith microconstituent analysis can identify new levels of stock structure. Microanalysis of Sr described seasonal and ontogenetic migrations and elemental fingerprint analysis showed the overall result of divergent migrations, a single phenotypic expression of environmental history (i.e., a natural tag). Other studies using otolith composition to describe anomalous migrations and stock structure are included in the next section.

Maintenance of Contingents

The striped bass contingent example leads us to the question: What causes divergent migrations to persist over generations? Contingents may be sub-populations, each sub-population persisting due to a degree of reproductive isolation (Kaitala et al. 1993). Alternatively, maintenance of divergent migratory forms could represent phenotypic plasticity--a result of an evolutionary stable polymorphism for alternate life cycles (e.g. Gross 1985). Heterogenous distribution of habitat could also result in divergent migrations within populations (MacCall 1990). Research on facultative or partial migrations is insufficient to support the primacy of any one of these mechanisms (Jonsson and Jonsson 1993). In this section, I review possible mechanisms of contingent maintenance and

regulation in case studies on Arctic char, Lake Biwa ayu, zander and bream, and bluefin tuna. My goal is to show that anomalous migrations occur for a diversity of taxa and systems. Thorpe's "developmental programme" (Thorpe 1987) is advanced as a mechanism which could regulate migration tactics over a range of taxa.

Genetics vs. Environment: The Char Problem

The "char problem" (Nordeng 1983) epitomizes the conundrum of co-existing life-styles or forms within the same population: Do such polymorphisms occur as discrete genetic entities or can they arise through varying phenotypic expression of the same underlying genetic architecture? Arctic char *Salvelinus alpinus* show discontinuous polymorphisms within populations involving growth rate, size at maturity, maximum size, spawning coloration, shape, and feeding behaviors. Many of these variations are related to two principal migration tactics: anadromy and residency. Residents often exhibit a dwarf phenotype, mature early, and tend to be males. A larger resident form also exists: these exhibit distinct feeding behaviors and spawning coloration. Anadromous forms, seasonally exploit more productive coastal habitats in summer, and tend to be large females. In autumn, both assortive (sexual selection based upon size of mate) and non-assortive mating has been reported for chars (Jonsson and Hindar 1982; Nordeng 1983; Jonsson 1985; Maekawa et al. 1994). Overwinter residency in rivers and streams is undertaken by all forms.

Evidence supports a positive relationship between juvenile (parr) growth rate and anadromous behaviors later in life (Svenning et al. 1992; Krisoffersen et al. 1994; Strand and Heggberget 1994). Early growth variations may reflect variations in habitat. Individuals or populations which utilize littoral rather than profundal lake habitats tend to become anadromous (Hindar and Jonsson 1982; Sandlung et al. 1987; Krisoffersen et al. 1994; Rikardsen et al. 1997). Similarly, populations in systems which have little or no littoral habitats tend to be entirely resident (Kristoffersen et al. 1994). In some instances, migration tactics are reversible; resident forms become anadromous later in life (Nordeng 1983; Jonsson and Jonsson 1993), and in rare instances migratory forms can become resident for several years (Hammar et al. 1989; Näslund 1990). Recently, otolith microprobe analysis of strontium has revealed patterns consistent with previous tagging studies including: 1) a positive relation between early growth and anadromy; and 2) anadromous behaviors comprised of short-term seasonal coastal migrations (Radtke et al. 1996; Babaluk et al. 1997). Occasional "lapses" in coastal migrations have been recorded, where an anadromous individual remained resident for 1-2 years (Radtke et al. 1996).

Nordeng (1983) demonstrated through crossing experiments that resident and migratory forms arise from the same gene pool. A degree of "totipotence" to produce all forms was observed within and across all breeding types (resident dwarf, resident large, or anadromous). Transplantations to new watersheds, comprised exclusively of either resident or migratory form resulted in offspring of both forms (Jonsson and Jonsson 1993). Nevertheless, offspring varied in the frequency of life history traits according to mating pairs, indicating polygenic inheritance of life history morphs (Nordeng 1983). Subsequent research corroborate that morphs vary within populations dependent upon the interaction between environment and genotype (Jonsson et al. 1988; Svedäng 1990; Kristoffersen et al. 1994; Jones et al. 1997).

Sympatric migratory and resident forms are well known for other Salmonidae (e.g. *Salmo salar*, *S. trutta*, *Oncorhynchus kisutch*, *O. mykiss*, *O. masou*, *O. nerka*). Genetic and behavioral evidence is equivocal on the existence of migratory sub-populations in these salmon species (Ferguson and Mason 1981; Jonsson 1985; Jonsson and Jonsson 1993; Birt et al. 1991). For example in Atlantic salmon, Verspoor and Cole (1989) showed evidence for separation between anadromous and resident gene pools. In addition, the resident sub-population showed lower heterozygosity, consistent with expectations for reduced gene flow. However, the resident migration tactic was shown to sometimes arise from the "anadromous" genotype. For some populations, assortive mating or temporal and spatial segregation in spawning grounds suggested reproductive isolation (Ferguson and Mason 1981; Child 1984 Verspoor and Cole 1989; Birt et al. 1991), but in other instances, clear examples were given for mating among migratory forms (Gross 1985; Hutchings and Myers 1985; Jonsson 1985). Growth rate is also not consistently related to the probability of early smoltification and anadromy. For coho salmon and Atlantic salmon, the fastest growing parr become precocial male residents (Myers et al. 1986; Gross 1991), but in masu salmon and brown trout and a separate study on Atlantic salmon, rapid early growth was observed to be related to anadromy (Jonsson 1985; Hirata et al. 1988; Økland et al. 1993). Thorpe (1989) and Jonsson and Jonsson (1993) have argued that rapid early growth or development enable either an anadromous behavior or early maturation, but not both. Thorpe (1987) further suggested that only intermediate early growth rates would result in early anadromy (Figure 6).

The char problem also occurs for marine spawners such as Atlantic cod *Gadus morhua*, which supports fisheries on both resident (e.g. "fjord cod," Harden Jones 1968) and migratory stocks. Migratory behaviors of cod have been recently studied with biotelemetry, verifying retentive behaviors of some individuals to inshore regions of Canada (Wroblewski et al. 1995). Two biochemical studies have led to opposed conclusions on the degree of genotypic difference between inshore and offshore Canadian contingents (Carr et al. 1995; Ruzzante et al. 1996). Research on fjord cod in Norway suggested that early life history differences may generate inshore and offshore forms of cod (Loeken et al. 1994). Interestingly, Campana et al. (1995), using ICPMS otolith composition analysis of Scotian Shelf cod observed greater stock structure than evinced by biochemical methods. It is conceivable that otolith composition, as a phenotypic expression of habitat use, detected divergent migratory patterns by Atlantic cod which were unrelated to lineage.

The char problem remains unresolved in the degree of environmental vs. genetic influence on ontogenetic and seasonal migrations. The literature supports the hypothesis that variation in early growth (and presumably, heterogenous distribution of habitat) causes divergent migration tactics in Arctic char. For Atlantic cod and other taxa, variation in expression of other critical phenotypic traits (e.g. antifreeze levels in blood; Ruzzante et al. 1996) may be associated with divergent migrations. Because individual populations vary in the proportion of migratory and resident behaviors (Kristoffersen et al. 1994), evidence suggests that migration tactics occur according to population-specific reaction norms. Jonsson and Jonsson (1993) argued that if genotypes solely governed expression of migration tactics, then normalizing selection should eventually eliminate one of the tactics. In the next section, I take up the issue of evolutionary stable strategies for migration.

Evolutionary Stable Strategies: Lake Biwa Ayu

Tsukamoto et al. (1987) described a remarkable system in which migratory and resident forms occurred as alternating generations. Ayu (pronounced "eye-you"), *Plecoglossus altivelis* is a small semelparous salmonid occurring throughout Japan. Adults spawn in down-river reaches, larvae and small juveniles utilize estuarine and coastal nursery habitats, and juveniles >60 mm TL migrate to upstream feeding grounds. A land-locked population exists in Lake Biwa; spawning occurs in stream inlets to the lake - dwarf resident forms reside in the lake throughout their lives, and large resident forms undertake a seasonal migration into stream habitats. The spawning season is protracted occurring between late August until mid-October. Resident and migratory forms spawn during early and late periods of the season, respectively. Spawning reaches utilized by either form are also different. Remarkably, early spawned fish, the progeny of resident fish, attain a large size during their first growth season which enables upstream migration. The progeny of late spawning migratory fish do not grow as large during their first summer and remain resident. Thus, offspring of migratory spawners become resident and offspring of resident spawners become migratory (Figure 7).

What could be gained by such a life history strategy? Evolutionary stable strategies and game theory have been used as a means to evaluate the equivalency of alternate life cycles within populations. For coho salmon, Gross (1985; 1991) showed that equivalent fitness (lifetime reproductive values) resulted for dwarf-resident ("jack") and large-migratory ("hooknose") males through disruptive selection (Figure 8). Both large size in hooknose or small size in jacks were positively correlated with access to females and fertilization success, and intermediate sizes showed lower mating success. In this mating system, the fitness of either mode would vary in a frequency dependent manner, according to factors which affect the relative survivorship of the two forms (Gross 1991). Disruptive selection has also been modelled as a mechanism to explain the regulation of resident and migratory forms of Atlantic salmon (Hutchings and Myers 1994). In contrast, Thorpe's hypothesis that early growth rate results in several mating forms (Figure 6) could be envisioned as the result of stabilizing selection for divergent migrations. For instance, specific ranges of early growth rate give rise to divergent migration tactics, each tactic resulting in mating forms which have equivalent reproductive success dependent upon the environment and the relative frequency of the forms (Figure 6).

Divergent migrations could serve as a mechanism to increase diversity of spatial and temporal placement of eggs and larvae and thereby reduce the probability of failed recruitments (Lambert 1990; Secor and Houde 1995; Secor, in press). Diversity of spawning behavior among migratory forms could increase the probability that offspring encounter favorable conditions. Considering the Lake Biwa ayu example, a protracted spawning period would serve as a bet-hedging strategy insuring some recruitment occurs under ephemeral and rapidly changing conditions. Iguchi (1996) found that female size and time of spawning were important determinants to ayu offspring mortality. The benefits of a protracted spawning season could result in stabilizing selection for divergent migrations. Ultimately, stabilizing selection for a range of spawning behaviors could apply to a broader range of estuarine and marine taxa than selection mechanisms which apply to specialized mating systems.

Exploratory Platoons: Invasive Freshwater Fish and Tuna Fleets

The dispersive nature of fish leads us to the question, is the anomalous fish merely an individual at or beyond the boundary of a population's normal habitat distribution? Shouldn't we expect that dispersive behaviors are continuous according to density dependent habitat selection? The question boils down to the biological attributes of the anomalous fish. If every fish in a population is similar in growth rate and behavior, then the assumptions of density dependent habitat selection should apply (MacCall 1990). However, if dispersive fish are unique in biological attributes, then a discontinuous distribution of migration modes might be supported.

Unique attributes of have been observed for freshwater fishes which invade temperate estuaries. These species (families Cyprinidae, Percidae, Centrarcidae) typically have limited home ranges, cannot breed in brackish water, and seasonally invade estuaries for feeding as adults (Thiel et al. 1995; Hölker and Thiel 1998). Kafemann et al. (1998; in review) used otolith microprobe analysis of Sr of a stenohaline common bream *Abramis brama* and zander *Stizostedion lucioperca* collected from the Kiel Canal (Germany) to show that those individuals captured in brackish waters were more likely to have invaded brackish water in previous years than those captured in freshwater habitats. They proposed that this exploratory behavior, occurred for specific portions of the bream and zander populations, and represented an important life history tactic. The tactic would engender increased metabolic costs due to osmoregulation but such costs could be outweighed by increased production in brackish water habitats (Hölker and Thiel 1998).

Invasive individuals may represent exploratory, dispersive segments of their populations. For Japanese sea bass (*Lateolabrax japonicus*), otolith microprobe analysis has shown that some larvae will ingress from coastal spawning grounds into high amplitude tidal freshwater portions of the Ariake Sea estuary (Secor et al. 1998). However, another fraction of juvenile sea bass persist in brackish nursery habitats (Tanaka et al., in review). Invasive juveniles would weigh increased metabolic costs against improved feeding conditions which may exist in tidal freshwater habitats of Ariake Sea (Secor et al. 1998). Limburg's (1998) demonstration of anomalous migrations for *Alosa spp.*; again, based upon otolith microprobe analysis of Sr, showed that fast growing juveniles undertook exploratory behaviors since they were energetically capable of early egress into coastal environments from freshwater nurseries.

Tunas often show anomalous occurrences, where migrations are highly variable and apparently related to the effects of climate change, ocean circulation and related changes in prey distribution (Povlina 1996; Kimura et al. 1997). The high maintenance demands by tunas engender a higher dependence on exploratory behaviors to attain sufficient energy. Bluefin tuna *Thunnus thynnus* are peculiar among tunas in having a temperate distribution, and in the Atlantic Ocean bluefin tuna historically ranged between Brazil and Norway. Since the 1980s, bluefin have not been harvested at the "frontiers" of their range. Fonteneau and Soubrier (1996) speculated that previous frontier fisheries for bluefin tuna occurred on unique segments of the population. These exploratory contingents may have been lost because they were more vulnerable to the effects of exploitation.

Habitat suitability over the geographic range of a population can be evaluated as the expected rate of biomass elaboration (Heath 1996) and is inversely related to the quotient of mortality divided

by growth rate, μ/g (Werner and Gilliam 1984). Here, growth rate represents surplus production and includes elaboration of reproductive tissues. Thus, μ/g can be considered to vary inversely with fitness. Conceptually, changes in μ/g over an habitat gradient should result in directional dispersals. Based on local variations in habitat suitability, MacCall (1990) proposed the "Basin Model" which stipulated that reduced marginal fitness, the result of local density, should drive individuals into less suitable habitats with increased density (Figure 9). We could envision a system with discontinuous habitat suitability, where a potentially more productive habitat was isolated due to surrounding regions of very poor or risky environments. Were all individual fish randomly responding to habitat in a like manner, then there would be no opportunity to exploit this adjacent habitat.

The "activation" energy required for some individuals to disperse across unfavorable habitats could be achieved by exploratory platoons, groups of fish which have an increased proclivity for dispersal. Such fish could have unique bioenergetic attributes, habitat or growth histories (perhaps related to initial spawning date or other early life history attributes); or represent discrete genotypes, preserved through assortive or discrete spawning behaviors. Intuitively, exploratory platoons would comprise those individuals most likely to colonize new habitats and increase a population's gene flow.

Ontogenetic Niche Shifts, Habitat Selection, and Developmental Programs

Over a single generation, migration is expected to be influenced most by ontogeny, population density and the distribution of habitat values. Over many generations, variable migratory behavior should be a key tactic in population persistence. Using μ/g , as a common currency, I have attempted to combine the concepts of ontogenetic niche shift, density-dependent habitat selection, and evolutionary stable strategies. As stated earlier μ/g serves as a proxy for fitness, particularly when g is considered as surplus production. Other features which make μ/g an useful fitness measure in migration studies is that it can be quantified over a range of life history stages and environments, and that growth rate and mortality risk are physiological and environmental factors which fish can assess (e.g., Werner et al. 1983a,b).

We begin by considering the ontogenetic habitat shift for an intermediate migration tactic (Figure 10; late migration curves). During juvenile growth within a nursery, increasing juvenile size may result in reduced predation and/or increased growth and μ/g initially declines. However, at some point the juvenile's consumption demands begin to exceed the carrying capacity of the nursery habitat and μ/g begins to rise. At a critical size or stage, μ/g in the nursery habitat is equivalent to μ/g in an adjacent more productive habitat and the juvenile migrates to the new habitat, represented by another size-dependent μ/g response. Surplus production and reproductive values should be inversely related to the area under these curves. In this example, we can consider an Atlantic salmon which smolts relatively late in its life history. The "decision" to smolt and egress is related to appetite and behavior (Metcalf and Thorpe 1992; Thorpe et al. 1992) and its physiological perception of it's own growth rate (e.g. allocation to surplus production or energy stores) (Thorpe 1987; Økland et al. 1993).

Next, consider a fish that migrates much earlier in it's ontogeny (Figure 10, early migration curves). Following the decline in μ/g in the nursery, μ/g is more influenced by growth rate relative to the late migrant. Increased growth necessitates increased consumption so that the equivalent point between nursery and sub-adult feeding habitat is attained earlier in life. For the early smolting

Atlantic salmon, increased appetite drives an early exploratory behavior, engendering higher mortality risk. Increased consumption is expected to result in higher mortality because higher energy and time allocations will be devoted towards prey search and digestion rather than those activities or behaviors which mitigate against predation. However, increased mortality may be compensated by increased growth in the new habitat. Such a fish is not necessarily larger in size when it makes the habitat shift, it is only capable, through its particular energetic tactic, of exploiting a new habitat early in ontogeny. It is important to recognize that this relatively risky behavior can result in the same overall fitness (e.g., surplus production or lifetime reproductive value) as the late migration strategy.

Finally, the resident behavior can be viewed as one resulting from conservative bioenergetic allocation. The μ/g curve never rises substantially in the nursery habitat because the fish consumption demands do not over-take the carrying capacity of the environment. A continuous negative or static relationship exists between size and μ/g occurs so that there is no advantage to change habitats. Converse to the early migration fish tactic, I am assuming that low growth rates result in low mortality rates. The resident Atlantic salmon allocates more energy towards standard metabolism and potential active respiration rather than growth. Despite expected lower surplus production, resident fish could experience reproductive values similar to migrants since they need not encumber energetic and survival costs related to a migratory life style.

While divergent migrations can be explained by ontogenetic changes in μ/g , we still have not accounted for the persistence of multiple migratory modes within populations. Discreteness of these modes may represent an early life decision as conceived by Thorpe (1989). The idea of an early decision is consistent with divergence of rate dependent processes such as growth and mortality which can lead to large differences in attributes later in life (e.g. Houde 1987). In particular, Thorpe (1989) proposed that fish could monitor early growth rates and storage of surplus production, and based upon thresholds, regulate energetic allocations to enable later life history decisions (rates of smoltification or maturation). Factors which Thorpe and his colleagues have proposed which might influence early surplus production rates (and later migration tactics) include spawning time, embryo and larval development rates, early behaviors (dominance structure), and early photoperiod and temperatures (Thorpe 1987, 1989; Thorpe et al. 1992; Metcalfe and Thorpe 1992). In the present scenario (Figure 10), I propose that migration tactics depend upon the energetic trade-off between maintenance and growth, under the assumption that maintenance allocations are inversely related to mortality risk.

Decisions on migratory tactics are not necessarily irreversible. Temporal and spatial variations in habitat suitability could cause large variation in μ/g for each tactic (Figure 1; clouds about each μ/g curve). Thus, a fish embarked on a fast-living strategy (high growth, high mortality) could delay migration if the nursery habitat is unusually productive. Similarly, particularly poor nursery conditions might cause a resident fish to migrate. Late-life reversals of migration tactics have been reported for migratory forms (Näslund 1990; Radtke et al. 1996). These inconsistencies between early decisions and realized tactic would suggest that a fish can modify the developmental plan based upon their ability to assess real-time changes in the environment (Thorpe 1989).

The char problem, i.e. the relative roles of genotype vs. phenotype in migration behaviors, remains a critical problem in investigating the maintenance of contingents. Under the early life

decision model, it seems most reasonable to search for a polygenic system of inheritance, one which leads to a population-specific reaction norm of phenotypic response and thresholds to environmental conditions. In the near term, much work is needed to establish the extent to which populations are structured into contingents. Currently, otolith composition analyses may provide the most precise means of discriminating contingents and understanding their interactions. The char problem may be productively addressed by coupling otolith composition measures of contingent discreteness with biochemical measures of contingent and population lineage.

Stocks and Contingents

Definition of Stock

Early fisheries science struggled to determine stock (population) origin because rigorous approaches were unavailable (Ihssen et al. 1981). Biochemical measures can now precisely measure lineage over several evolutionary and ecological time scales (Wirgin and Waldman 1994). This has resulted in synonymy between population and stock terms (Table 3). However, even with sophistication in stock separation techniques, confusion in term usage persists (Table 3; see also Waldman and Begg, this issue). If we can now precisely know the lineage of a stock, why not simply label stocks as populations, which has clear meaning in fisheries science (Sinclair 1988), and be done with the confusing legacy of the term stock?

The stock concept continues to guide fisheries science and management because stocks are not simply populations. Historically, considerations of the catchable or accessible portions of populations were implicit in the definition of stock (Russell 1931; Marr 1957; Saila and Martin 1987; Gauldie 1991). How do individuals, cohorts, or contingents within populations become accessible to fisheries? What component of a population is affected by habitat alterations-- pollution? The definition of stock lies at the spatiotemporal intersection between the extent of population occurrence and those human activities which affect population productivity. Recent examples of studies specifying points of spatial intersection between exploitation and population behaviors include reproductive subsidy between exploited and relatively unexploited groups of Atlantic cod and American lobster (Frank 1992; Fogarty 1998) and increased catchability of Atlantic cod at low population size due to more clumped distribution around favorable habitats (Hutchings 1996).

Dependent upon the human activity, the biological levels which are pertinent to management will scale from individual to species (Table 4). Recent determinations of stock center on lineage of individuals within populations, rather than ecological attributes which affect accessibility. While lineage sets the stage for patterns of migration and habitat use by populations, ecological attributes (population density, year-class strength, migratory behaviors) have remained relatively unevaluated in issues related to stock. In general, levels critical to understanding the effects of exploitation and habitat change will be governed by both lineage and accessibility (year-class to meta-population levels).

Contingent-Thinking

The ultimate value of the stock concept is in its utility (Booke 1981). Does another level in the hierarchy of stock organization provide a tractable means to evaluate the effect of fishing and habitat degradation on fish populations? Let us return to the striped bass case study to demonstrate the utility of contingent thinking. Hudson River striped bass, classified as resident, showed much higher contamination by polychloride biphenyl hydrocarbons (PCBs) than the other migratory groups (Zlokovitz and Secor, in press), consistent with a known point source of PCBs upriver to the estuary. Currently, due to high contamination of striped bass captured in the Hudson River, no exploitation is permitted. Alternatively, total PCBs in striped bass captured in Long Island Sound is below the U.S. federal action limit and exploitation is permitted on the coastal contingent of Hudson River striped bass. If resident striped bass produce progeny some of which become coastal migratory fish, then coastal fisheries are subsidized by reproduction of the highly contaminated resident contingent. Thus, it would be impossible to recruit over-fish the coastal contingent with this "pollution refuge" from exploitation (Figure 11).

The function of contingents may be to maintain divergent life-cycle pathways and thereby confer resiliency against spatial variation in mortality risk. Examples of temporal bet-hedging in the strategies of teleosts are well known. I have already reviewed Hjort's (1914) pioneering contribution, which led to profound insights on control of population dynamics through year-class strength. Since Hjort's synthesis, many instances have been shown for compensatory mechanisms which dampen population variations. In particular, reproductive schedules of teleosts can be generalized as modes of associated life history attributes which confer resiliency to temporal variation in recruitment success (Adams 1980; Kawasaki 1980; Winemiller and Rose 1992). Along similar lines of reasoning, I speculate that multiple modes of retentive and dispersive behaviors may minimize risks associated with use of unpredictable and variable habitats within a population's range. Returning to the concept of hydrographic containment of populations, the function of contingents can be exhibited as multiple migration triangles, a set of migration circuits originating and returning to the same spawning ground (Figure 12). In the extreme case, should one feeding or wintering ground result in complete mortality, then other contingents persist - an effective means of bet hedging. Contingent structure could also promote effective colonization of new habitats. For instance, the invasion of striped bass from the Sacramento system, California (where they were introduced from the Atlantic Ocean in 1879 and 1881) to the Coos Bay system, Oregon (Waldman et al. 1998) may have involved a migratory contingent from the source population (presumably either Chesapeake Bay or Hudson River populations).

Contingent thinking will not always provide a tractable or useful means to understand the dynamics of human-fish interactions. For instance, intrapopulation migrations of freshwater eels (*Anguillidae*) or reef damselfish (*Pomacentridae*) would require tracking innumerable contingents, with little apparent benefit. However, across freshwater, estuarine, and marine systems, I have cited many examples where relatively few migratory contingents can be generalized with potentially useful insight to population processes which affect accessibility. An underlying theme of this paper is that otolith composition studies will aid in the measurement of patterns of migration and habitat use, and thereby provide a means to evaluate points of intersection between fish populations and human activities. Because the application of otolith composition studies in fisheries science is now quite

popular (Moksness 1998), the next decade of research should bear out whether this prediction is correct.

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REFERENCES

- Adams, P. B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fish. Bull.* 78:1-11.
- Alperin, I. M. 1966. Dispersal, migration and origins of striped bass from great South Bay, Long Island. *NY Fish and Game J.* 13:79-112.
- Austin, H. M. and O. Custer. 1977. Seasonal migration of striped bass in Long Island Sound. *NY Fish and Game J.* 24:53-68.
- Babaluk, J. A., N. M. Halden, J. D. Reist, A. H. Kristofferson, J. L. Campbell and W. J. Teesdale. 1997. Evidence for non-anadromous behavior of arctic charr (Salvinus alpinus) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada, based on scanning probe microprobe analysis of otolith strontium distribution. *Arctic* 50:224-233.
- Berggren, T. J. and J. T. Liebman. 1978. Relative contribution of Hudson, Chesapeake, and Roanoke striped bass, Morone saxatilis, to the Atlantic coast fishery. *Fish. Bull.* 76:335-345.
- Biette, R. M., D. P. Dodge, R. L. Hassinger and T. M. Stauffer. 1981. Life history and timing of migrations and spawning behavior of rainbow trout (Salmo gairdneri) populations of the Great Lakes. *Can. J. Fish. Aquat. Sci.* 38:1759-1771.
- Birt, T. P., J. M. Green and W. S. Davidson. 1991. Mitochondrial DNA variation reveals genetically distinct sympatric populations of anadromous and nonanadromous Atlantic salmon, Salmo salar. *Can. J. Fish. Aquat. Sci.* 48:577-582.
- Booke, H. E. 1981. The conundrum of the stock concept - Are nature and nurture definable in fishery science? *Can. J. Fish. Aquat. Sci.* 38:1479-1480.
- Boreman, J. and R. R. Lewis. 1987. Atlantic coastal migrations of striped bass. *Am. Fish. Soc. Symp.* 1:331-339.
- Campana, S. E., A. J. Fowler and C. M. Jones. 1994. Otolith elemental fingerprinting for stock identification of Atlantic cod (Gadus morhua) using laser-ablation ICPMS. *Can. J. Fish. Aquat. Sci.* 51:1942-1950.

Campana, S. E., J. A. Gagne and J. W. McLaren. 1995. Elemental fingerprinting of fish otoliths using IDICPMS. *Mar. Ecol. Prog. Ser.* 122:115-120.

Carr, S. M., A. J. Smellen, K. A. Howse and J. S. Wroblewski. 1995. Mitochondrial-DNA sequence variation and genetic stock structure of Atlantic cod (Gadus morhua) from bay and offshore locations on the Newfoundland and continental shelf. *Molec. Ecol.* 4:79-88.

Casselman, J. M. 1982. Chemical analyses of the optically different zones in eel otoliths. *Proc. 1980 N. Amer. Eel Conf.* :74-82.

Chapoton, R. B. and J. E. Sykes. 1961. Atlantic coast migration of large striped bass as evidenced by fisheries and tagging. *Trans. Am. Fish. Soc.* 90:13-20.

Child, A. R. 1984. Biochemical polymorphism in char (Salvelinus alpinus L.) from three Cumbrian Lakes. *Heredity* 53:249-257.

Clark, J. 1968. Seasonal movements of striped bass contingents of Long Island Sound and the New York Bight. *Trans. Am. Fish. Soc.* 97:320-343.

Dorazio, R. M., K. A. Hattala, C. B. McCollough and J. E. Skjeveland. 1994. Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. *Trans. Am. Fish. Soc.* 123:950-963.

Edmonds, J. S., N. Caputi and M. Morita. 1991. Stock discrimination by trace element analysis of otoliths of orange roughy (Hoplostethus atlanticus), a deep-water marine teleost. *Aust. J. Mar. Freshw. Res.* 42:383-389.

Edmonds, J. S., R. C. J. Lenanton, N. Caputi and M. Morita. 1992. Trace elements in the otoliths of yellow-eye mullet (Aldrichetta forsteri) as an aid to stock identification. *Fish. Res.* 13:39-51.

Edmonds, J. S., M. J. Moran, N. Caputi and M. Morita. 1989. Trace element analysis of fish sagittae as an aid to stock identification: Pink snapper (Chrysophrys auratus) in Western Australian waters. *Can. J. Fish. Aquat. Sci.* 46:50-54.

Fabrizio, M. C. 1987a. Contribution of Chesapeake Bay and Hudson River stocks of striped bass to Rhode Island coastal waters as estimated by isoelectric focusing of eye lens protein. *Trans. Am. Fish. Soc.* 116:588-593.

Fabrizio, M. C. 1987b. Growth-invariant discrimination and classification of striped bass stocks by morphometric and electrophoretic methods. *Trans. Am. Fish. Soc.* 116:728-736.

Ferguson, A. and F. M. Mason. 1981. Allozyme evidence for reproductively isolated sympatric populations of brown trout Salmo trutta L. in Lough Melvin, Ireland. *J. Fish Biol.* 18:629-642.

- Fogarty, M. J. 1998. Implications of migration and larval interchange in American lobster (Homarus americanus) stocks: spatial structure and resilience. *Can. Spec. Publ. Fish. Aquat. Sci.* 125:273-283.
- Fonteneau, A. and P. P. Soubrier. 1996. Interactions between tuna fisheries: a global review with specific examples from the Atlantic ocean. *In: Shomura, R. S., J. Majkowski and R.F. Harmon (eds.), Status of Pacific tuna fisheries in 1995. Proceeding of the second FAO Expert Consultation in Interactions on Pacific Tuna Fisheries.* FAO Fish. Tech. Paper No. 365:84-123.
- Fowler, A. J., S. E. Campana, C. M. Jones and S. R. Thorrold. 1995a. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using solution-based ICPMS. *Can. J. Fish. Aquat. Sci.* 52:1421-1430.
- Fowler, A. J., S. E. Campana, C. M. Jones and S. R. Thorrold. 1995b. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser-ablation ICPMS. *Can. J. Fish. Aquat. Sci.* 52:1431-1441.
- Frank, K. T. 1992. Demographic consequences of age-specific dispersal in marine fish populations. *Can. J. Fish. Aquat. Sci.* 49:2222-2231.
- Gardiner, M. N. and T. B. Hoff. 1982. Diet of striped bass in the Hudson River Estuary. *NY Fish and Game J.* 29:152-165.
- Gauldie, R. W. 1991. Taking stock of genetic concepts in fisheries management. *Can. J. Fish. Aquat. Sci.* 48:722-731.
- Goodyear, C. P. 1985. Relationship between reported commercial landings and abundance of young striped bass in Chesapeake Bay, Maryland. *Trans. Am. Fish. Soc.* 114:92-96.
- Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* 313:47-48.
- Gross, M. R. 1991. Salmon breeding behavior and life history evolution in changing environments. *Ecology* 72:1180-1186.
- Gunn, J. S., I. R. Harrowfield, C. H. Proctor and R. E. Thresher. 1992. Electron microanalysis of fish otoliths - evaluation of techniques for studying age and stock discrimination. *J. Exp. Mar. Biol. Ecol.* 158:1-36.
- Hammar, J., R. Porter, E. Skjold and E. Verspoor. 1989. Mixed or reversed anadromy - life history strategies of Arctic charr in southern Labrador. *Physiol. Ecol. Japan. Spec., Vol.* 1:169.
- Harden Jones, F. R. 1968. *Fish Migration.* St. Martin's Press, New York, 325 pp.

Heath, M. R. 1996. The consequences of spawning time and dispersal patterns of larvae for spatial and temporal variability in survival to recruitment. pp. 175-208, *In*: Watanabe, Y., Y. Yamashita and Y. Oozeki (eds.), Survival strategies in early stages of marine resources. A. A. Balkema, Rotterdam, the Netherlands.

Heincke, F. 1898. Naturgeschichte des Herings I. Die Lokalformen und die Wanderungen des Herings in den europäischen Meeren. Abhandlung der deutschen Seefischereivereins. Vol. 2.0. Salle, Berlin.

Hindar, K. and B. Jonsson. 1982. Habitat and food segregation of dwarf and normal Arctic charr (Salvelinus alpinus) from Vangsvatnet Lake, western Norway. Can. J., Fish. Aquat. Sci. 39:1030-1045.

Hirata, T., A. Goto and F. Yamazaki. 1988. Individual growth and smoltification of juvenile masu salmon, Oncorhynchus masou Brevoort, under rearing conditions. J. Fish Biol. 32:77-84.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe. Conseil Permanent International Pour L'exploration de la Mer 20:1-228.

Hjort, J. and E. Lea. 1914. The age of herring. Nature 94:60-61.

Hölker, F. and R. Thiel. 1998. Biology of ruffe (Gymnocephalus cernuus (L.)) - a review of selected aspects of the European literature. J. Great Lakes Res. 24:186-204.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17-29.

Hutchings, J. A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. 53:943-962.

Hutchings, J. A. and R. A. Myers. 1985. Mating between anadromous and non-anadromous Atlantic salmon, Salmo salar. Can. J. Zool. 63:2219-2221.

Hutchings, J. A. and R. A. Myers. 1994. The evolution of alternative mating strategies in variable environments. Evol. Ecol. 8:256-268.

Iguchi, K. 1996. Size-specific spawning pattern in ayu, Plecoglossus altivelis. Ichthyol. Res. 43:193-198.

Ihssen, P. E., H. E. Booke, J. M. Casselman, J. M. McGlade, N. R. Payne and F. M. Utter. 1981. Stock identification: Materials and methods. Can. J. Fish. Aquat. Sci. 38:1838-1855.

Ingram, B. L. and D. Sloan. 1992. Strontium isotopic composition of estuarine sediments as paleosalinity-paleoclimate indicator. Science 255:68-72.

- Jones, M. W., R. G. Danzmann and D. Clay. 1997. Genetic relationships among populations of wild resident, and wild and hatchery anadromous brook charr. *J. Fish Biol.* 51:29-40.
- Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Trans. Am. Fish. Soc.* 114:182-194.
- Jonsson, B. and K. Hindar. 1982. Reproductive strategy of dwarf and normal Arctic charr (Salvelinus alpinus) from Vangsvatnet Lake, western Norway. *Can. J. Fish. Aquat. Sci.* 39:1404-1413.
- Jonsson, B. and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Rev. Fish Biol. Fish.* 3:348-365.
- Jonsson, B., S. Skúlason, S. S. Snorrason, O. T. Sandlund, H. J. Malmquist, P. M. Jónasson, R. Gydemo and T. Lindem. 1988. Life history variation of polymorphic Arctic charr (Salvelinus alpinus) in Thingvallavatn, Iceland. *Can. J. Fish. Aquat. Sci.* 45:1537-1547.
- Jung, Y.-J. 1816. Fishes in Huk-San Island. (Reference provided by Dr. S. Kim).
- Kafemann, R., J. E. Finn, S. Alderstein and R. Neukamm. In review. Variation in otolith strontium and calcium ratios as indicator of life-history strategies of freshwater fish species within a brackishwater system. *Fish. Res.*
- Kaffemann, R., R. Thiel, J. E. Finn and R. Neukamm. 1998. The role of freshwater habitats for the reproduction of common bream Abramis brama (L.) in a brackish water system. *Pol. Arch. Hydrobiol.* 45:225-244.
- Kaitala, A., V. Kaitala and P. Lundberg. 1993. A theory of partial migration. *Am. Nat.* 142:59-81.
- Kalish, J. M. 1990. Use of otolith microchemistry to distinguish progeny of sympatric anadromous and non-anadromous salmonids. *Fish. Bull.* 88:657-666.
- Kawasaki, T. 1980. Fundamental relations among the selections of life history in the marine teleosts. *Nipp. Suis. Gakk.* 46:289-293.
- Kimura, S., M. Nakai and T. Sugimoto. 1997. Migration of albacore, Thunnus alalunga, in the North Pacific Ocean in relation to large oceanic phenomena. *Fish. Oceanogr.* 6:51-57.
- Kohlenstein, L. C. 1981. On the proportion of the Chesapeake stock of striped bass that migrates into the coastal fishery. *Trans. Am. Fish. Soc.* 110:168-179.
- Kristoffersen, K., M. Halvorsen and L. Jørgensen. 1994. Influence of parr growth, lake morphology, and freshwater parasites on the degree of anadromy in different populations of arctic char (Salvelinus alpinus) in Northern Norway. *Can. J. Fish. Aquat. Sci.* 51:1229-1246.

- Lambert, T. C. 1990. The effect of population structure on recruitment in herring. *J. Cons. int. Explor. Mer.* 47:249-255.
- Limburg, K. E. 1998. Anomalous migrations of anadromous herrings revealed with natural chemical tracers. *Can. J. Fish. Aquat. Sci.* 55:431-437.
- Loeken, S., T. Pedersen and E. Berg. 1994. Vertebrae number as an indicator for recruitment mechanism of coastal cod of northern Norway. *ICES mar. Sci. Symp.* 198:510-519.
- MacCall, A. D. 1990. *Dynamic Geography of Marine Fish Populations*. Washington Sea Grant, Seattle, WA. 155 pp.
- Maekawa, K., S. Nakano and S. Yamamoto. 1994. Spawning behavior and size-assortative mating of Japanese charr in an artificial lake-inlet stream system. *Environ. Biol. Fishes.* 39:109-117.
- Margraf, F. J. and L. M. Riley. 1993. Evaluation of scale shape for identifying spawning stocks of coastal Atlantic striped bass (Morone saxatilis). *Fish. Res.* 18:163-172.
- Marr, J. C. 1957. Contributions to the study of subpopulations of fishes. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. No. 208, La Jolla, California. 6 pp.
- McKown, K. A. and M. Penski. 1994. An investigation of the movements and growth of the 1989 Hudson River Year Class. pp. 59-120, *In: A Study of the Striped Bass in the Marine District of New York*. NY Dept. Environ. Conserv., Albany.
- McLaren, J. B., J. C. Cooper, T. B. Hoff and V. Lander. 1981. Movements of Hudson River striped bass. *Trans. Am. Fish. Soc.* 110:158-167.
- Merriman, D. 1941. Studies of the striped bass (Roccus saxatilis) of the Atlantic coast. U.S. Fish Wildl. Serv. Fish. Bull. 50:1-77.
- Metcalf, N. B. and J. E. Thorpe. 1992. Early predictors of life-history events - the link between 1st feeding date, dominance and seaward migration in Atlantic salmon, Salmo salar L. *J. Fish Biol.* 41:93-99.
- Milton, D. A. and S. R. Chenery. 1998. The effect of otolith storage methods on the concentration of elements detected by laser-ablation ICPMS. *J. Fish Biol.* 53:785-794.
- Moksness, E. 1998. Second International Symposium on Fish Otolith Research and Application, Abstracts. Institute of Marine Research, Bergen, Norway. 280 pp.
- Mugiya, Y. and N. Watabe. 1977. Studies on fish scale formation and resorption-II. Effect of estradiol on calcium homeostasis and skeletal tissue resorption in the goldfish, Carassius auratus, and the killifish, Fundulus heteroclitus. *Comp. Biochem. Physiol.* 57:197-202.

Myers, R. A., J. A. Hutchings and R. J. Gibson. 1986. Variation in male parr maturation within and among populations of Atlantic salmon, Salmo salar. Can J. Fish. Aquat. Sci. 43:1242-1248.

Näslund, I. 1990. The development of regular seasonal habitat shifts in a landlocked Arctic charr, Salvelinus alpinus L., population. J. Fish Biol. 36:401-414.

Nordeng, H. 1983. Solution to the "Char Problem" based on Arctic char (Salvelinus alpinus) in Norway. Can. J. Fish. Aquat. Sci. 40:1372-1387.

Økland, F., B. Jonsson, A. J. Jensen and L. P. Hansen. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? J. Fish Biol. 42:541-550.

Pitcher, T. J. and J. K. Parish. 1993. Functions of shoaling behavior in teleosts. pp. 171-200, *In*: Pitcher, T. J. (ed.), Behavior of Teleost Fishes. Chapman & Hall, London.

Povlina, J. J. 1996. Decadal variation in the trans-Pacific migration of northern bluefin tuna (Thunnus thynnus) coherent with climate-induced change in prey abundance. Fish. Oceanogr. 5:114-119.

Proctor, C. H. and R. E. Thresher. 1998. Effects of specimen handling and otolith preparation on concentration of elements in fish otoliths. Mar. Biol. 131:681-694.

Radtke, R., R. A. Kinzie and S. D. Folsom. 1988. Age at recruitment of Hawaiian freshwater gobies. Environ. Biol. Fishes 23:205-213.

Radtke, R., M. Svenning, D. Malone, A. Klements, J. Ruzicka and D. Fey. 1996. Migrations in an extreme northern population of Arctic charr Salvelinus alpinus: insights from otolith microchemistry. Mar. Ecol. Prog. Ser. 136:13-23.

Radtke, R. L., D. W. Townsend, S. D. Folsom and M. A. Morrison. 1990. Strontium:calcium concentration ratios in otoliths of herring larvae as indicators of environmental histories. Environ. Biol. Fishes 27:51-61.

Raney, E. C., W. S. Woolcott and A. G. Mehring. 1954. Migratory pattern and racial structure of Atlantic Coast striped bass. Trans. N. Amer. Wildl. Conf. 19:376-396.

Rikardsen, A. H., M.-A. Svenning and A. Klemetsen. 1997. The relationships between anadromy, sex ratio and parr growth of Arctic charr in a lake in North Norway. J. Fish Biol. 51:447-461.

Russell, E. S. 1931. Some theoretical considerations on the "overfishing" problem. Conseil Permanent International Pour L'exploration de la Mer 6:3-20.

Ruzzante, D. E., C. T. Taggart, D. Cook and S. Goddard. 1996. Genetic differentiation between inshore and offshore Atlantic cod (Gadus morhua) off Newfoundland: microsatellite DNA variation and antifreeze level. Can. J. Fish. Aquat. Sci. 53:634-645.

Saila, S. B. and B. K. Martin. 1987. A brief review and guide to some multivariate methods for stock identification. pp. 149-173, *In*: Kumpf, H. E. (ed.), Proceedings of the Stock Identification Workshop, November 5-7, 1985, Panama City Beach, Florida. National Marine Fisheries Service NOAA, Panama City Beach, FL.

Sandlung, O. T., B. Jonsson, H. J. Malmquist, R. Gydemo, T. Lindem, S. Skulason, S. S. Snorrason and P. M. Jonasson. 1987. Habitat use of the Arctic charr Salvelinus alpinus in Thingvallavatn, Iceland. *Environ. Biol. Fishes* 20:263-274.

Secor, D. H. In press. Spawning in the nick of time? Effect of adult demographics on spawning behavior and recruitment of Chesapeake Bay striped bass. *ICES J. Mar. Sci.*

Secor, D. H. 1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass Morone saxatilis. *Fish. Bull.* 90:798-806.

Secor, D. H. 1995. Otolith-based demographic and migration studies of Chesapeake Bay striped bass. Final Rept. to National Biological Service for F&W Contract 14-48-0009-92-934, 94 pp.

Secor, D. H., A. Henderson-Arzapalo and P. M. Piccoli. 1995a. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? *J. Exp. Mar. Biol. Ecol.* 192:15-33.

Secor, D. H. and E. D. Houde. 1995. Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). *Estuaries* 18:527-544.

Secor, D. H. and E. J. Chesney. 1997. Summary of a workshop: Otolith microconstituent analysis of Atlantic bluefin tuna. *Int'l. Comm. Cons. Atl. Tunas Collective Volume of Scientific Papers SCRS/97/62*.

Secor, D. H. and P. M. Piccoli. 1996. Age- and sex-dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. *Estuaries* 19:778-793.

Secor, D. H. and J. R. Rooker. In review. Is otolith strontium a useful scalar of life-cycles in estuarine fishes? *Fish. Res.*

Secor, D. H., T. Ota and M. Tanaka. 1998. Use of otolith microanalysis to determine estuarine migrations of Ariake Sea Japanese seabass. *Fish. Sci.* 64:740-743.

Secor, D. H., T. M. Trice and H. T. Hornick. 1995b. Validation of otolith-based ageing and a comparison of otolith and scale-based ageing in mark-recaptured Chesapeake Bay striped bass, Morone saxatilis. *Fish. Bull.* 93:186-190.

Secor, D. H., J. R. Rooker, E. Zlokovitz and V. Zdanowicz. In press. Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. Mar. Ecol. Prog. Ser.

Sinclair, M. 1988. Marine Populations: An essay on population regulation and speciation. Washington Sea Grant Program, Seattle, WA. 252 pp.

Sinclair, M. and P. Solemdal. 1988. The development of 'population thinking' in fisheries biology between 1878 and 1930. Aquat. Living Resour. 1:189-213.

Smith, T. D. 1994. Scaling Fisheries, the science of measuring the effects of fishing, 1855-1955. Cambridge Univ. Press, Cambridge, UK. 392 pp.

Strand, R. and T. G. Heggberget. 1994. Growth and sex distribution in an anadromous population of Arctic char in northern Norway. Trans. Am. Fish. Soc. 123:377-384.

Svedäng, H. 1990. Genetic basis of life-history variation of dwarf and normal Arctic charr, Salvelinus alpinus (L.), in Stora Rösjön, central Sweden. J. Fish Biol. 36:917-932.

Svenning, M.-A., A. Smith-Nilsen and M. Jobling. 1992. Sea water migration of Arctic charr (Salvelinus alpinus L.) - correlation between freshwater growth and seaward migration, based on back-calculation from otoliths. Nord. J. Freshw. Res. 67:18-26.

Tanaka, M., T. Ohta and D. H. Secor. In review. Freshwater entry of Japanese sea bass: amphidromous migration or accidental immigration. Fish. Sci.

Thiel, R., A. Sepúlveda, R. Kafemann and W. Nellen. 1995. Environmental factors as forces structuring the fish community of the Elbe estuary. J. Fish Biol. 46:47-69.

Thompson, D. W. 1914. The age of a herring. Nature 94:60-61.

Thorpe, J. E. 1987. Smolting versus residency: developmental conflict in salmonids. Am. Fish. Soc. Symp. 1:244-252.

Thorpe, J. E. 1989. Developmental variation in salmonid populations. J. Fish Biol. 35:295-303.

Thorpe, J. E., N. B. Metcalfe and F. A. Hutingford. 1992. Behavioral influences on life-history variation in juvenile Atlantic salmon, Salmo salar. Environ. Biol. Fishes 33:331-340.

Thresher, R. E., C. H. Proctor, J. S. Gunn and I. R. Horrowfield. 1994. An evaluation of electron-probe microanalysis of otoliths for stock delineation and identification of nursery areas in a southern temperate groundfish, Nemadactylus macropterus (Cheilodactylidae). Fish. Bull. 92:817-840.

Townsend, D. W., R. L. Radtke, M. A. Morrison and S. D. Folsom. 1989. Recruitment implications of larval herring overwintering distributions in the Gulf of Maine, inferred using a new otolith technique. *Mar. Ecol. Prog. Ser.* 55:1-13.

Townsend, D. W., R. L. Radtke, S. Corwin and D. A. Libby. 1992. Strontium:Calcium ratios in juvenile Atlantic herring Clupea harengus L. otoliths as a function of water temperature. *J. Exp. Mar. Biol. Ecol.* 160:131-140.

Townsend, D. W., R. L. Radtke, D. P. Malone and J. P. Wallinga. 1995. Use of otolith strontium:calcium ratios for hind-casting larval cod Gadus morhua distributions relative to water masses on Georges Bank. *Mar. Ecol. Prog. Ser.* 119:37-44.

Tsukamoto, K., R. Ishida, K. Naka and T. Kajihara. 1987. Switching of size and migratory patterns in successive generation of landlocked ayu. *Am. Fish. Soc. Symp.* 1:492.

Verspoor, E. and L. J. Cole. 1989. Genetically distinct sympatric populations of resident and anadromous Atlantic salmon, Salmo salar. *Can. J. Zool.* 67:1453-1461.

Waldman, J. R. 1986. 1986 Hudson River Striped Bass Tag Recovery Program. Hudson River Foundation Report, NY, NY, 50 pp.

Waldman, J. R., R. E. Bender and I. I. Wirgin. I. I. 1998. Multiple population bottlenecks and DNA diversity in populations of wild striped bass, Morone saxatilis. *Fish. Bull.* 96:614-620.

Waldman, J. R., D. J. Dunning, Q. E. Ross and M. T. Mattson. 1990. Range dynamics of Hudson River striped bass along the Atlantic Coast. *Trans. Am. Fish. Soc.* 119:910-919.

Werner, E. E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15:393-425.

Werner, E. E., J. F. Gilliam, D. H. Hall and G. G. Mittelbach. 1983a. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540-1548.

Werner, E. E., G. G. Mittelbach, D. J. Hall and J. F. Gilliam. 1983b. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* 64:1525-1539.

Winemiller, K. O. and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* 49:2196-2218.

Wirgin, I. I. and J. R. Waldman. 1994. What DNA can do for you. *Fisheries* 19:16-27.

Wirgin, I., L. Maceda, J. R. Waldman and R. N. Crittenden. 1993. Use of mitochondrial DNA polymorphisms to estimate the relative contributions of the Hudson River and Chesapeake Bay striped bass to the Mixed fishery on the Atlantic Coast. *Trans. Am. Fish. Soc.* 122:669-684.

Wroblewski, J. S., S. V. Goddard, R. K. Smedbol and W. L. Bailey. 1995. Movements of Atlantic cod (Gadus morhua) within the spring thermocline in Trinity Bay, Newfoundland. J. Mar. Biol. Assoc. U.K. 75:265-284.

Zlokovitz, E. R. and D. H. Secor. In press. Effect of habitat use on PCB body burden in Hudson River striped bass (Morone saxatilis). Can. J. Fish. Aquat. Sci.

Table 1. Studies measuring composition of New York Bight mixed stock of striped bass using morphometric, protein, and biochemical analyses. HR = Hudson River, Ches = Chesapeake Bay; LI = Long Island; RI = Rhode Island coastal waters; % HR = % of mixed stock sample attributed to Hudson River population

Approach	Mixed Stock	Sample Site	% HR	Reference study period
Fin ray counts	HR, Ches	Upper HR, Lower HR	"Hudson Race" Hudson Race + Ches	Raney et al. 1954 1936-1953
Meristics	HR, Ches	LI Sound	51%,	Waldman et al. 1997 1989
Morphometrics (truss analysis)	HR, Ches	LI Sound	81%	Waldman et al. 1997 1989
Morphometrics + Meristics	HR, Ches	LI Sound	79%	Waldman et al. 1997 1989
Body, scale, meristics and morphometrics	HR, Ches, Roanoke	LI Sound (<40 cm FL) HR-winter (<40 cm FL)	>80% >95%	Berggren and Lieberman 1978 1975
Eye lens proteins and morphometrics	HR, S. Stock	RI (1982) LI Sound (1984-1985)	46% 36-67%	Fabrizio et al. 1987a,b 1982, 1984, 1985
Immunoassay	HR, Ches	LI Sound	70%	Waldman et al. 1997 1989
scale shape	HR, Ches	LI Sound RI	53% 45%	Margraf and Riley 1993 1982
scale shape	HR, Ches	LI Sound	47%	Waldman et al. 1997 1989
mt DNA	HR, Ches	LI Sound	73%	Wirgin et al. 1993 1989

Table 2. Mark-recapture studies on a coastal stock of striped bass. Recapture percentages by site indicate the proportion the total recapture sample. TL = total length (cm), n = no. tagged; NE = New England (RI, MA, NH, and ME), LI = Long Island, HR = Hudson River, S. LI = Southern LI coast (including Great South Bay), S. Locations = States south of Cape May (Delaware, Maryland, Virginia and North Carolina = DE, MD, VA, NC, respectively).

Tagging Site; n (Study Period)	TL	Recaptures	Proposed Migration Patterns	Source
LI, Sound: 2,573 (1936-1938)	30-51	2% NE ~0% HR 51% LI Sound 29% S. LI 8% NJ 10% S. Locations	1. N. Spring and S. Fall migration by coastal stock 2. Summer quiescent period of feeding by coastal stock 3. Winter dormancy; occasional winter residence of non-natal fishes in spawning tributaries 4. Coastal sample mostly immature females 5. Early spawning runs in fall 6. Persistent schools 7. Abundance of coastal stocks dependent upon Chesapeake recruitments	Merriman 1941
LI Sound: 555 (1948-1952)	21-43	67% HR 28% LI Sound 5% outside LI, HR	1. Large upriver migrations in fall and spring 2. Late spring migration to W. L.I. Sound 3. Wintering group in HR= "Hudson race"	Raney et al. 1954
lower HR: "numerous" (1948-1952)	?	97% HR		
Great S. Bay L.I.: 1,917 (1956-1964)	29-68	5% HR 58% LI (S. Bay, Sound) 21% NJ 11% NE 5% "S. Stocks"	1. S. Bay stock of mixed origin 2. Stock origin dependent upon recruitments elsewhere	Alperin 1966
NE: 272 LI Sound: 2,816 S. LI: 1,191 NY Harbor: 1,697 NJ: 700 (1959-1963)	28-56	12% NE 23% LI 8% S. LI 24% NY Harbor, HR 18% NJ 15% DE and Ches	1. Three contingents by HR origin fish. 2. Discrete migrations of NY Harbor and W. LI Sound contingents 3. NY Harbor contingent winters in HR 4. HR pop. contributes most to mixed stock north of DE Bay.	Clark 1968
LI Sound: ? (1966-1972)	"short"	4% NE 58% LI Sound 14% S. LI 5% NY Harbor 3% NJ 16 % Ches and NC	1. Spring ingress E. and W. entrances to Sound. 2. Summer residency in Sound. 3. Fall egress through W. entrance of Sound 4. Fall migration of NE fish into LI Sound 5. Stock origin dependent upon Chesapeake Bay recruitments	Austin and Custer 1977

Table 2. (Continued)				
HR: 5,219 (1976-1977)	40-65	48% HR 50% NY Harbor/LI Sound	1. NY Harbor and LI Sound serve as important feeding ground 2. Wintering group in HR after upriver fall migration 3. Freshwater resident group 4. No size or sex dependency in dispersal from tagging sites. 5. HR population does not support S. mixed stock	McLaren et al. 1981
LI: 9,851 S. LI: 1,099 NY Harbor: 8,558 (1964-1985)	15-76	LI ¹ 52% S. LI ¹ 41% NY Harb ¹ 36%	1. Confirmation of Merriman's coastal migration hypothesis 2. HR population does not support S. mixed stock 3. Ches fish do not overwinter in HR	Boreman and Lewis 1987
HR & NY Harb.: 28,667 (1984-1986)	20-72	10% NE 23% LI Sound 48% NY Harbor 33% HR <1% elsewhere	1. Larger fish more dispersive 2. Wintering group in lower HR 3. Clark's contingents likely due to size-dependent migrations rather than contingent behaviors	Waldman 1986; Waldman et al. 1990
HR Females: 1,224 HR Males: 1,801 (1988-1991)	60-110 30-100	50-70% LI Sound, NY Harbor, HR 92-96% LI Sound, NY Harbor, HR	1. Rare migration of HR pop. to S. mixed stocks. 2. Coastal mixed stocks mostly female 3. Size dependent emigration to coastal regions	Dorazio et al. 1994
LI Sound & S. Bay: 3,240 (1987-1992)	15-50	10% NE 86% LI Sound, NY Harb, HR 3% NJ 1% Ches	1. Young-of-the-year recruit to western LI embayments 2. Yearlings occur throughout LI Sound and S. Bay.	McKown and Penski 1994

¹Proportion of recaptures for Boreman and Lewis 1987 is given as proportion of recapture sample by site, rather than the proportion of recapture sample from combined sites.

Table 3. Phrases describing a fishery occurring on multiple populations. Phrases reported from primary literature 1978 - 1998 (Institute for Scientific Information[®]).

Stock (n.) = Population	Stock (adj.) = Population Origin	Stock (n.) + Population
mixed stocks	mixed stock fishery(ies)	mixed stock
stock mixtures	mixed stock analysis	mixed population of stocks
	mixed stock origin	mixed stock populations
	mixed stock model	mixed stock comprised of "x" and "y" stocks

Table 4. Hierarchy of the stock concept.

Accessibility	Biological Level	Examples for Striped Bass
Accessibility most determined by lineage	Species	<i>Morone saxatilis</i>
	Sub-Species	None yet observed
	Meta-population	Mid-Atlantic migration corridors
	Population	Hudson River lineage
	Sub-population	None yet observed
Accessibility most determined by ecological attributes	Contingent	Resident freshwater contingent
	Year-class	Dominant 1987 and 1988 cohorts
	School/Shoal	Seasonally persistent shoal by Troy Dam
	Brood	Hatchery released striped bass
	Individual	Stray from Chesapeake Bay population

Migration Triangle in Diffusive Environment

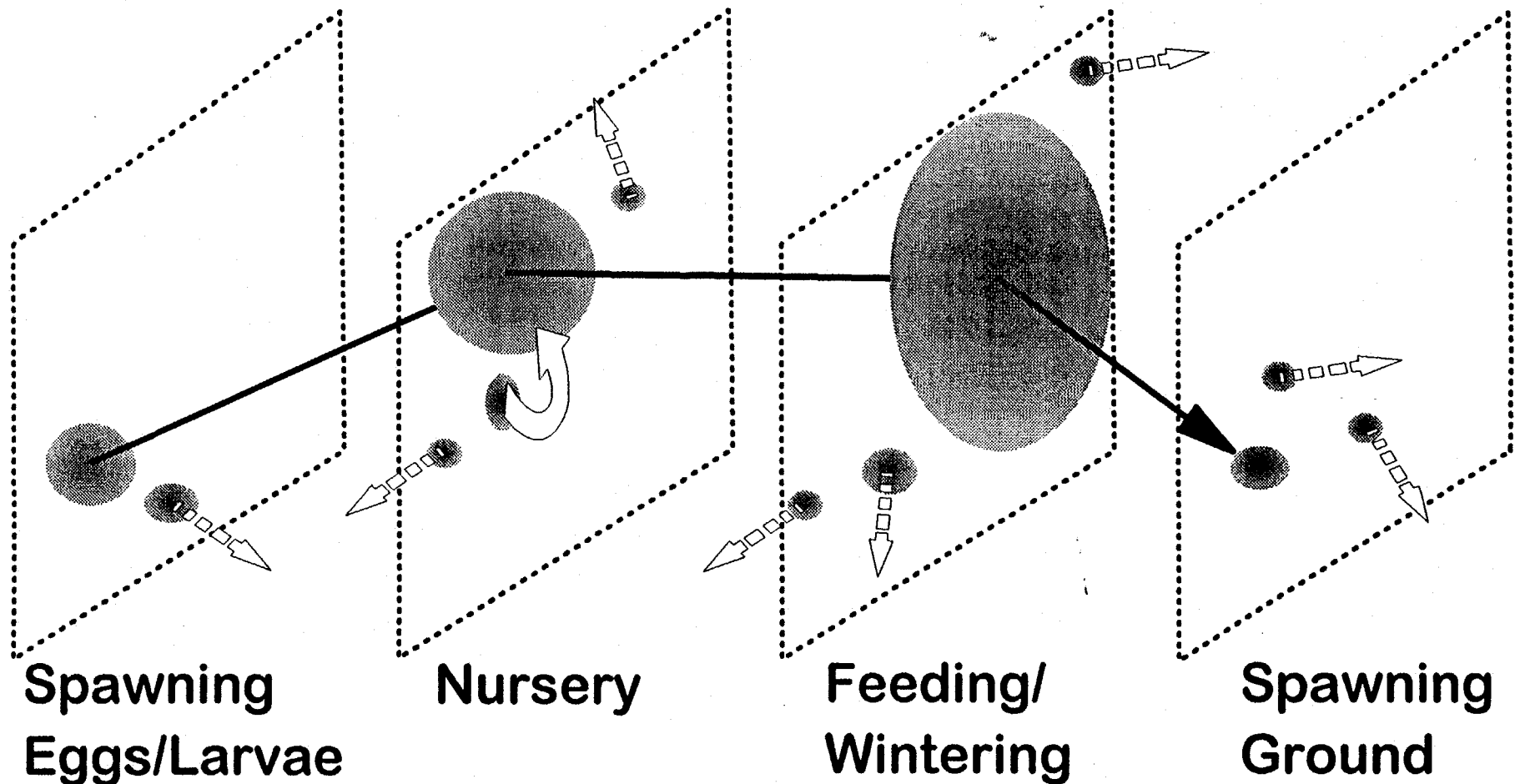


Figure 1. Migration triangle in a diffusive environment. Each pane represents a cross-sectional profile of spatial occurrence (for example, horizontal and vertical axes of each pane could represent latitude and longitudes). Panes are arranged left to right to show ontogenetic pattern of migration. Mean migratory circuit is shown by the bold line. Centroids exhibit numerical density of the population aggregations. Open arrows indicate possible migratory fates of vagrant aggregations. Note that collapsing all panes into a single framework would cause the mean migratory circuit to circumscribe a migration triangle (*sensu* Harden Jones 1968).

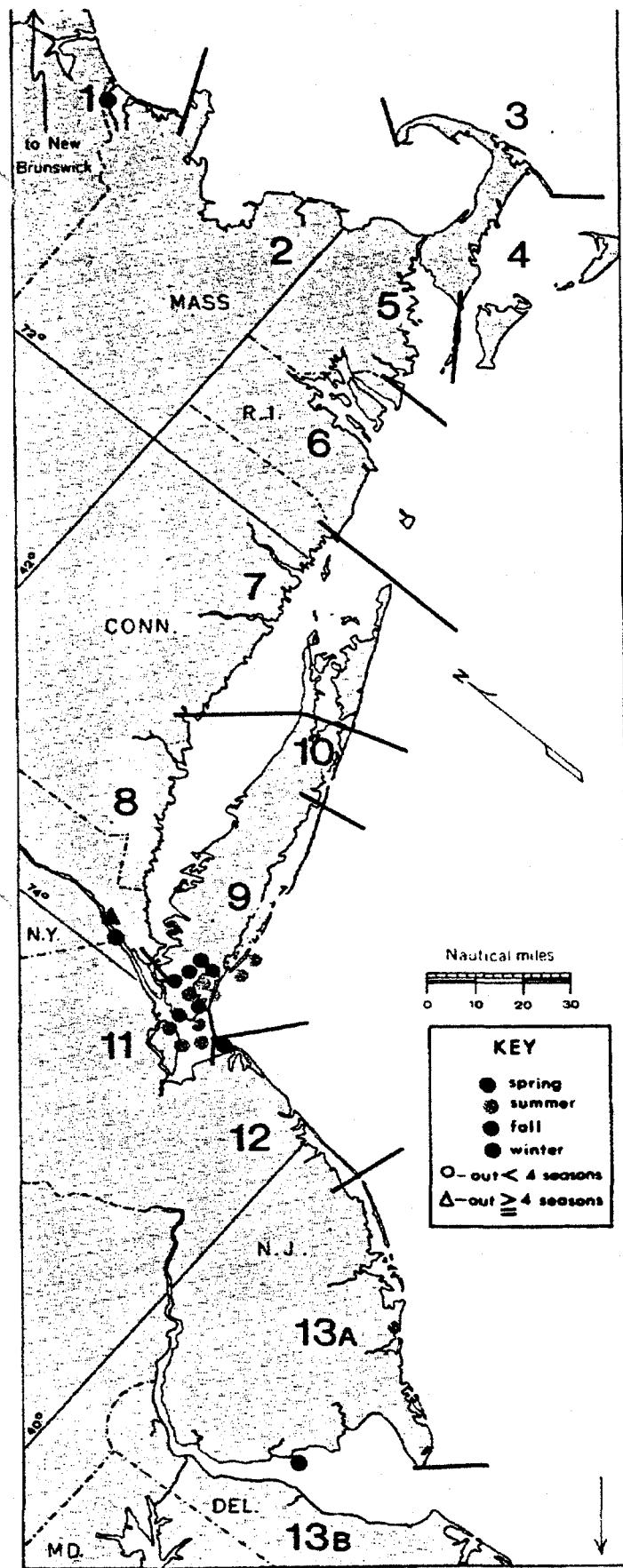


FIGURE 18.—Recaptures from spring tagging, Area 11, New York Bay.

A

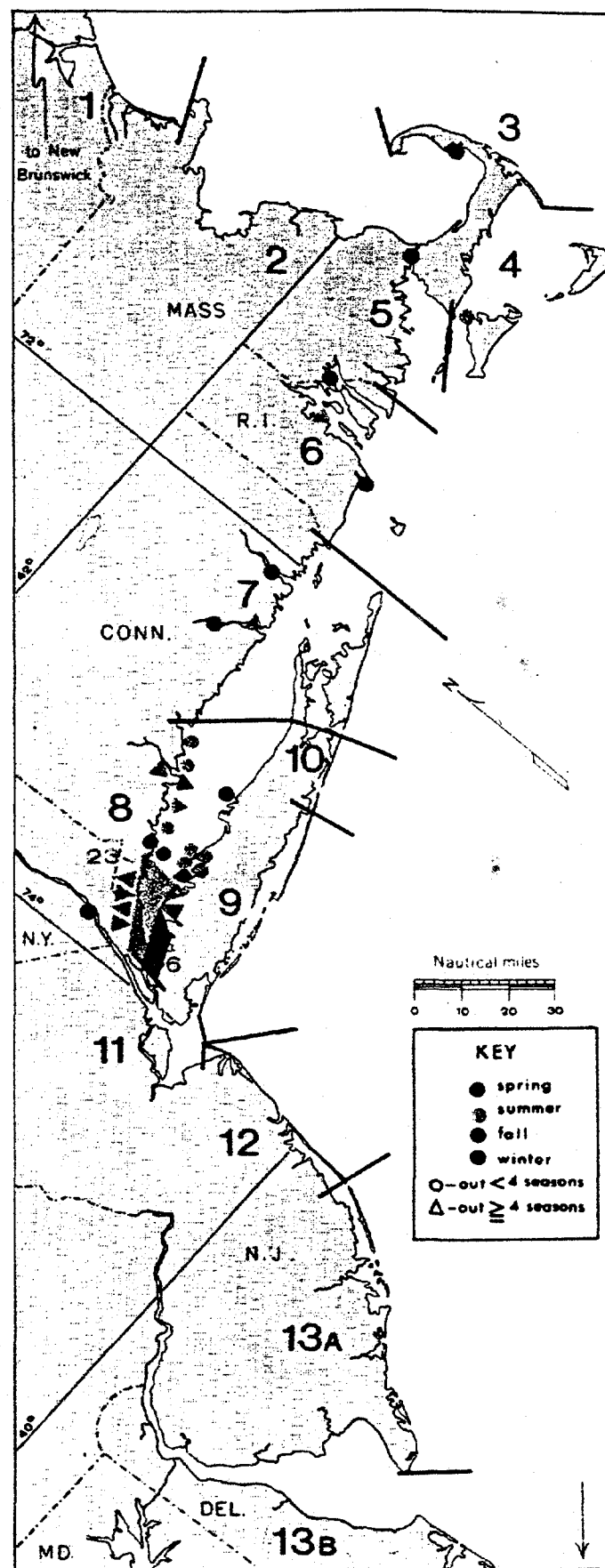


FIGURE 12.—Recaptures from spring tagging, Area 8, West Sound.

B

Figure 2. Map of New York Bight showing striped bass tagging and recapture location for Clark's 1959-1963 study. (A) Fish tagged in New York Harbor region and subsequently recaptured, by season. (B) Fish tagged in Long Island Sound region and subsequently recaptured, by season.

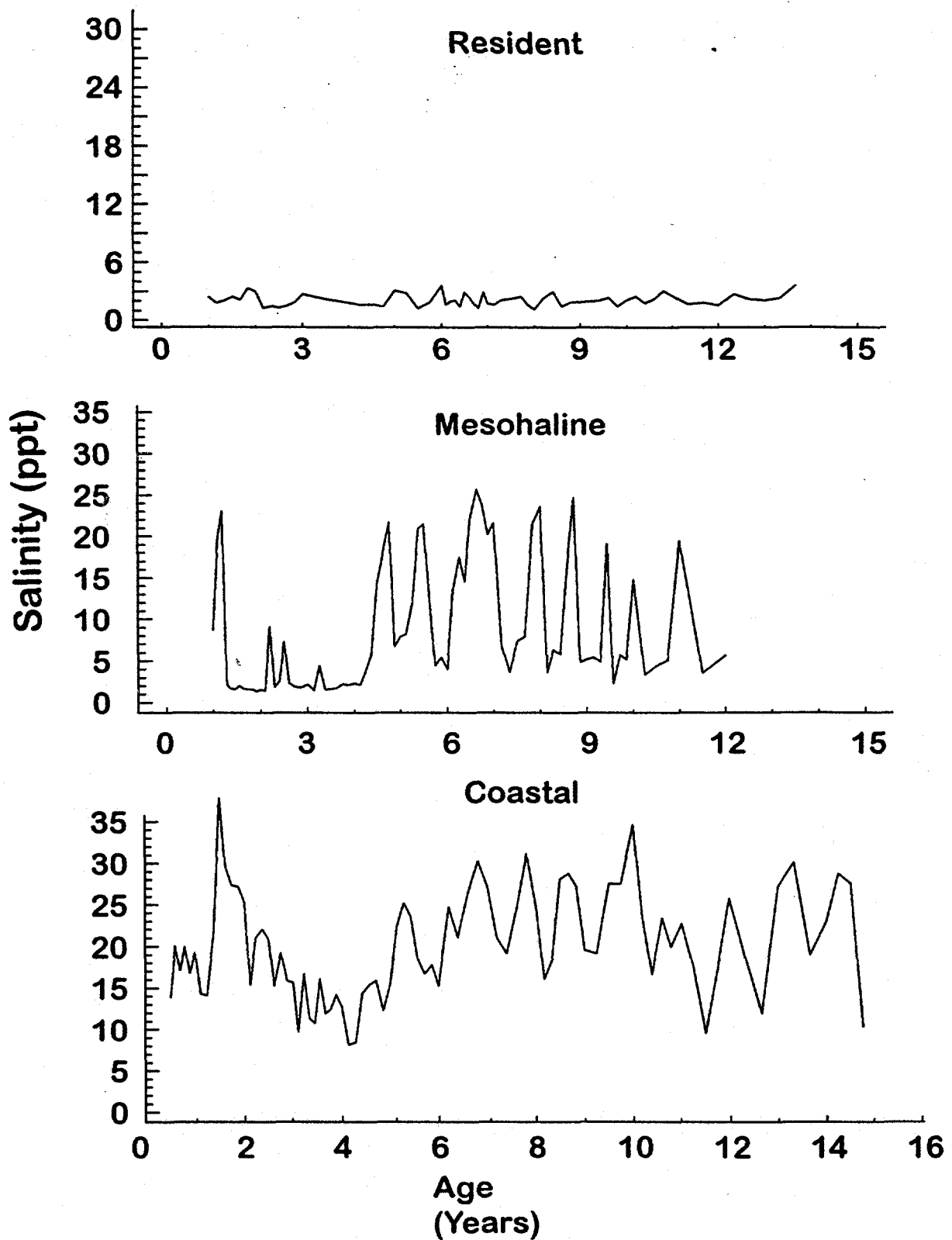


Figure 3. Representative lifetime salinity chronologies for Hudson River striped bass. Chronologies were constructed from otolith microprobe analysis of Sr (Secor et al. 1995). Migratory classifications (resident, mesohaline, or coastal) are indicated. Modified from Secor et al., in press.

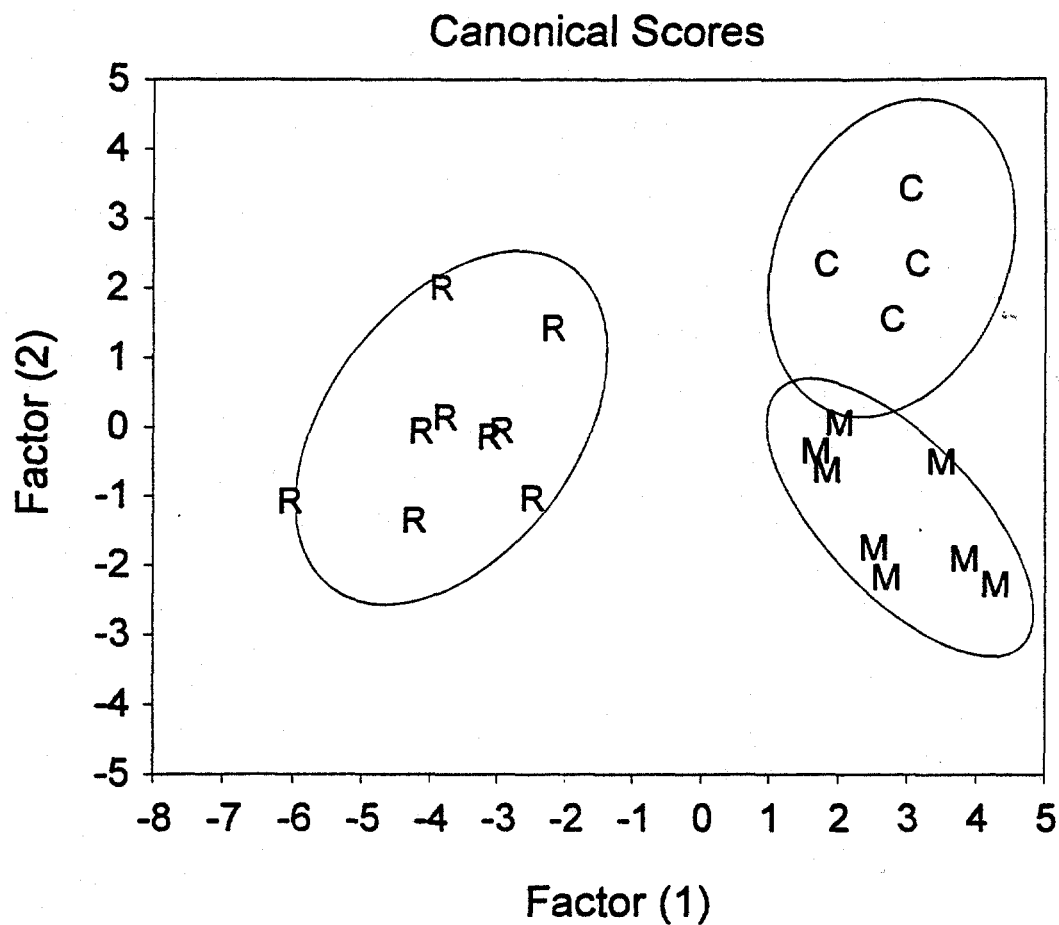


Figure 4. Canonical variable plot of striped bass migratory contingents. R = Resident; M = Mesohaline; C = Coastal. 95% confidence ellipses for each group are presented. Modified from Secor et al., in press.

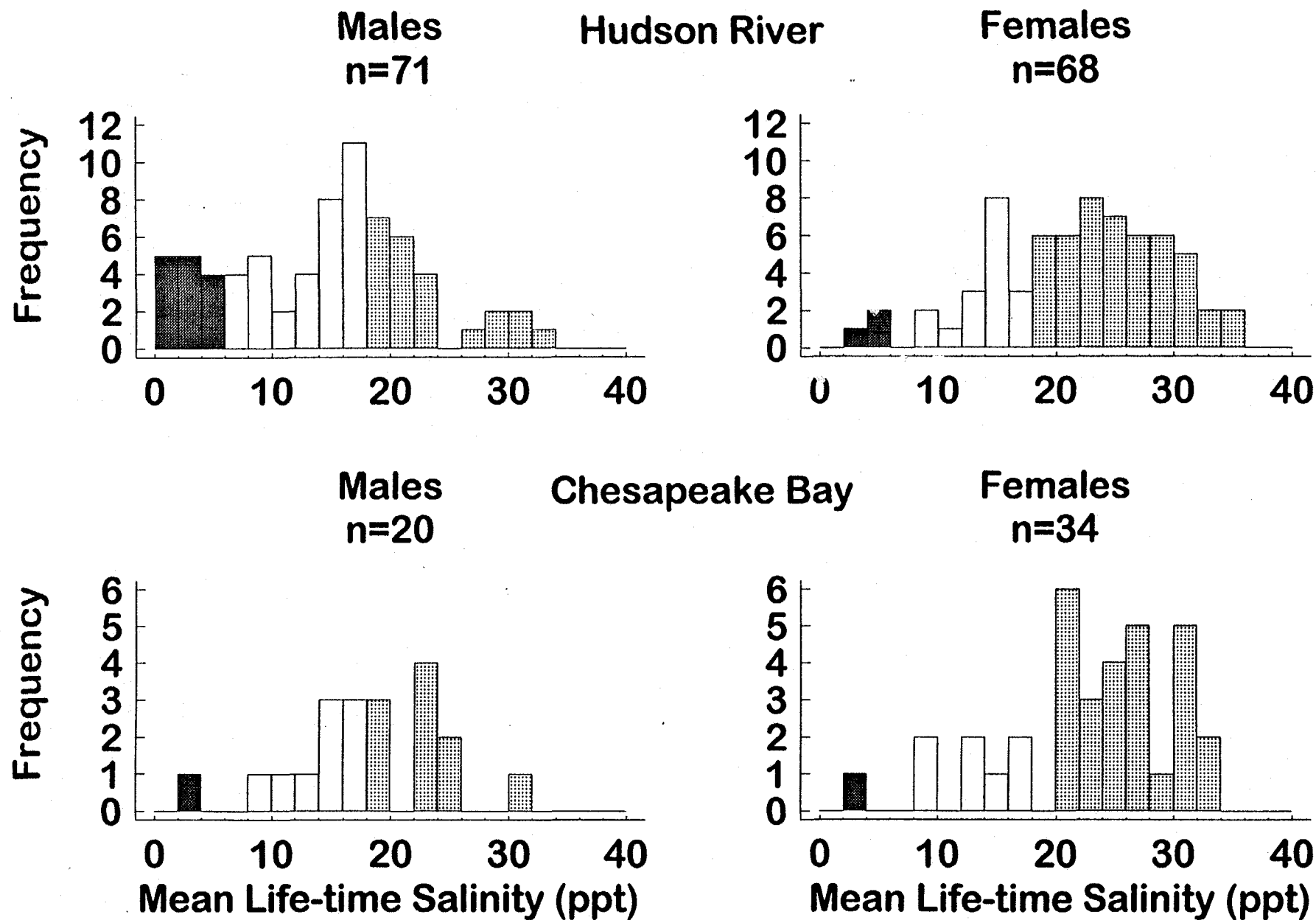


Figure 5. Frequency histogram of individual life-time salinity habitat values (see text) for Hudson River and Chesapeake Bay striped bass. Resident, mesohaline, and polyhaline/marine ranges are indicated by shaded, open, and stippled bars, respectively.

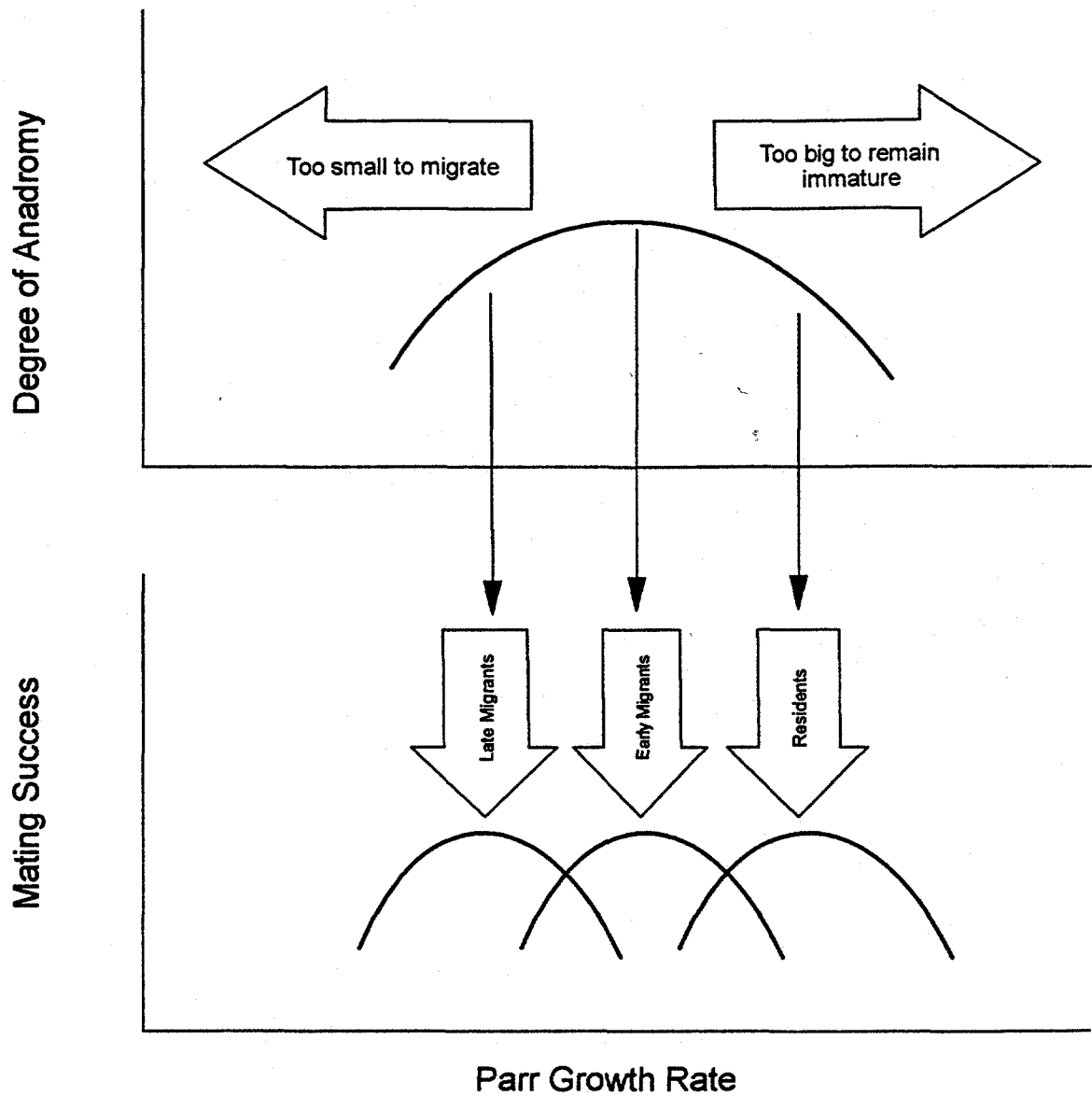


Figure 6. Idealized relationships between early growth rate, migratory tactic and mating success (see text).

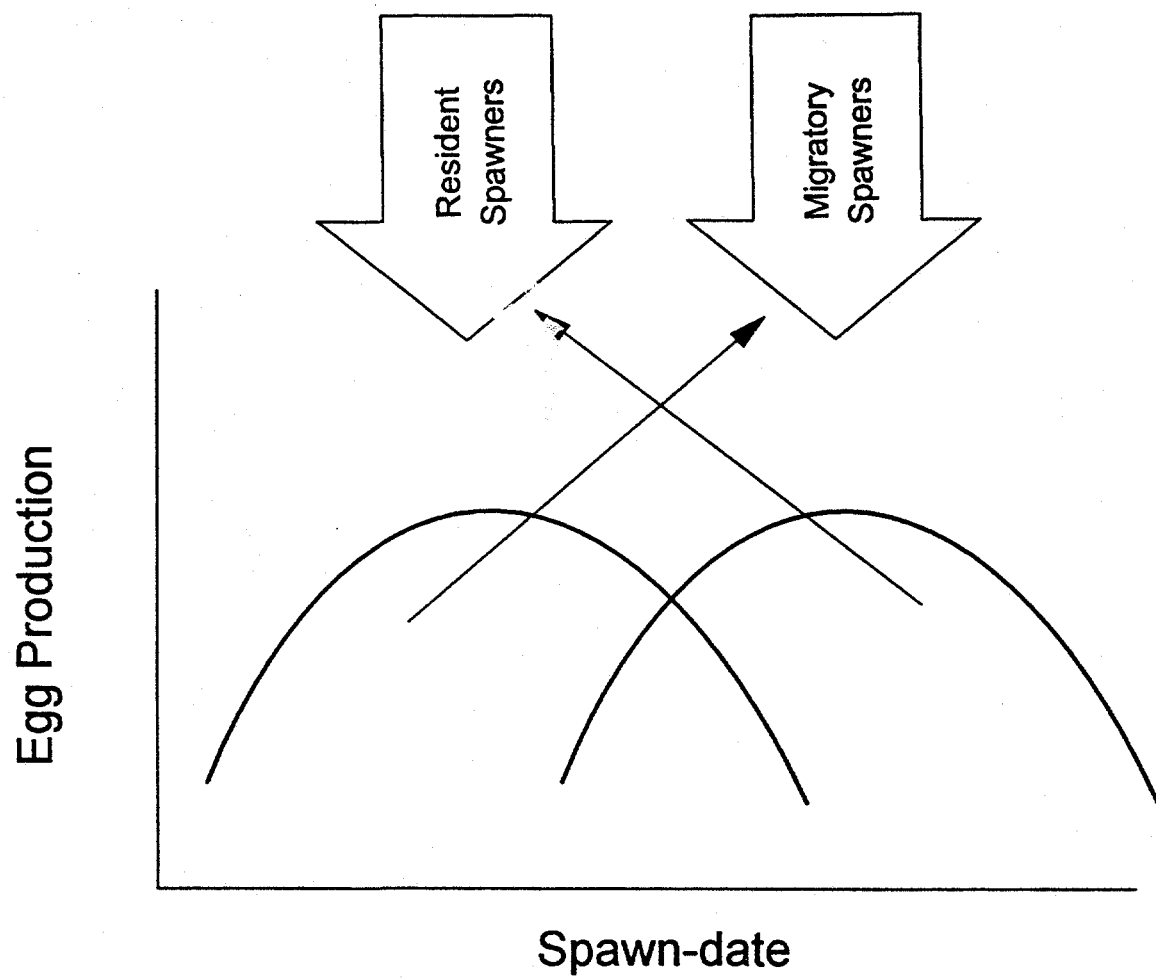


Figure 7. Tsukamoto et al.'s (1987) system for Lake Biwa ayu in which migratory and resident forms occurred as alternating generations.

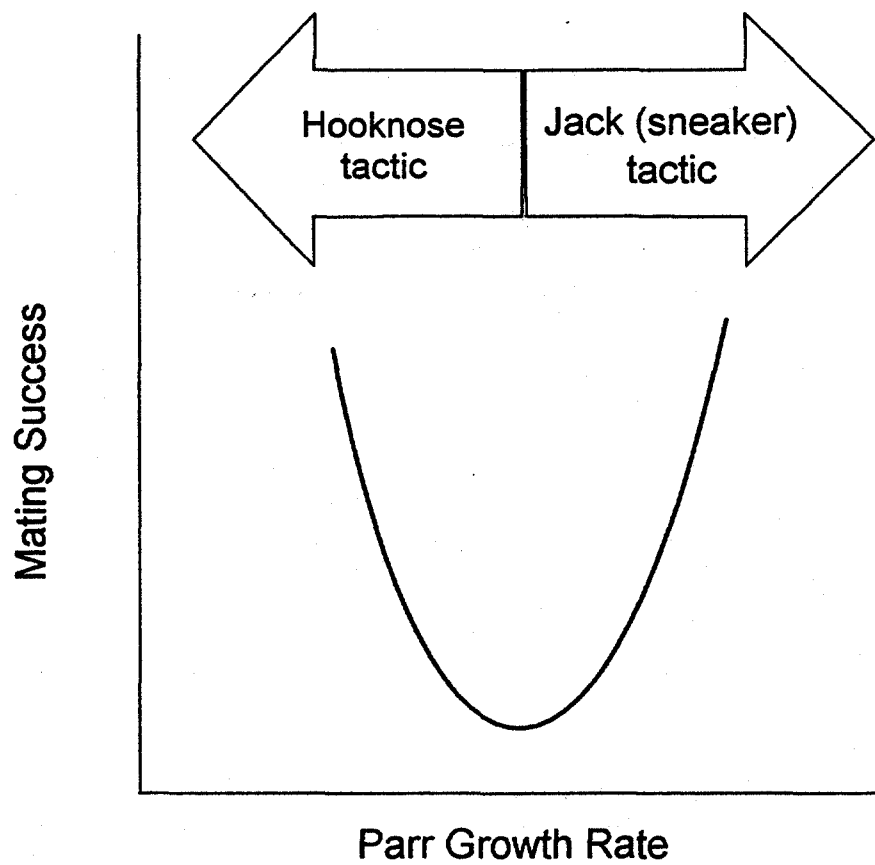


Figure 8. Idealized diagram showing disruptive selection for migratory tactics based upon mating success (adapted from Gross 1985).

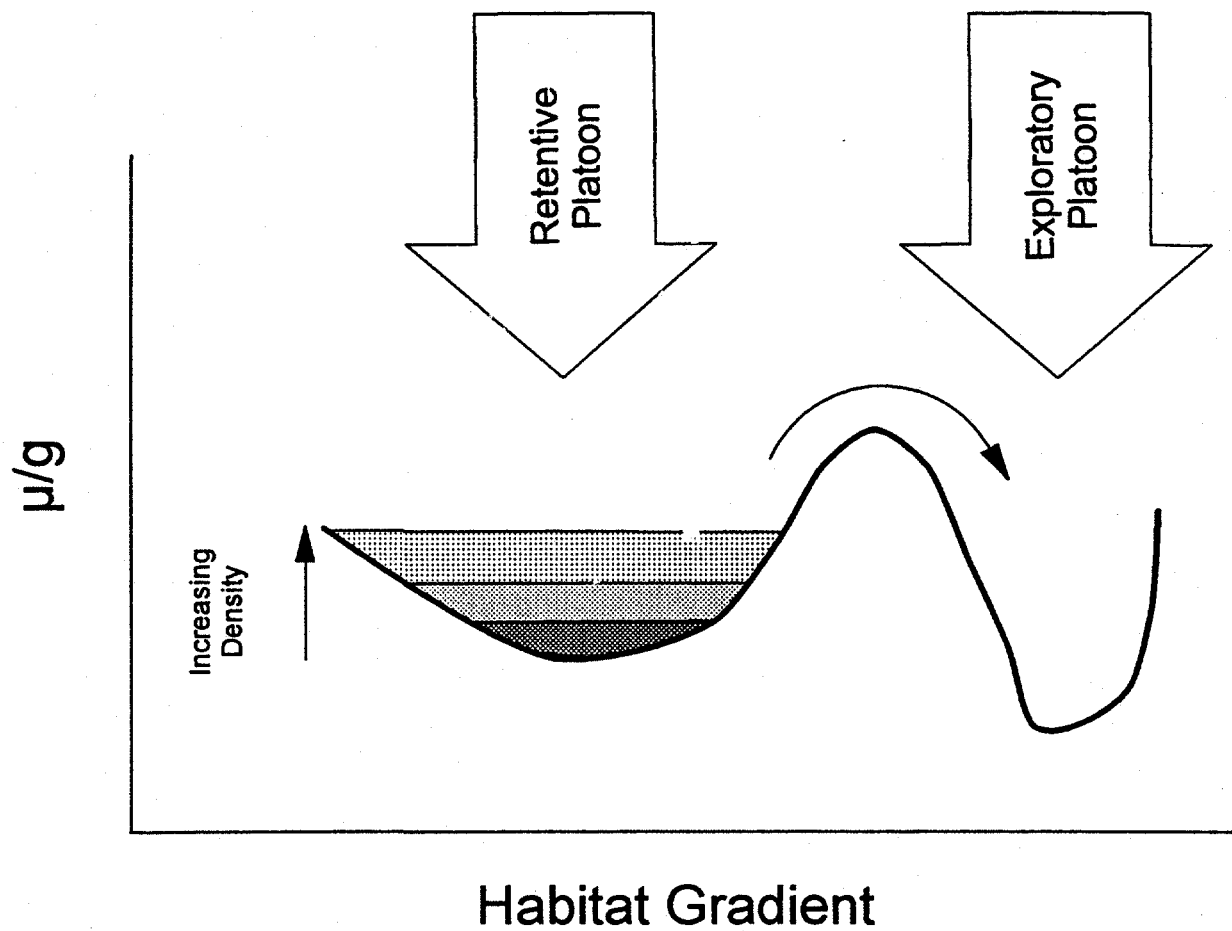


Figure 9. Modification of MacCall's (1990) Basin Model, considering μ/g as a fitness criterion and barriers to dispersal into adjacent favorable habitats. Within the basin, habitat values are inversely related to degree of shading.

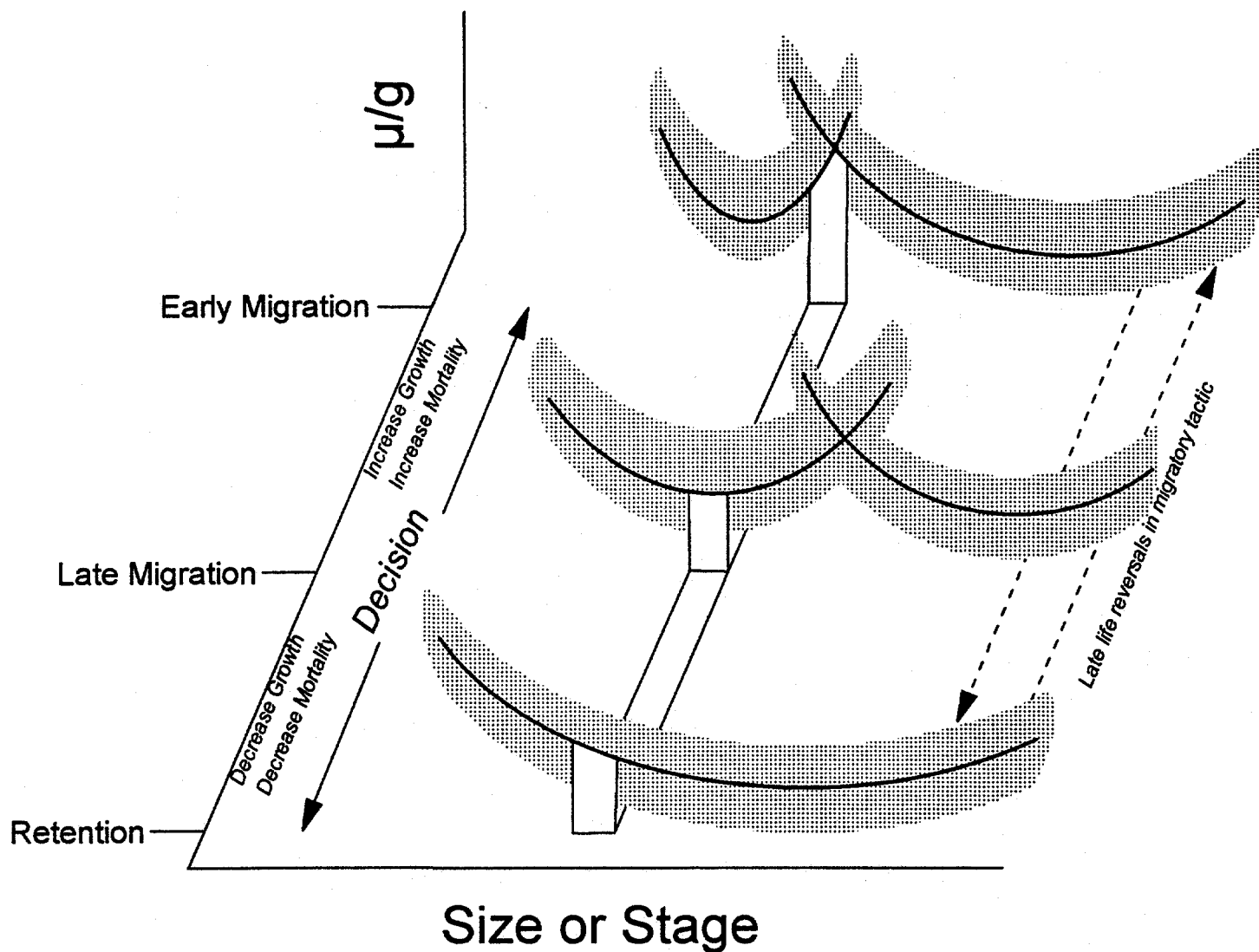


Figure 10. Curves describing idealized responses of μ/g to ontogeny and migration tactics. Three hypothetical migratory tactics are presented which correspond to early, late coastal migrations and resident behavior. The initial curves represent nursery habitat and the second curve for the early and late migration tactic correspond to the marine habitat. Stippled areas about the response curves indicate the effect of variable habitats variation on μ/g . Early decision by juveniles based upon metabolic allocations are represented as the open bar intersecting with all migration tactics. In this example, decreasing ratios of μ/g ratio would cause resident behavior, static or slightly increasing μ/g ratio would cause delay in migration, and rapidly increasing μ/g ratio would accelerate migration. Dependent upon realized μ/g (stippled clouds) individuals may "decide" not to be guided by early decisions, resulting in reversals in migratory tactics shown by broken arrows.

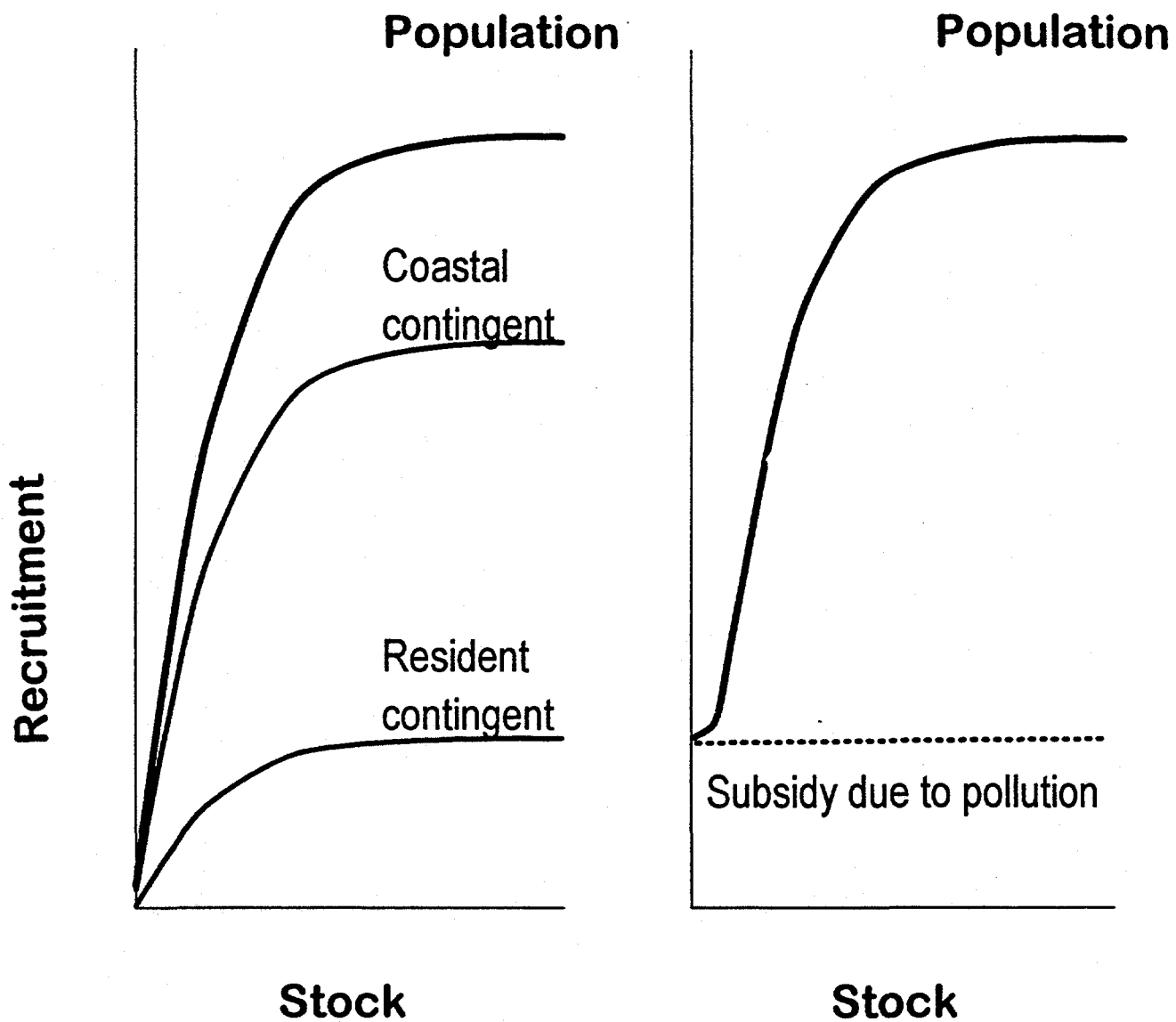


Figure 11. Example of hypothetical stock-recruitment curves for contingents of Hudson River striped bass. In this example, the resident contingent does not experience exploitation and provides reproductive subsidy to the exploited coastal contingent.

Migratory Modes

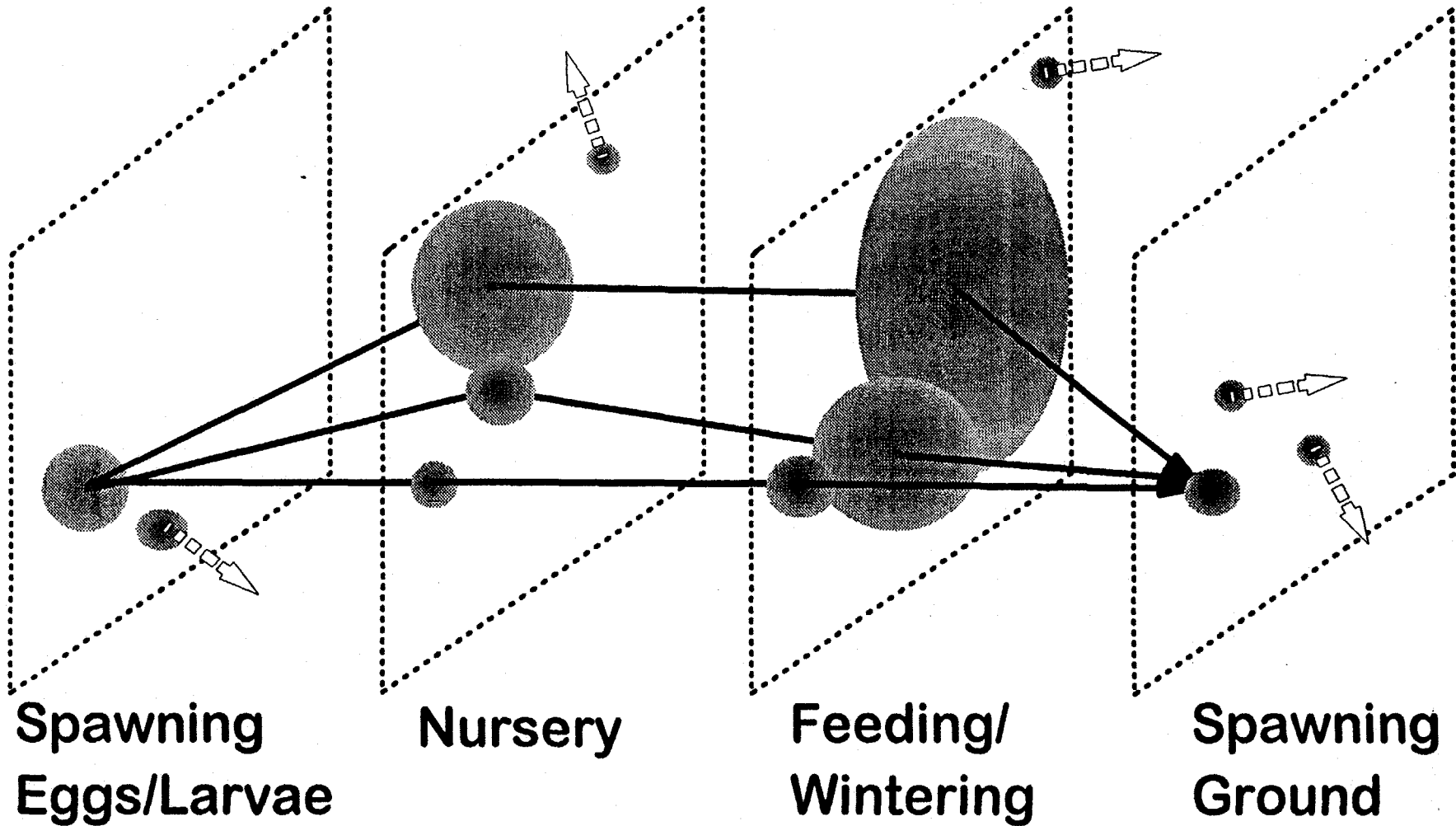
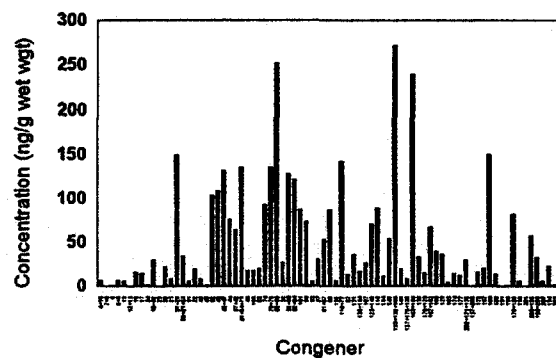
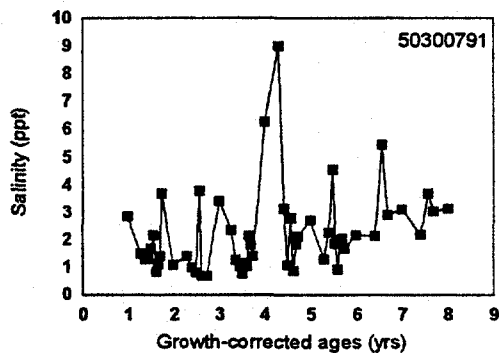
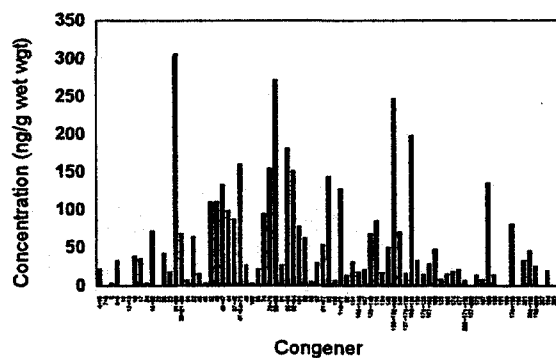
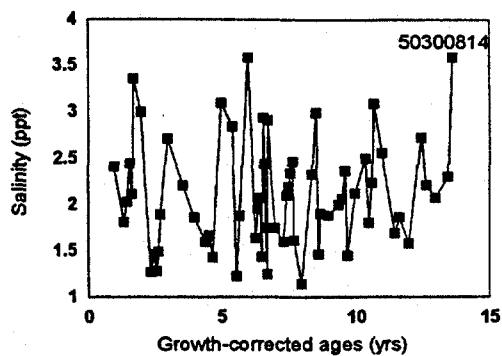
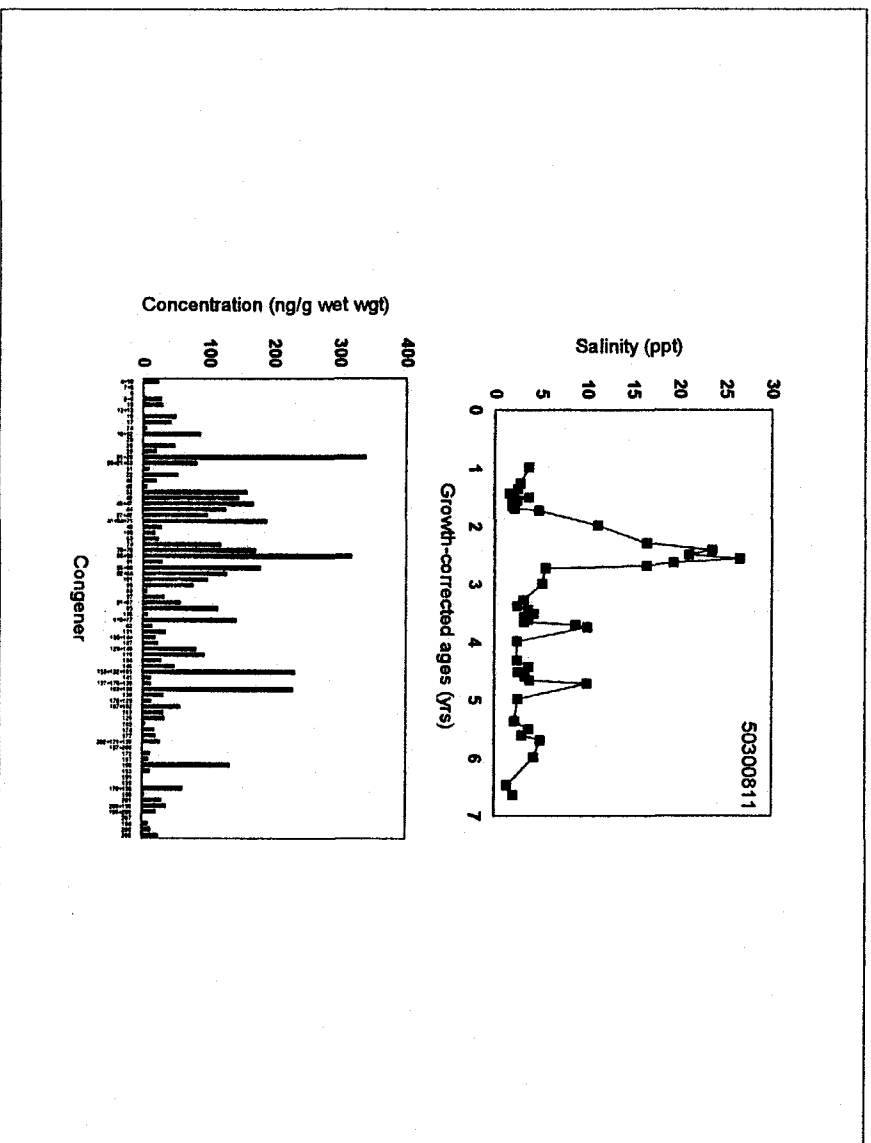
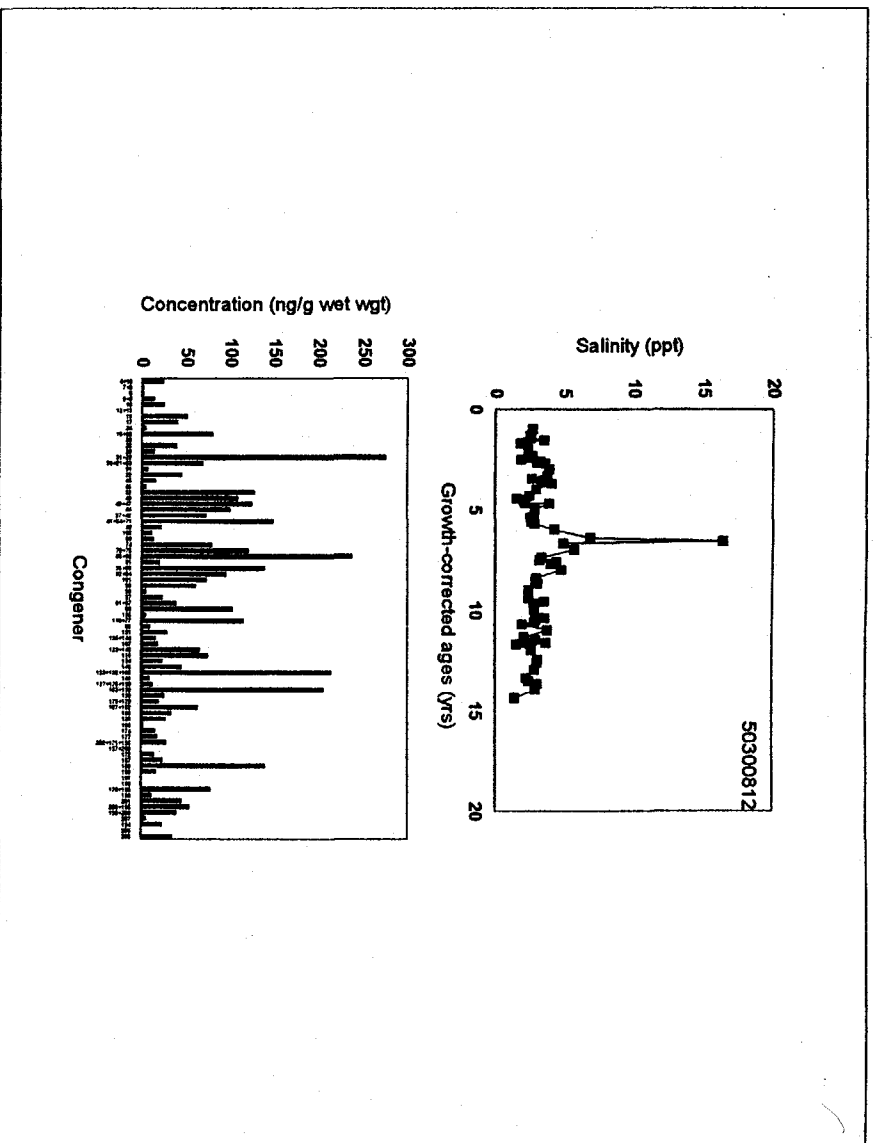
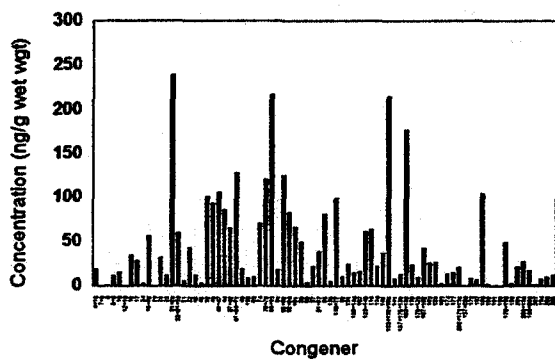
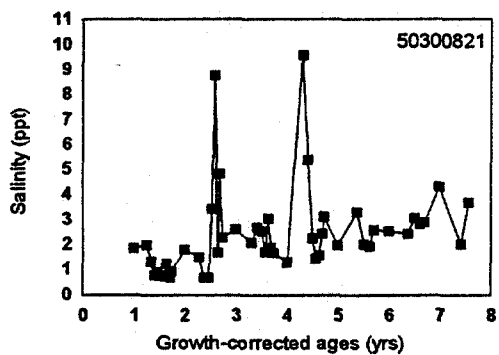
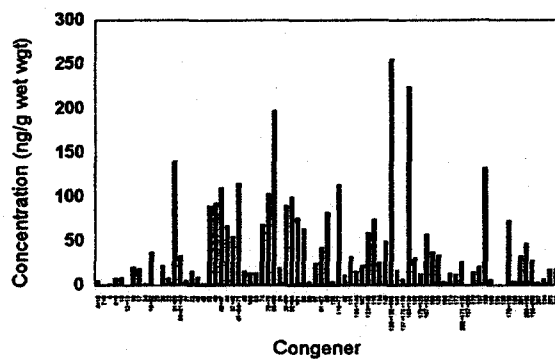
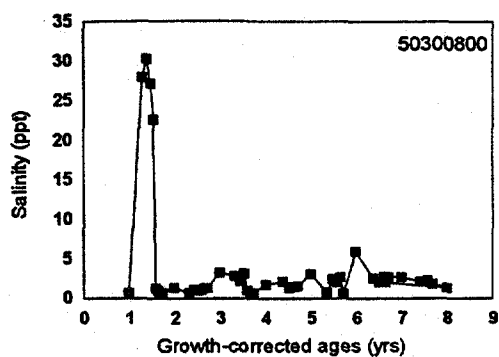


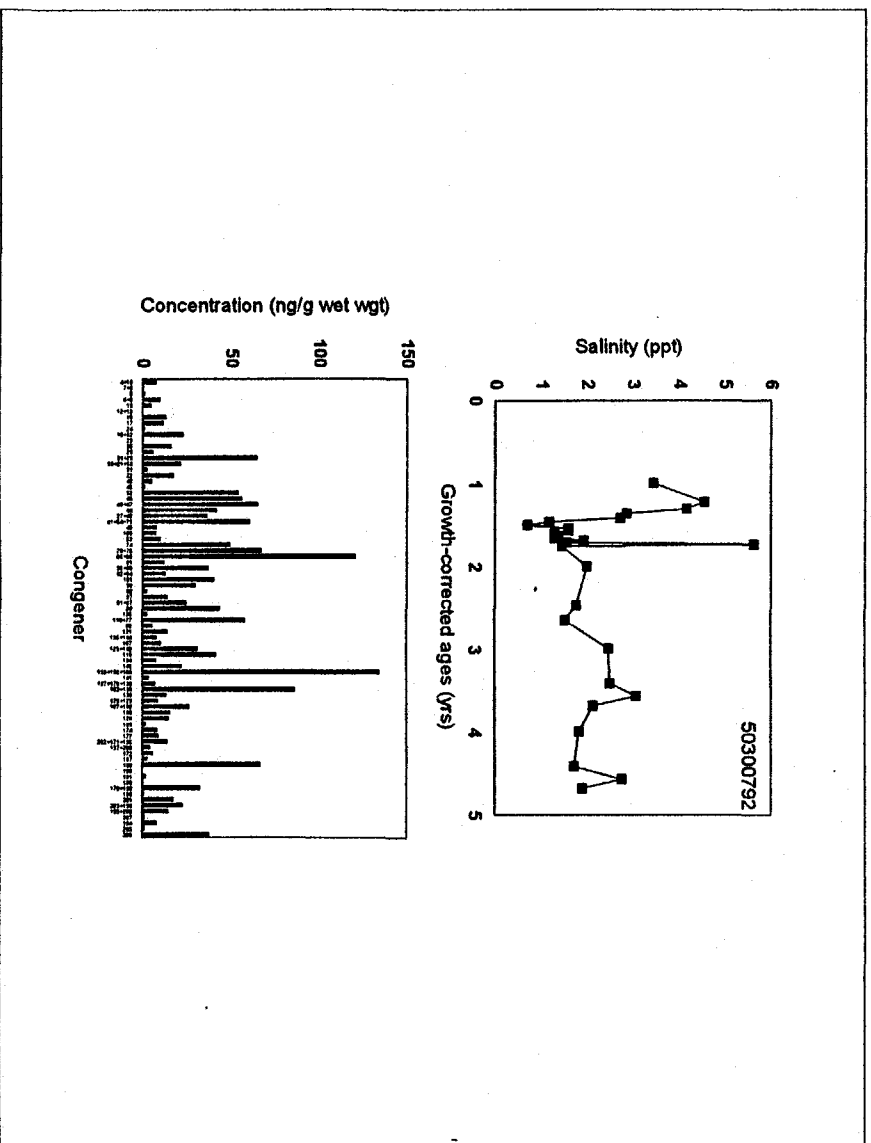
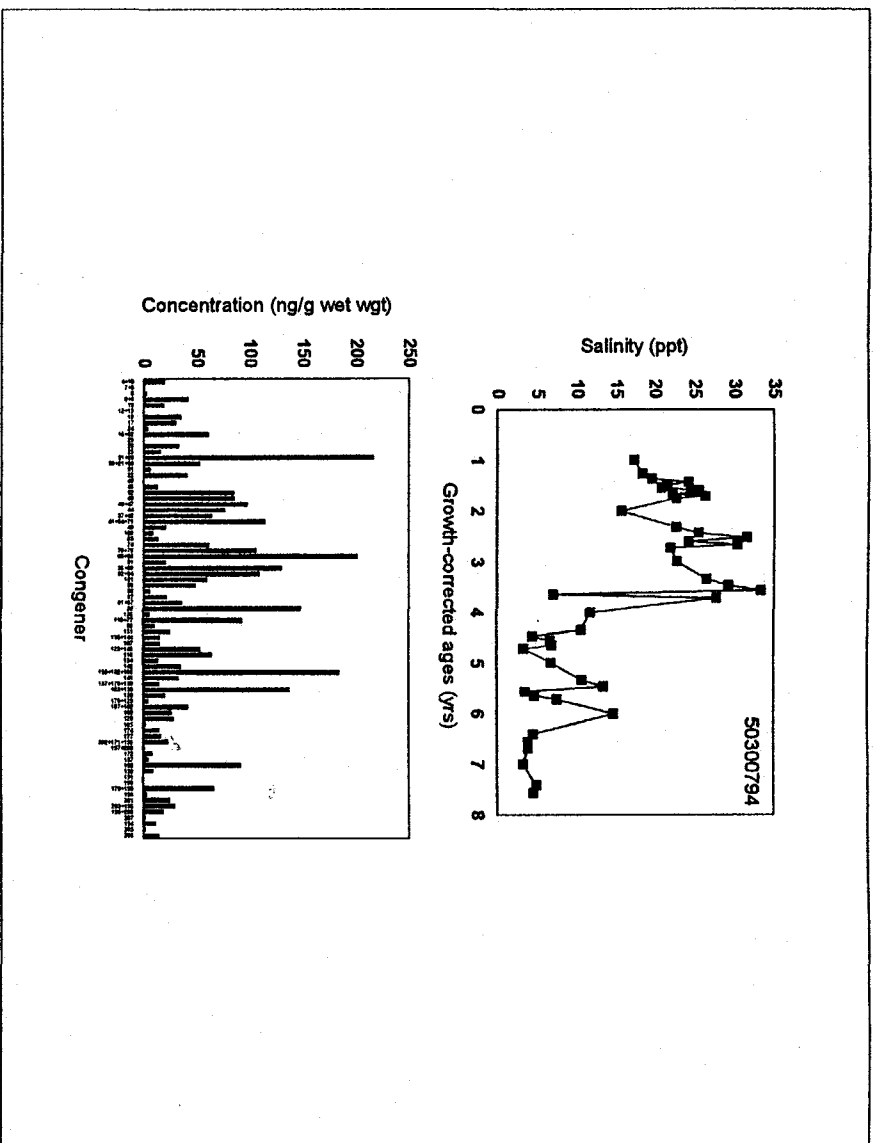
Figure 12. Set of migration trajectories caused by contingent behaviors within a population. See Figure 1 for description of plot. Note that collapse of the panes into an overall framework results in multiple migratory triangles with a single common point at the origin (spawning ground).

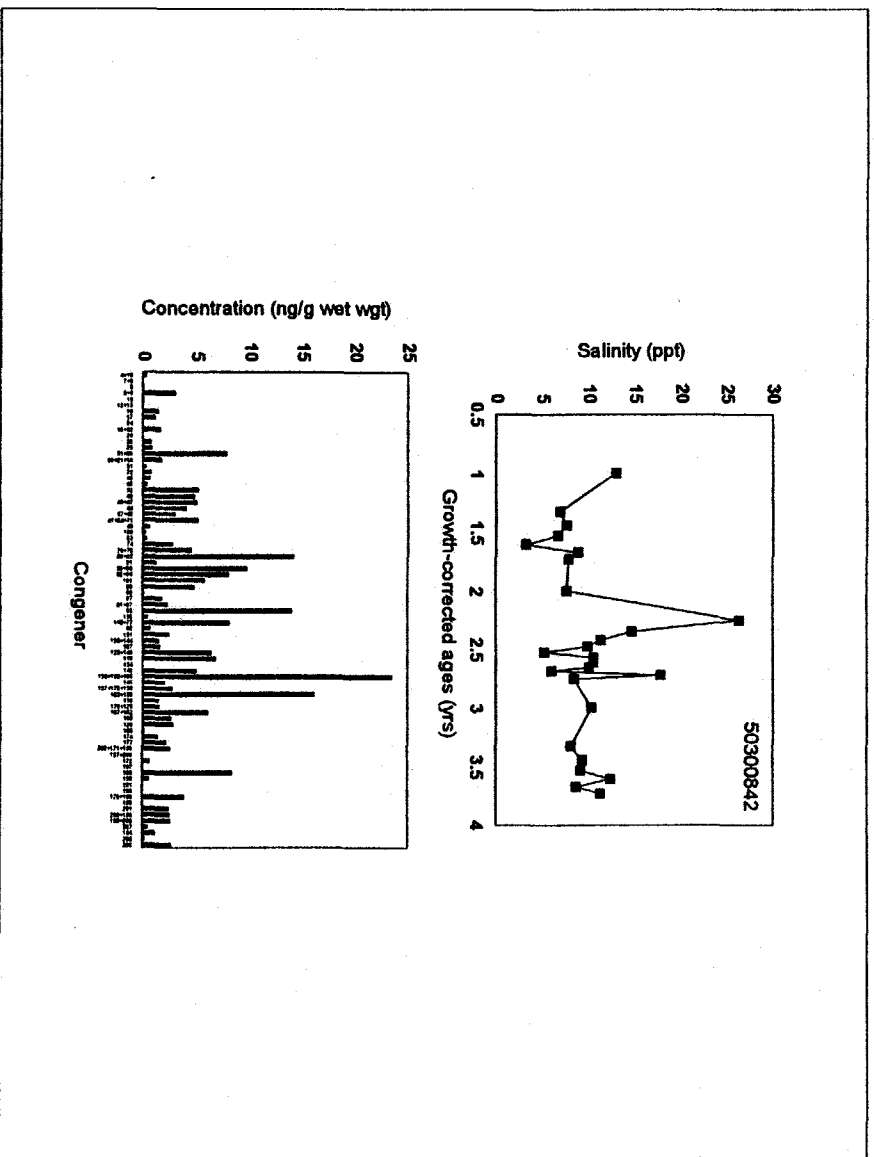
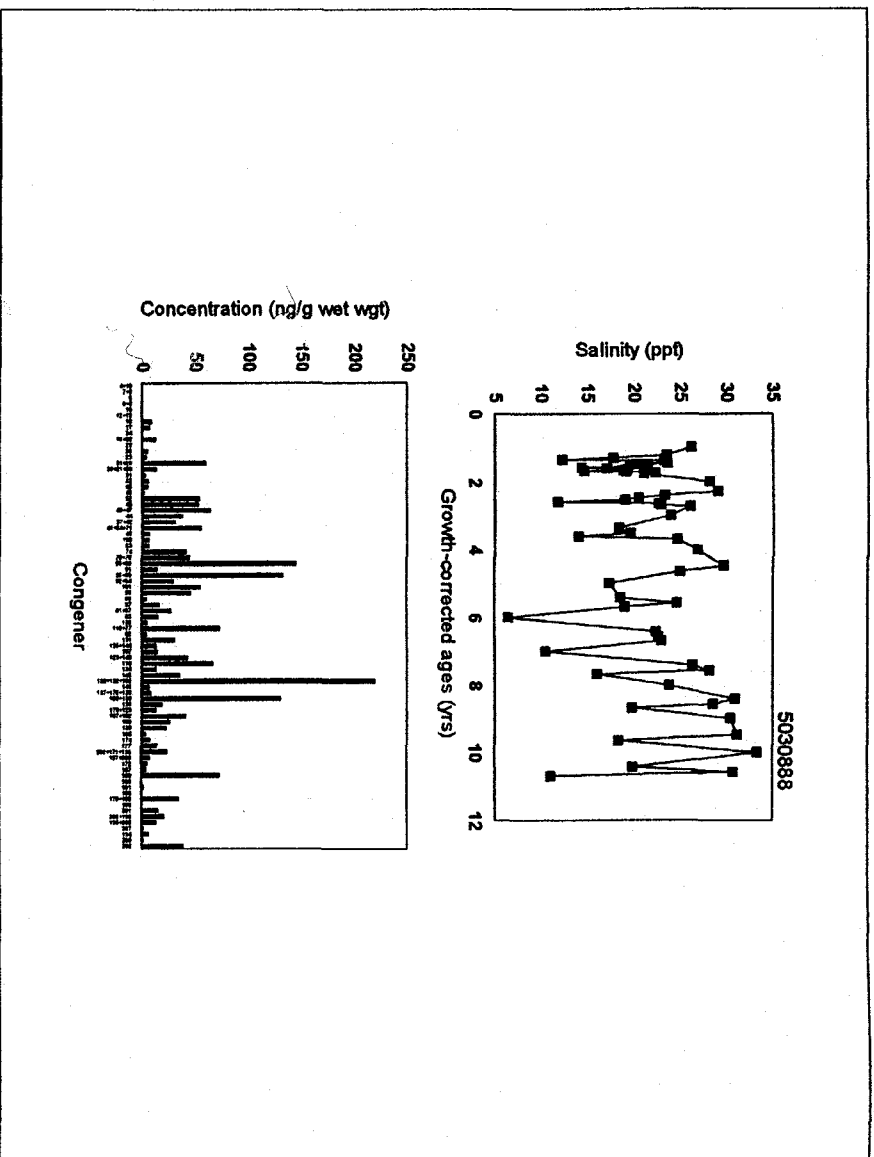
APPENDIX I. **Salinity Chronologies and PCB Congener Profiles for
Hudson River Striped Bass Collected During Fall Season**

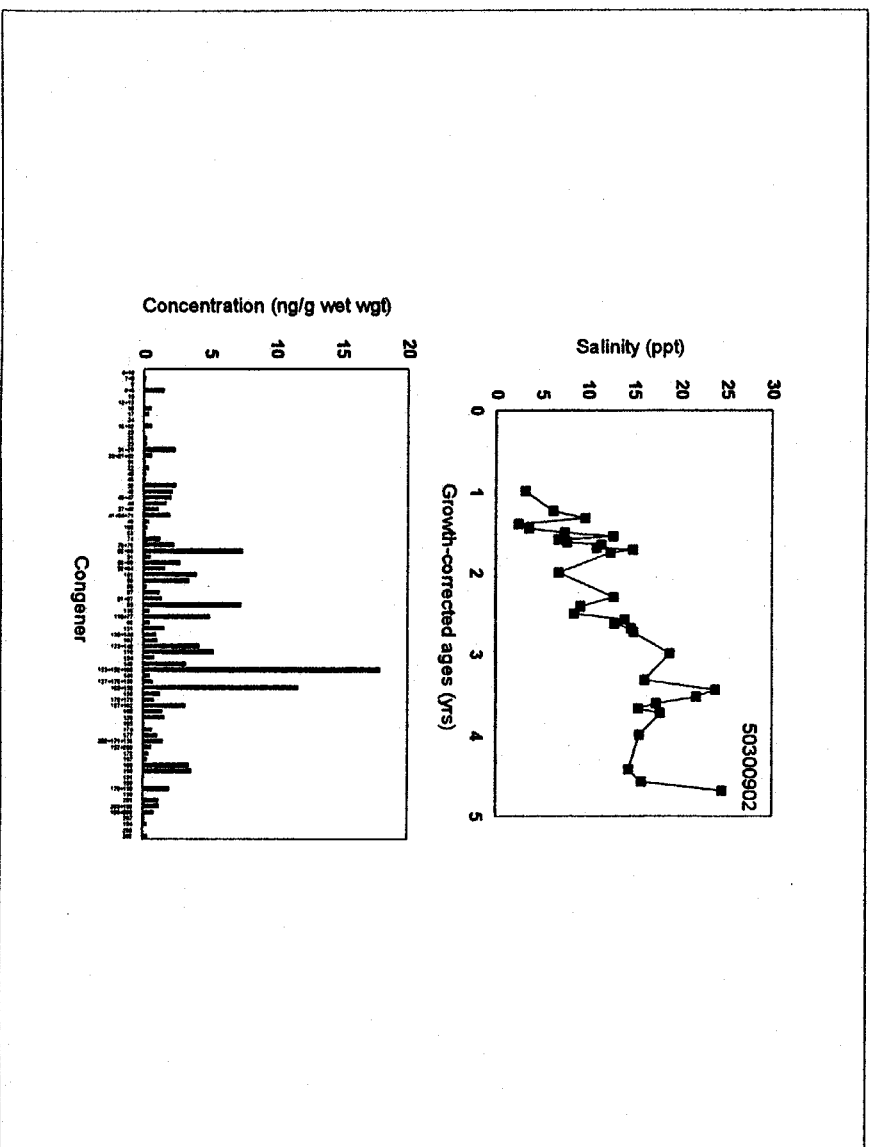
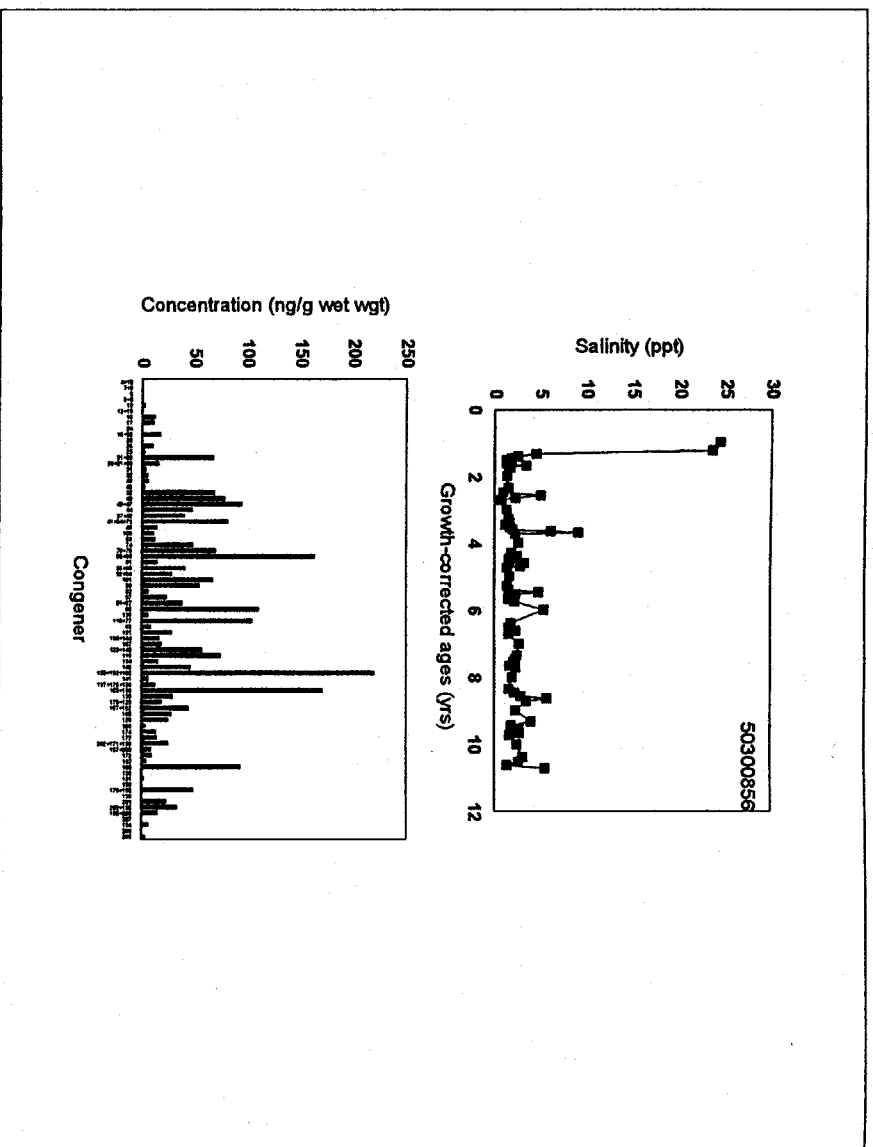


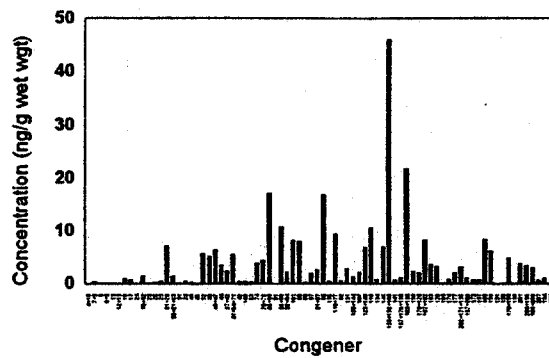
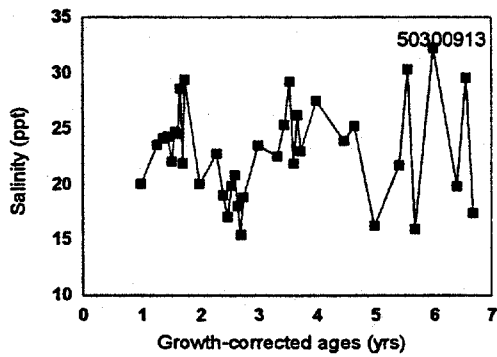
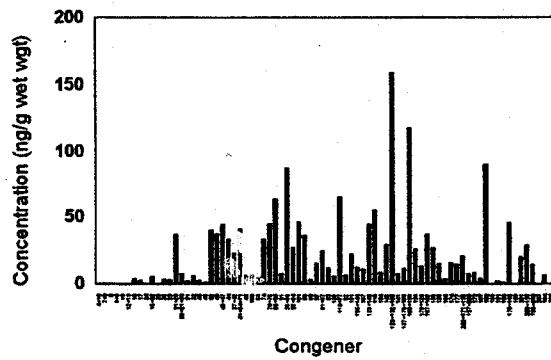
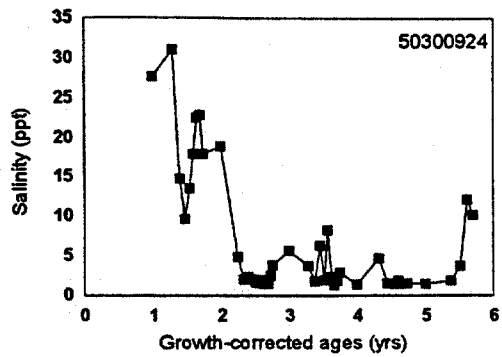


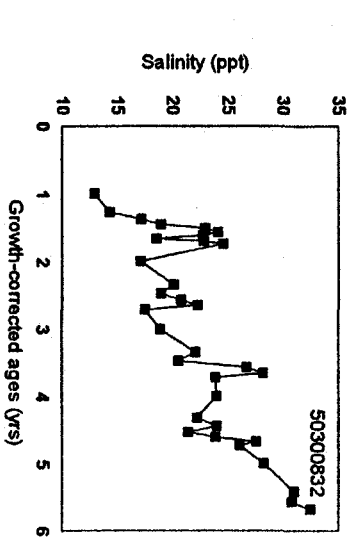
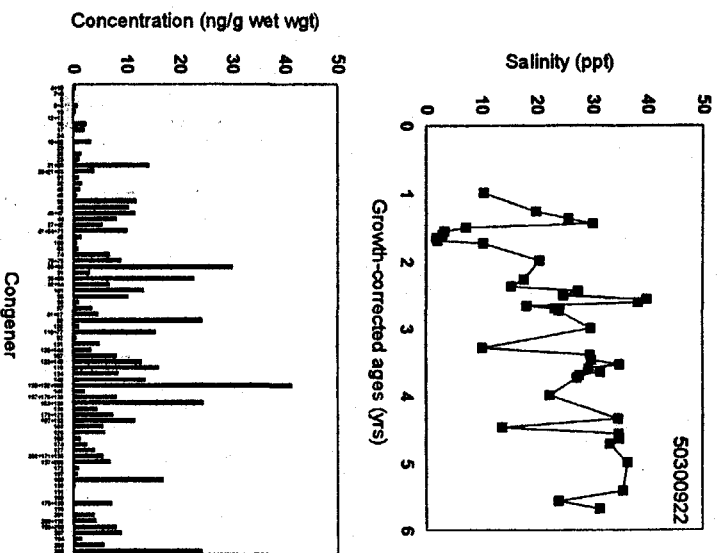


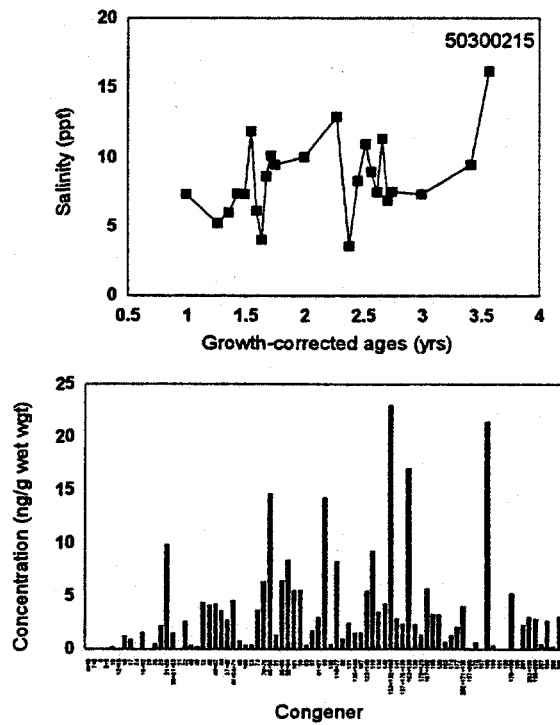
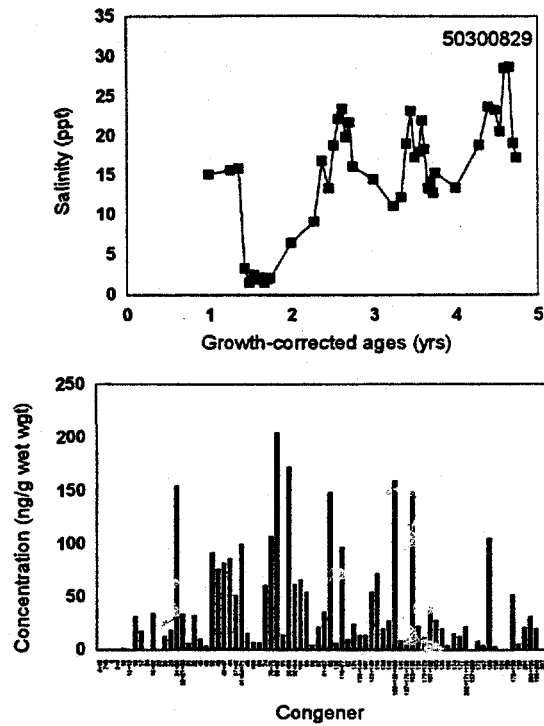


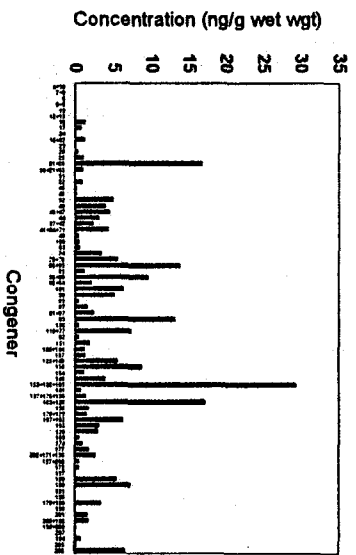
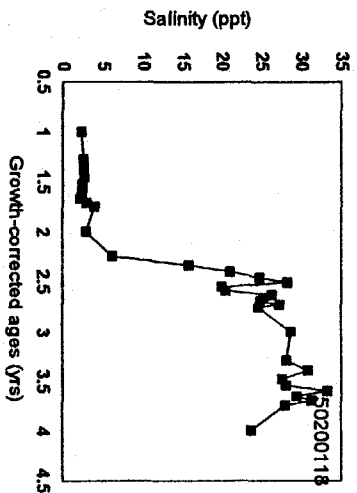
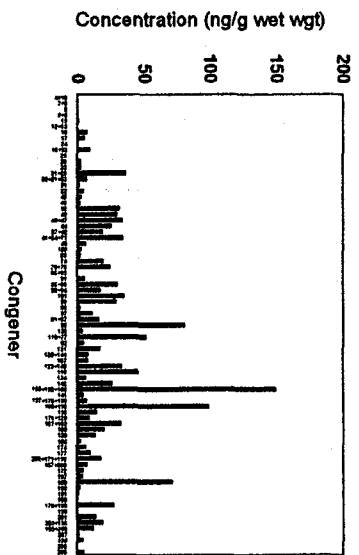
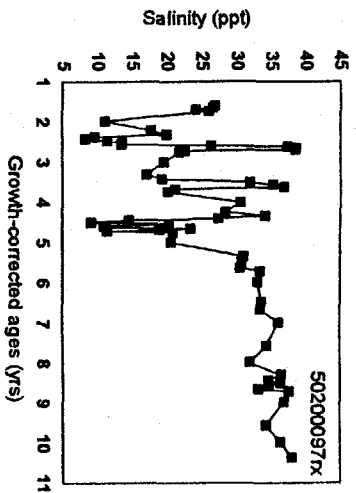


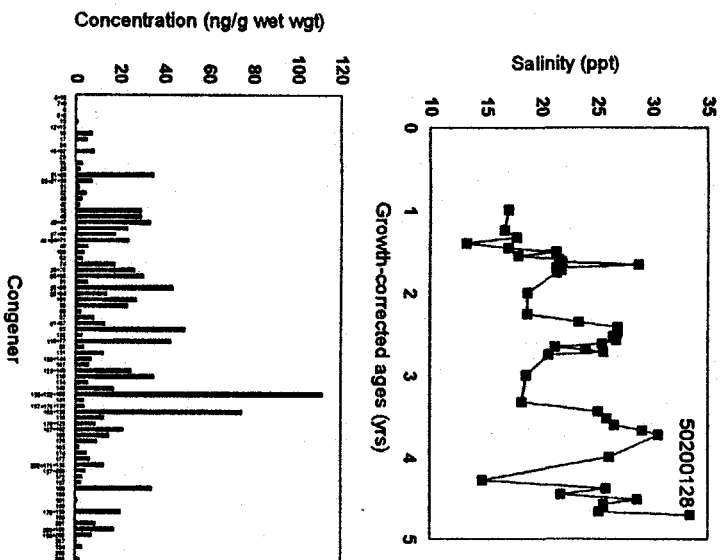
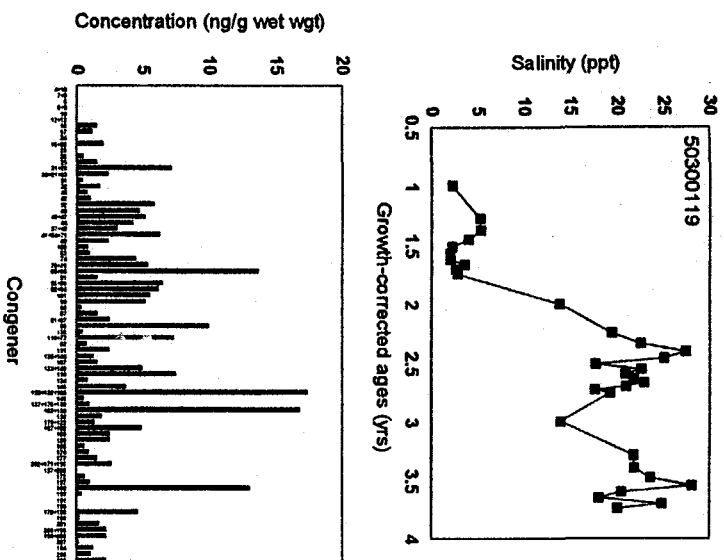


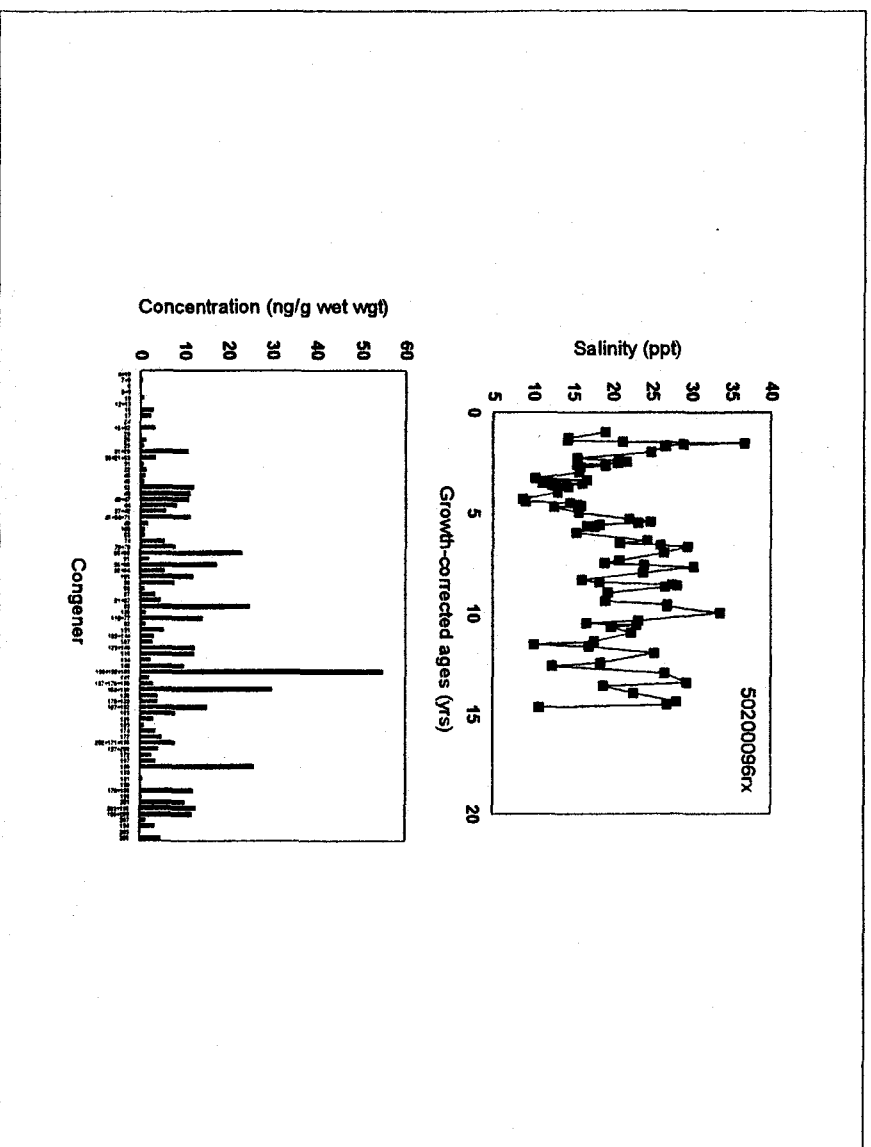
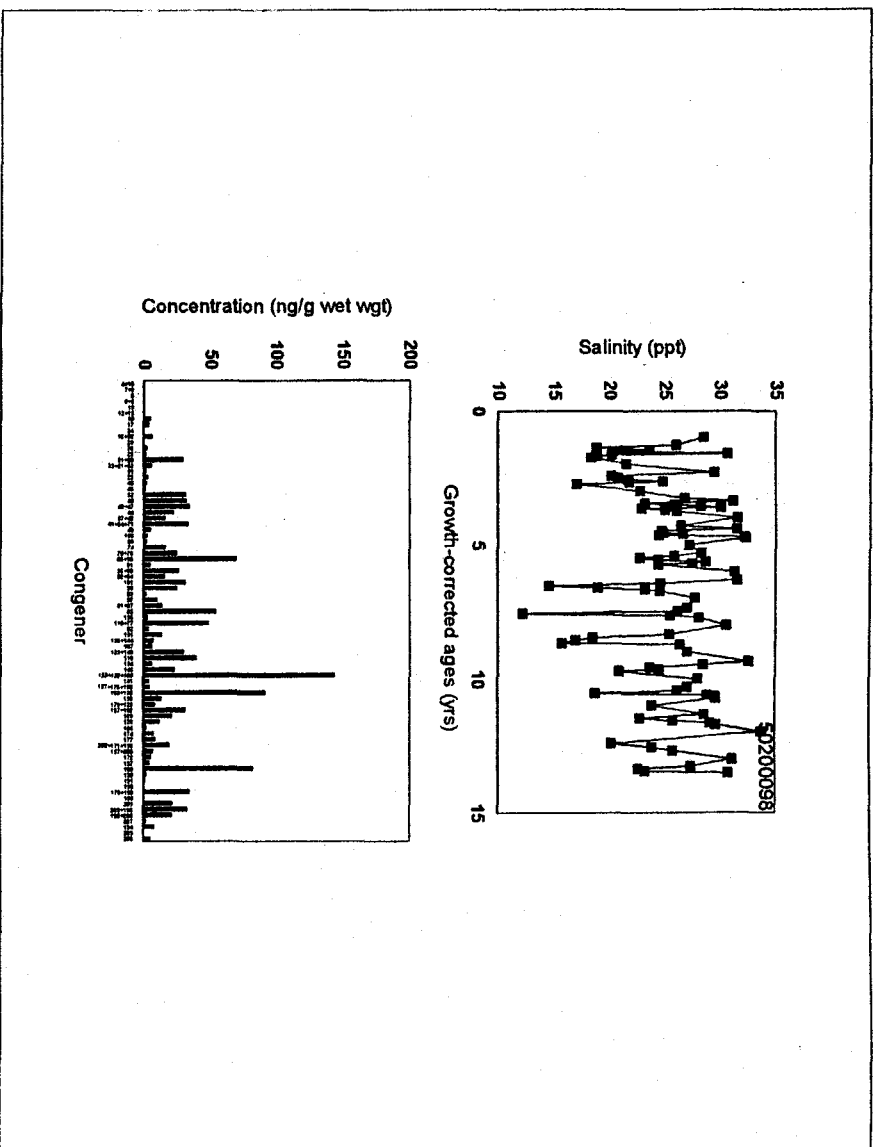


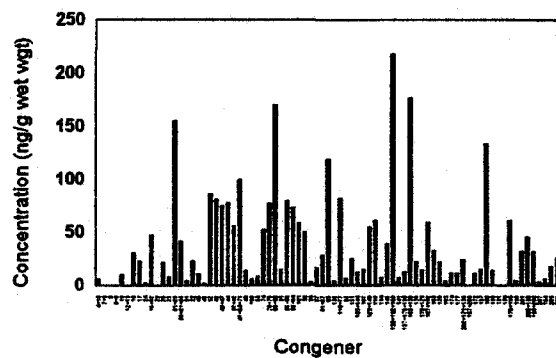
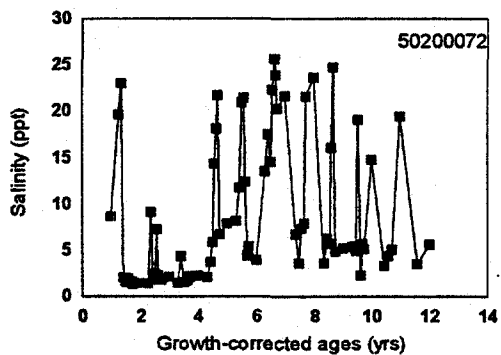
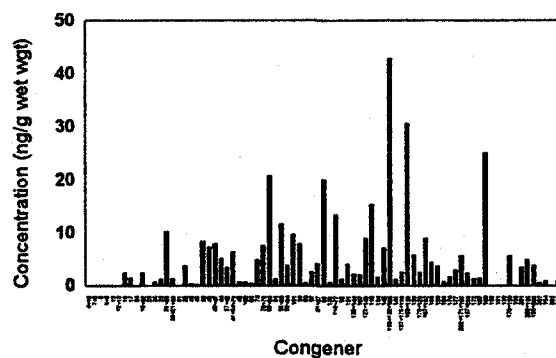
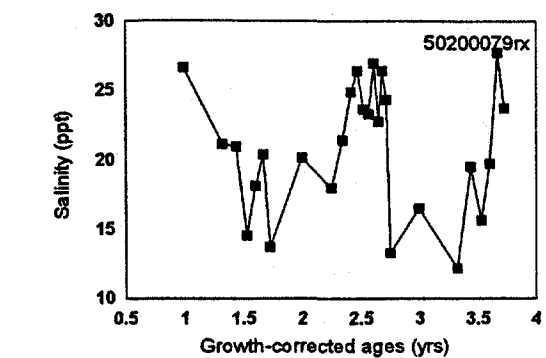


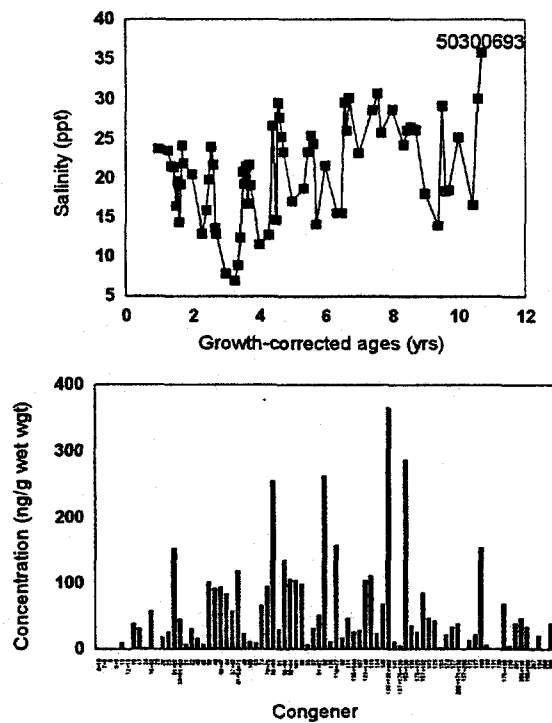
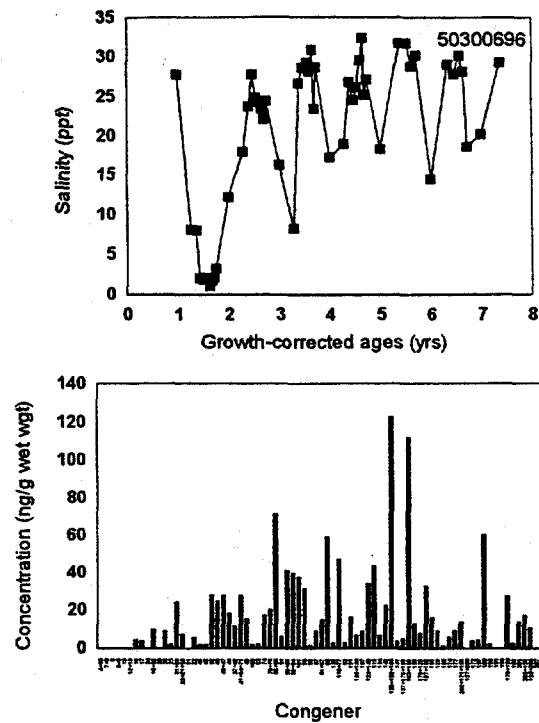


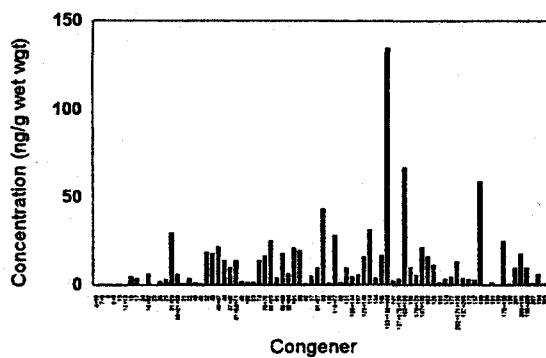
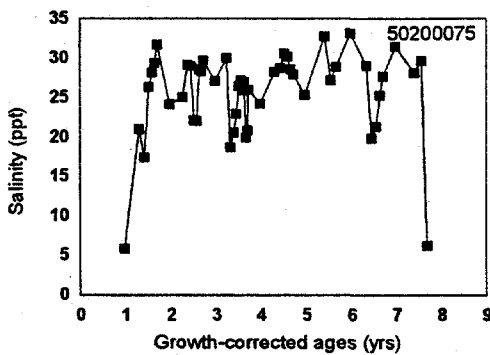
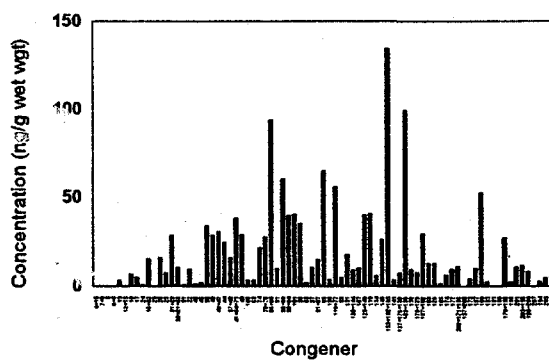
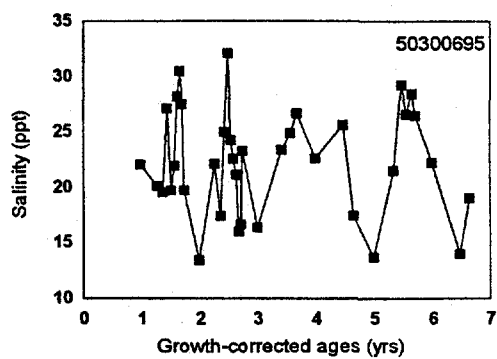


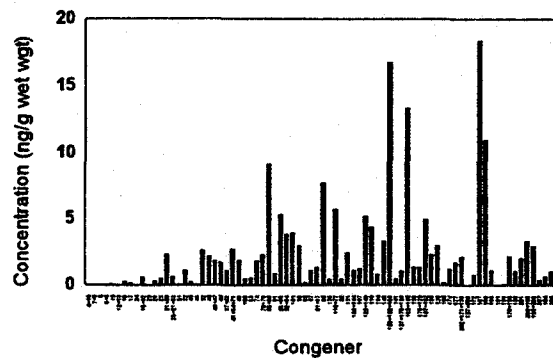
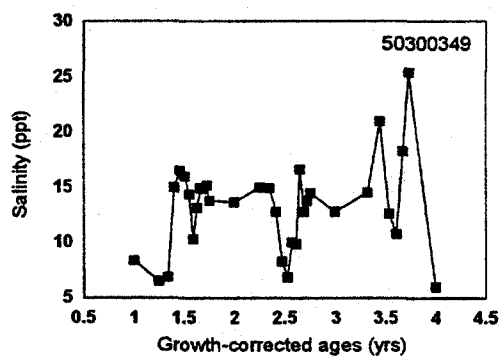
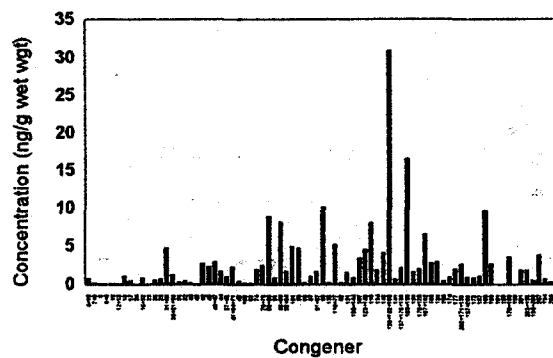
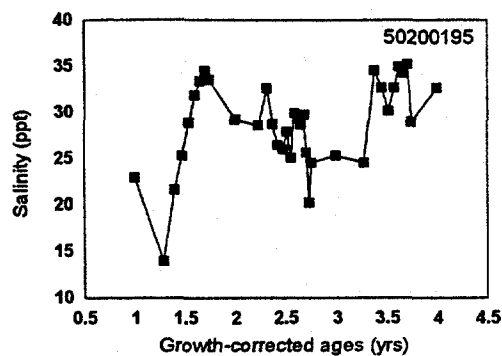


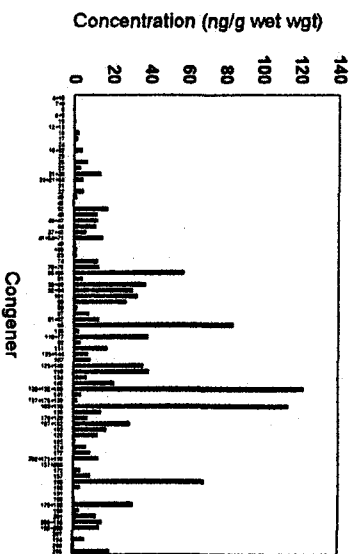
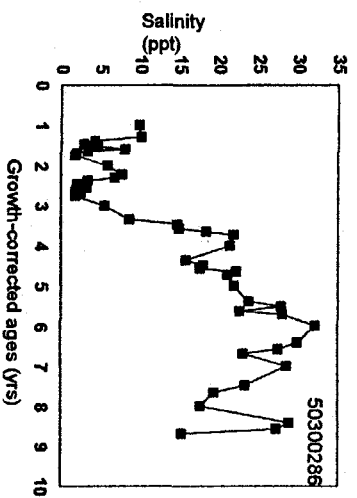
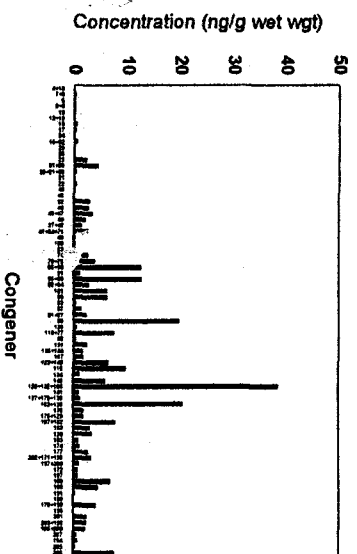
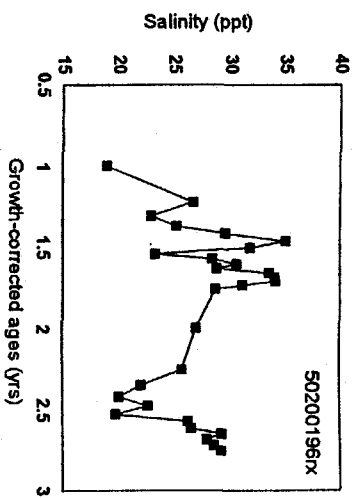


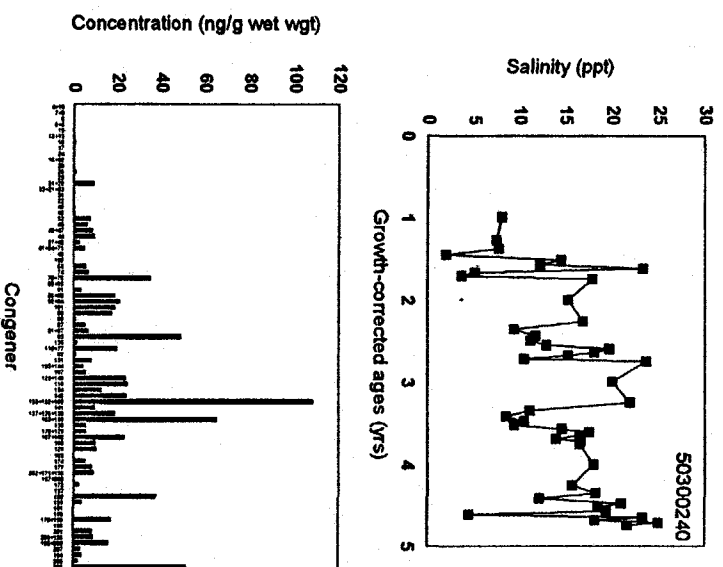
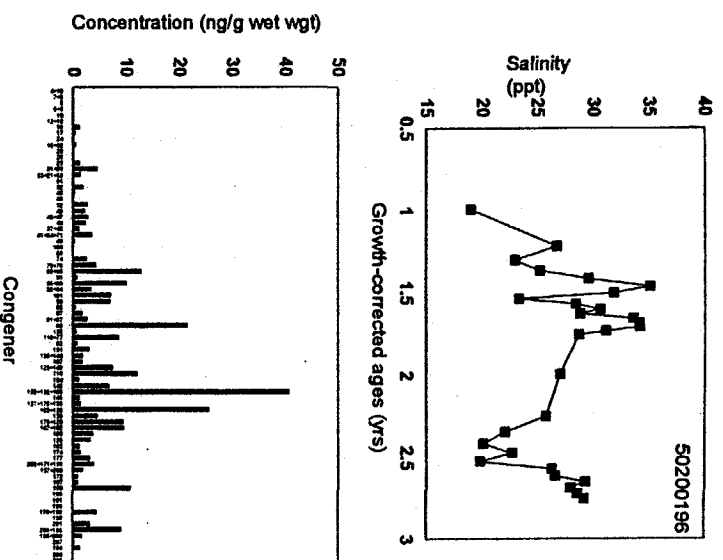


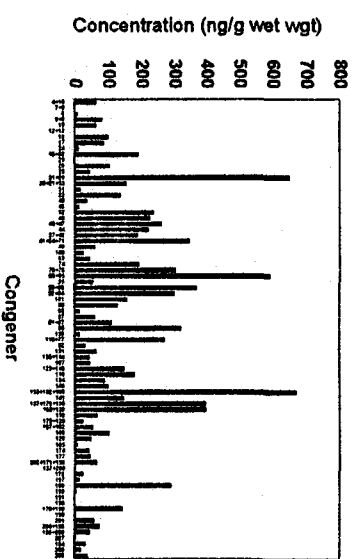
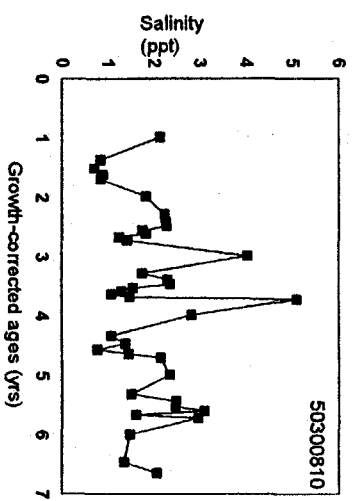
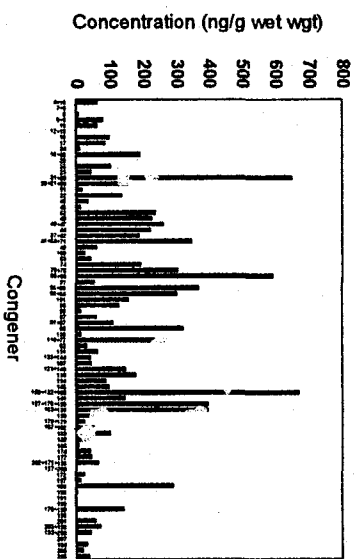
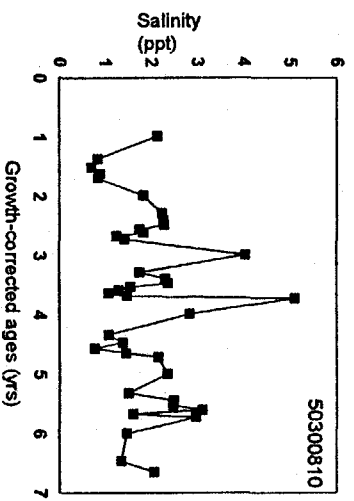












APPENDIX II.

Salinity Chronologies and PCB Congener Profiles for Hudson River Striped Bass Collected During Spring Season

