ABSTRACT

Title of Thesis: MARINE INFLUENCE ON JUVENILE FISH TROPHIC ECOLOGY AND COMMUNITY DYNAMICS IN MARYLAND'S NORTHERN COASTAL LAGOONS

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Marine influence on Maryland's juvenile lagoon fish community was examined under varied levels of internal and external forcing. In 2009, stable isotope analysis showed increasing marine carbon dependency by bay anchovy with decreasing distance to the marine inlet. Following large seagrass losses, no similar trend was detected in 2012. Weakfish showed no structured dependence on marine carbon in either year. Diet contents lacked corresponding year-to-year changes in pelagic versus benthic prey items. In 2009, serial changes with distance to the inlet occurred in species assemblage, which may have been associated with internal seagrass structure. No gradient occurred in 2012. Analysis of a 24-year survey indicated a shift from marine-pelagic to structure-oriented species, associated with increased seagrass and tide level, and decreased North Atlantic Oscillation index. In Maryland's northern lagoon, the strength of marine influence on juvenile assemblages depended on the interplay between internal bay structure and external marine forcing.

MARINE INFLUENCE ON JUVENILE FISH TROPHIC ECOLOGY AND COMMUNITY DYNAMICS IN MARYLAND'S NORTHERN COASTAL LAGOONS

by

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Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Master of Science
2013

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Acknowledgements

I would first like to thank my advisor, Dr. Dave Secor, who, through hard work, mental fortitude, and unending compassion, provided a role model of what a scientist can and should be. I would also like to thank Ryan Woodland, whose insight and curiosity in the workings of fish nurseries formed the basis and impetus of this thesis. Without Dave and Ryan, it is safe to say that I would not have found myself completing a master's thesis at the Chesapeake Biological Laboratory.

I would also like to thank the other members of my committee, Drs. Lora Harris and Mike Wilberg. With suggestions, help, and support always on offer, they helped make any scattered thoughts a coherent whole.

A special "thanks" goes out to the Secor Lab—Ryan Woodland, Chris Conroy, and Ben Gahagan for help with the initial stages of my project, and Matt Siskey and Alex Atkinson for help wrapping it up.

Thank you to Angel Willey from Maryland DNR's Coastal Fisheries Program for patience with my numerous data requests. Thank you to Captain Harold Martin for his expertise and artful piloting of a large boat through the shallow waters of the coastal bays.

Finally, I cannot thank my parents, Mike and Rita O'Brien, and my sister, Bridget O'Brien, enough for their unending support. I find it impossible to put into words the love and sacrifice needed from them in order for me to get to this moment.

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Thesis Overview

Coastal Lagoon Connectivity

Coastal lagoons represent estuaries that are heavily influenced by their connection to marine environments. Estuaries are commonly defined through a combination of three attributes: the presence of tides, the dilution of seawater, and some degree of enclosure; the least restrictive definition of an estuary requires only enclosure (Tagliapietra et al. 2009). Authors disagree as to whether coastal lagoons should be considered estuaries, as the input of freshwater may not be great enough to produce a large gradient in salinity (Kjerfve 1994, Tagliapietra et al. 2009). Others, however, group brackish estuaries and coastal lagoons as "estuarine systems" (Tagliapietra et al. 2009, Elliott and Whitfield 2011), a classification adopted here.

All estuarine systems provide (at least intermittently) a connection to the marine environment (Tagliapietra et al. 2009, Elliott and Whitfield 2011) and possess an intrinsic amount of connectivity. Connectivity describes the rate of exchange of individuals across or between predetermined spatial units or subpopulations (Herzka 2005, Cowen and Sponaugle 2009) and can thus be defined as the degree to which the landscape or seascape facilitates movement among these units (Ray 2005). Should a particular subpopulation possess more individuals than are needed to be self-sustaining, surplus individuals can move into other accepting subpopulations or spatial units. As such, a "source-sink" dynamic is created, wherein one subpopulation provides individuals to another. Similarly, species pools in adjacent regions could exhibit source-sink behaviors based on their relative carrying capacity and the capacity of constituent species to move from one region to another. Coastal lagoons often possess little freshwater input, so most species flow occurs through the corridor connecting the lagoon to the nearshore marine environment. Whereas brackish estuaries possess species gradients across both freshwater-estuarine and estuarine-marine transitions (Wagner and Austin 1999), coastal lagoons principally possess a species gradient across a lagoon-marine gradient (Tagliapietra et al. 2009).

As a result of lagoon-marine connectivity, changes in the marine or lagoonal environment may alter species composition in the alternate habitats. Similar fish assemblages have been found between coastal lagoons and nearshore ocean habitats, indicating that lagoon assemblages are influenced by the recruitment of and resulting influx from the adjacent pool of marine species (Yáñez-Arancibia et al. 1994, Able 2005, Able et al. 2011). Indicators of recruitment and ecosystem health however are limited to measures taken solely within lagoons (Wazniak et al. 2007, Dennison et al. 2009). Should there be a large degree of connectivity between the ocean and coastal lagoons, such indicators are likely influenced by the coastal ocean, leading to a biased assessment of the role of lagoon ecosystem properties on the abundance of living resources.

Maryland Coastal Bays

The Maryland Coastal Bays are a coastal lagoon complex located along the Atlantic coast of the state of Maryland. The system is composed of six separate sub-embayments: Assawoman Bay, St. Martin’s River, and Isle of Wight Bay to the north of Ocean City Inlet and Sinepuxent, Newport, and Chincoteague Bays to the south. The northern sub-embayments have flushing times of 21, 12, and 9 days, respectively, decreasing in duration with proximity to the inlet. The flushing time of the southern subwatersheds are >2 months and are mostly influenced by the Chincoteague inlet (Virginia) (Dennison et al. 2009). This system has seen increasing human population growth over the last 30 years and currently produces ~ $1 billon/yr. in tourism (http://www.mdcoastalbays.org). The internal structure of the bays has changed concurrently with this period, as water quality and seagrass coverage decreased in the first decade, followed by a resurgence of seagrass in the northern bays in the 1990s and rapid decline in 2011. Due to the artificially-maintained Ocean City Inlet, the northern coastal bays also experience anthropogenically-reinforced connectivity with the coastal ocean. This connectivity allows for the constant exchange of water, sediment, and species between the two environments.

Since 1972, the Maryland Department of Natural Resources (MDDNR) has conducted a monthly finfish survey to monitor the health of living resources (Dennison et al. 2009). As in other systems, the distribution and connectivity of juvenile finfish species between the lagoon complex and nearshore ocean remains largely unexplored. A previous analysis of this historical monitoring program indicated that assemblages were structured among the coastal lagoons in a manner dependent upon the lagoon's distance from the inlet (Murphy and Secor 2006). Murphy and Secor suggested that the structure of assemblages was due to species spawning outside of the coastal bays and passively or actively entering through an inlet.

Thesis Objectives

I hypothesize that the nearshore ocean and coastal bays act together as a species "source-sink," with the Ocean City Inlet creating a corridor for species exchange.

Similarly, the lagoon metacommunity framework outlined by Mouillot (2007) suggests that the fish assemblage within a lagoon is part of a larger-scale coastal metacommunity, in which all coastal species are able to permanently or transiently colonize the lagoon. The rate and permanence of colonization depends on species exchange between the lagoon and the larger metacommunity and the quality, number, and diversity of niches within the lagoon. This colonization effect can vary over space and time with changes in habitat quality and species availability. As the structure of the lagoon metacommunity changes, the effect of community alteration can influence trophic, biophysical, and socioeconomic interactions.

This thesis addresses how assemblage structure and food web dependencies vary along the estuarine-marine ecocline of Maryland's northern coastal bays. Targeted trawl sampling of juvenile-stage fishes occurred during August and September 2009 and August 2012 to support (1) trophic analysis of two dominant species *Cynoscion regalis* (weakfish) and *Anchoa mitchilli* (bay anchovy) and (2) assemblage analysis of coastal bay and nearshore fish communities. The shorter-term assemblage analysis was complemented with analysis of MDDNR's long-term finfish survey.

Thesis Structure

Chapter 1 investigates trophic connectance between the nearshore ocean and the Maryland northern coastal bay system between the summer and fall seasons of 2009 and the summer seasons of 2009 and 2012. I hypothesized that separate food web dependencies occurred in representative coastal bay and nearshore juvenile fishes (bay anchovy and weakfish). Further, due to the semi-enclosed nature of the lagoon complex, the carbon source of the fishes would become more pelagic with increasing proximity to the ocean, and that prey items within the coastal bays versus nearshore juveniles would reflect respectively benthic and pelagic food webs. In addition, due in part to the recent collapse of seagrass in the lagoons and beach replenishment in the nearshore, I hypothesized that coastal bay fish in 2012 would reflect a higher dependence on marine prey and carbon sources. Bay anchovy in the Northern bays conformed to some of these expectations, showing increased marine carbon with increased proximity to the inlet and greater homogeneity in carbon sources in 2012 versus 2009. Weakfish did not show the hypothesized carbon-source patterns in either year. Diet data showed differences between habitats, seasons, and years but not in accord with my predictions of benthic versus pelagic food web dependencies. Because the two fish species varied in the degree of spatial isotopic change and displayed no discernable trends in diet items, changes in the trophic landscape and habitat structure of the bays seem to have differential effects according to species.

Chapter 2 examines coastal bay fish community dynamics and their interaction with the nearshore ocean and a suite of environmental drivers. Analyses were conducted at both small and large scales in time and space (months and kilometers, years and whole-bay, respectively). I hypothesized that, due to the connection between the coastal bays and the nearshore ocean, coastal bay assemblage would lack spatial structure and be characterized by marine, pelagic species when marine influence was high or untempered. Conversely, bay assemblage would show spatial structure and a demersal, structure-oriented assemblage when marine influence was low or curtailed. At a small spatial scale, the 2009 coastal bay assemblage was found to change in a serial manner with increasing distance from the nearshore ocean. In 2012, however, a progressive change in assemblage was not found. At a large scale, coastal bay assemblage seemed to experience a wholesale shift to a more structure-oriented in 2007, which may have been triggered by changes in environmental parameters. In addition, increased seagrass coverage during the recent decade was associated with a shift from pelagic, marine to structure-oriented species, suggesting that seagrass may temper the effect of ocean forcing.

Recommendations

With the completion of this thesis, future research directions became apparent. First, spatially-explicit, temporally-dynamic baseline modeling for carbon and nitrogen isotopes within the coastal bays and associated nearshore ocean would be invaluable for future research into the isotopic properties of the coastal lagoon environment. As research using stable isotopes has been conducted within the Maryland coastal bays (Fertig et al. 2009, Fertig et al. 2013) and surrounding nearshore ocean (Woodland and Secor 2011), knowledge of the dynamic properties of common isotopes in time and space can be used to increase the scope of more-focused studies.

Similar to increasing the scope of inference from isotopic analyses, the expansion of the current study from two to several species could more clearly elucidate the trophic properties of the lagoon complex. For instance, macroinvertebrate species such as the blue crab *Callinectes sapidus* and the longfin inshore squid *Doryteuthis pealeii* were common in our samples and support targeted fisheries, but were not considered in this study. Consideration of these species, as well as other finfish species, would provide increased resolution to the trophic analyses conducted in this and other studies.

As this thesis focused solely on Maryland’s northern coastal bays, an expansion into the southern bays would be a worthwhile exercise. Sinepuxent Bay, a small bay connecting the Chincoteague Bay in the south to the Ocean City Inlet in the north, could be similarly investigated for variable trophic dynamics and spatially-explicit assemblage structure. A similar, more lateral expansion of sampling within the northern coastal bays to include associated seagrass beds would be useful to more-directly assess the impact of these habitats on lagoon assemblage and trophic dynamics. In fact, the Coastal Bays Fisheries Investigation has recently added within-seagrass bed sites to their monthly surveys (MDDNR, personal communication).

As the influence of adjacent environments, species exchange, and food web dynamics are further investigated within Maryland’s coastal lagoon complex, management of the coastal bay system can become more efficient, targeted, and effective. It is my hope that this thesis adds to the growing literature explaining the intricacies of Maryland’s coastal living resources.

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Chapter 1: Trophic connectance between the coastal ocean and Maryland's northern coastal lagoons as exhibited by two fish species

Introduction

The role of tidal lagoons as fish nurseries depends on their internal dynamics and exchange with adjacent nearshore marine habitats. Like most coastal water bodies, lagoons are strongly influenced in geomorphology, water chemistry, and nutrient flow by their connection to associated watersheds and marine environments, but marine influences typically dominate over watershed effects (Kjerfve 1994). Fish living within coastal lagoons are affected by species flux and nutrient exchanges from marine sources, as well as production internal to the lagoon. Similarly, fish living in nearshore marine environments adjacent to lagoonal nutrient pools may be influenced, in part, by trophic exports from the lagoon environment. The extent to which estuarine fish, including those from lagoons, act as nutrient vectors into the surrounding marine environment has been studied (Deegan 1993, Mouillot et al. 2000, Miranda et al. 2005). However, the influence of the marine environment on the trophic ecology of lagoon fish has received less attention.

During the first year of life, many coastal marine fish species develop within sheltered, productive areas that provide high prey abundance and adequate water quality before recruiting to the adult population (Dahlgren et al. 2006). Coastal lagoons are considered "nursery" habitats for this reason, as the increased productivity and shelter found within shallow lagoons afford increased growth and predation refugia for juvenile fishes (Beck et al. 2001, Ray 2005). Often, lagoons are well-surveyed due to their recognized role in the recruitment of commercial and recreational fish species (Dahlgren et al. 2006, Chícharo et al. 2012). The nearshore ocean (<10 m depth) has also been recognized as providing nursery habitat (Able 2005) and recent studies have shown that larval and juvenile fish assemblages occupying estuaries are often similar to those found in the nearshore and surf zone ocean (Able et al. 2011). However, due to a historical assumption that estuaries and lagoons provide principal nursery systems, this region has been understudied.

The nursery value and structure of nearshore ocean and coastal lagoon habitats are often influenced by human activities (Mellbrand et al. 2011, Chícharo et al. 2012). As human development associated with a coastal lagoon increases, physical, chemical, and biological connections between the lagoon and the coastal ocean are often reinforced. Using the example of the Ria de Aviero complex in Portugal, Duck and da Silva (2012) noted that as the human population of the area grew, the once-ephemeral ocean inlets became permanent fixtures maintained by the surrounding community. As ocean connections were reinforced, tidal action increased within the lagoon, and lagoon sediments transitioned from organically-active mud to organically-inactive sand. Other studies have noted that similar transitions are marked with physical homogenization and a shift away from benthic-oriented food webs (Silva et al. 2004) within the affected lagoon. In other words, reinforced coastal lagoons become increasingly similar to the adjacent marine environment in both physiochemical structure and food web composition.

The loss of natural physical and biotic structure and associated niches can lead to homogenization of lagoon habitats. When compared to marine systems, coastal lagoon food webs are more-strongly driven by benthic production arising from macroalgae, benthic microalgae, and seagrasses (Joyeux and Ward 1998, Nixon et al. 2001). The relative level of benthic dominance over pelagic production, however, often depends on the system being investigated, with more-closed systems often dominated by benthic production and more-open systems dominated by pelagic production (Pérez-Ruzafa and Marcos 2012). The strength of marine influence, then, may control the balance between autochthonous benthic and allochthonous pelagic production within the lagoon (Duck and da Silva 2012). In systems where a shift from benthic to pelagic primary production has occurred, a corresponding shift in nutrient availability and trophic pathways to consumers is expected (McGlathery et al. 2007, Hardison et al. 2010). Differences in the proportion of benthic versus pelagic prey in juvenile fish diets can in turn have consequences on the growth and production of juvenile fish communities (Woodland and Secor 2011).

Food webs of both the nearshore ocean and coastal bays are differentially influenced by dynamic anthropogenic and natural pressures (Chapman 2012), which influences the physical and nutrient exchange between the systems. These exchanges can be assessed using carbon and nitrogen stable isotopes to study the feeding history of consumers in both time and space (Lajtha and Michener 1994, Herzka 2005, Fry 2006). The processes of C3, C4, and CAM carbon fixation, as well as fractionation due to trophic enrichment, cause variation in the proportion of heavy (^{13}C) to light (^{12}C) carbon isotopes found in food items (Tieszen et al. 1983) (The ratio of the heavier to lighter isotope takes the notation $\delta^{13}C$, see Methods). In addition, variation in metabolic activity between tissues can permit investigation of dietary history over multiple timescales for an individual consumer and provide a source of redundancy for isotopic information. The high metabolic activity of liver tissue, for instance, causes isotopes to reflect more-recent dietary patterns than muscle tissue, which is less metabolically active than liver. In fish species, these relationships have been used to investigate trophic dependency on certain types of food webs, diet shifts, larval settlement, migration, residency, growth, condition, and habitat use (Herzka and Holt 2000, Herzka et al. 2001, Church et al. 2009, Woodland et al. 2012a).

As carbon fractionation between prey and consumer is often minimal (Pinnegar and Polunin 1999), the $\delta^{13}C$ of a selected tissue can be used to infer the source of carbon in an organism's diet (in this study, ocean or lagoon; and benthic or pelagic). Most ocean carbon isotope values arise from an phytoplankton-based trophic system, which is enriched in the heavy isotope when compared to other systems (Fry 2006). Due to C_3-plant derived organic carbon in lagoons, a lagoonal carbon source is depleted in ^{13}C when compared to an ocean source. Because of this, increasingly positive $\delta^{13}C$ values with increasing proximity to the ocean has been observed in several estuarine systems (Litvin and Weinstein 2004, Suzuki et al. 2008a, Suzuki et al. 2008b, Woodland et al. 2012a). Due to isotopic mixing, compound-specific fractionation, and other processes which cause variation in the isotopic makeup of tissues, isotopic analysis alone may be misleading. As such, direct diet analyses, where prey items are removed from the gut, identified, and quantified through assorted metrics, are often utilized to complement the results of stable isotope analyses (Fry 2006, Suzuki et al. 2008b, Woodland and Secor 2011).

Maryland's northern coastal bays are a system of coastal lagoons perennially connected to the nearshore ocean through an artificially reinforced inlet (Fig. 1.1). The Ocean City inlet was opened during a hurricane in 1933 and has since been maintained via dredging and shoreline restructuring by the US Army Corps of Engineers (USACE

1998). Tidal currents through the inlet (often 1.8 m/s, Schwartz (1964)) cause significant exchange of water and species between the ocean and Northern bays, with the southernmost Isle of Wight bay possessing a residence time of 9.5 days (Murphy and Secor 2006, Love et al. 2009). There has been a recent history of perturbation within the Northern bays, including a collapse of lagoon seagrass in 2011 (Orth et al. 2012) and periodic 4-year beach replenishment on the ocean side of Fenwick Island, the most recent in 2011 (USACE 1998). Similar to the Ria de Aviero complex (Duck and da Silva 2012), the reduction of seagrass within the coastal bays and increase of mobile sand influx through the Ocean City inlet from the nearshore ocean could accelerate a shift from benthic to pelagic food webs within the lagoons.

To investigate the degree of trophic connectance between nearshore ocean and coastal bay environments through the Ocean City inlet, I used stable isotope and gut content analyses to characterize the diet across time and space of two species that occur in both nearshore and lagoon habitats. Weakfish (*Cynoscion regalis*) and bay anchovy (*Anchoa mitchilli*) were chosen for this study, because the species are ubiquitous in both environments and represent different trophic levels (TL = 4 and 3) and food webs (demersal versus pelagic). These target species were sampled during summer and fall 2009 and summer 2012. A summer 2009 v. summer 2012 comparison was made specific to the lagoon environment to test for the generality of trophic ecology between years. Comparisons in trophic ecology were made (1) across years within the coastal bays; and in 2009, (2) across seasons separately for each habitat, and (3) across habitats separately for summer and fall seasons.

I hypothesized that, due to a spatial shift from benthic, autochthonous carbon to pelagic, allochthonous carbon with increasing proximity to the ocean, $\delta^{13}C$ values of fish tissue would increase from the most inshore coastal bays to nearshore ocean within both seasons of 2009. Both muscle and liver tissue were analyzed to measure carbon dependency during the 1-2 months (muscle) and 1-2 weeks (liver) (Herzka 2005) prior to sampling. I further hypothesized that prey items consumed by fish within the coastal bays should be more reflective of benthic-oriented food webs than those from the ocean. In 2012, I hypothesized a change in trophic dependence by coastal bay fish, due in part to the 2011 collapse of seagrass. In this year, under increased marine influence, the spatial trend in $\delta^{13}C$ and diet should be absent, representing a more-homogeneous environment, with increased influence of allochthonous, pelagic-based carbon and a decrease of benthic prey species.

Methods

Field sampling was completed in August (summer) and September (fall) 2009, and August (summer) 2012. Although separated by only a month, sampling was designated as occurring during separate seasons, as August represents the summer period of lagoon residence and growth, and fall (beginning in September) represents a period of species turnover where many juveniles initiate a fall egress from lagoon nursery habitats (Able and Fahay 1998). A 7-m benthic balloon trawl (3.8 cm body mesh, 0.64 cm mesh cod-end liner) was towed for 6 minutes (approx. 0.5 km) in north-south transects at each site to target juvenile fish within the Maryland coastal bay-nearshore ocean complex. The coastal bays and associated nearshore ocean were sampled according to a stratified random sampling design, with sites randomly selected from a pre-established grid of sampling sites within discrete strata (Fig. 1.1a). Twelve sites were sampled in the nearshore marine zone (8-15 m depth) during each season in 2009, with four sites randomly selected from each of three strata (Fig. 1.1b,c). Seven sites were sampled in the northern coastal bay complex (<2 m depth) in summer 2009, nine sites were sampled in fall 2009, and nine sites were sampled in summer 2012 (approximately 3 per lagoon strata, Fig. 1.1b,c,d). Three sites associated with the Ocean City Inlet (2-5 m depth) were sampled in summer 2009 and five sites were sampled in fall 2009 (Fig. 1.1b,c). Young-of-year weakfish (*Cynoscion regalis*) and bay anchovy (*Anchoa mitchilli*) were immediately frozen under dry ice and held in a -20°C freezer until processing. Catch of each species were compared across habitats on both a per-site and per-strata basis.

Stomachs were removed from partially thawed specimens and placed in ethanol in preparation for direct diet analysis. After allowing at least 24 hours for the preservation of prey tissue, stomachs were dissected and prey items removed. Prey items were identified to the lowest taxon possible, enumerated, air-dried, and weighed to the nearest hundredth of a mg (10^{-5} g). According to a pre-determined inclusion rule, prey items making up less than 3% of total items, weight, or occurrence within at least one month-stratum combination were joined into higher taxonomic levels or functional groups until the 3% threshold was met. Immediately after removal of the stomach, the liver and dorsal white musculature were excised using separate sets of ethanol-rinsed surgical scalpels and tweezers. All muscle tissue was cleaned of residual intramuscular bones. Tissue was rinsed in de-ionized water and held at 60°C for >48 hours or until dry. Dry tissue was ground into a fine powder using a mortar and pestle, and 0.2-1.2 mg was stored in tin capsules until stable isotope analysis.

Due to frequent variations in the isotopic values of primary producers (Cabana and Rasmussen 1996, Post 2002), the baseline isotopic value of coastal bay and nearshore habitats were represented by concurrently-collected primary consumers. As fleshy primary consumers have slower tissue turnover rates than primary producers, the isotopic values of their tissues often reflect the average, integrated isotopic value of the system (Post 2002, Woodland et al. 2012a). The ribbed mussel, *Geukensia demissa*, and the blue mussel, *Mytilus edulis*, were collected from one bay and one ocean location, respectively. The average isotopic value of the mussels was assumed to represent the isotopic value of their respective systems.

Tissue samples of fish and bivalve specimens were analyzed for carbon and nitrogen isotopic ratio using a continuous-flow isotope ratio mass spectrometer at the Colorado Plateau Stable Isotope Laboratory in Flagstaff, Arizona. Measured ^{13}C was reported in the delta notation relative to Vienna Pee-Dee Belemnite and air standards, respectively. Delta notation is represented as follows, where X represents the heavy isotope species and R represents the ratio of heavy to light isotope in the sample or standard:

$$\delta X = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

Due to fractionation during acetyl-CoA formation by pyruvate dehydrogenase in lipid synthesis, high lipid-content tissues can appear depleted in the heavy carbon isotope (Deniro and Epstein 1977). Because of this, many studies opt to extract lipids from sample tissue prior to isotopic analysis (Smyntek et al. 2007, Buchheister and Latour

2010). However, if lipid content within the tissue is low, variation introduced by the process of lipid extraction is often greater than the isotopic correction gained (Mintenbeck et al. 2008). The ratio of atomic carbon to nitrogen (C:N) within the sample is often used as a proxy for lipid content, and a cut-off of C:N ~4 is commonly used to guide the need for lipid extraction (McConnaughey and McRoy 1979, Kiljunen et al. 2006), with extraction necessary at higher values (>10) and suggested at intermediate values (5-10). As the C:N ratio of coastal bay and nearshore samples was low (<4.5) for both tissues in both species, lipid extraction and subsequent correction was not conducted.

An important source of bias in using stable isotope ratios to infer trophic dependency is constancy in isotopic baselines used to represent food webs. As the dissolved organic carbon (DIC) pool is reduced with seasonal growth of primary producers, algae exhibit less discrimination against the heavy carbon isotope (Woodland et al. 2012a). Because of this, the $\delta^{13}C$ values of primary producers within temperate systems tend to increase throughout the spring and early summer, peak in the late summer and early fall, and decrease through the winter as the DIC pool is renewed through algal death. This seasonal oscillation has been shown to propagate to higher trophic levels, with tissue growth and turnover times of target species determining the level bias. If the food web baseline changes at a rate greater than consumer tissue turnover, the consumer's isotopic values will be biased and unstable, reflecting the of seasonal baseline change (Woodland et al. 2012b). To assess this level of bias, I compared seasonal baseline changes to consumer tissue turnover rate.

The most common model describing the progress of isotopic turnover, developed by Hesslein et al. (1993), represents the proportion of heavy isotope within tissues as decaying exponentially via a combination of isotopic dilution through growth (represented by the instantaneous growth rate, G) and removal through metabolic processes (a fitted parameter, M).

$$\delta X_t = \delta X_\infty + (\delta X_0 - \delta X_\infty)e^{-(G+M)t}$$

Due to an overwhelmingly large instantaneous growth rate, the rate of removal through metabolic processes can be considered negligible in fast-growing life stages such as the juvenile fish in this study (Herzka 2005). As such, the instantaneous growth rate of the target species between two periods was assumed to reflect the concurrent rate of isotopic change.

The monthly instantaneous growth rate (*G*) for each fish species was calculated for the period concurrent with and previous to sampling (i.e., July, August, and September) in 2009, 2011, and 2012. *G* was calculated using bay anchovy and weakfish lengths from the Maryland Department of Natural Resources' Coastal Bay Fisheries Investigation survey (Capossela et al. 2010). Lengths were converted to weight using the following equation:

$$W = aL^b$$

with *a* and *b* taken from the per-species fitted length-weight relationship of this survey. The instantaneous growth rate was then calculated using the following:

$$G = \frac{\ln\left(\frac{W_{t+n}}{W_t}\right)}{n}$$

where W_t is mean average weight in month t and W_{t+n} is mean weight in month $t+n$. For the baseline bivalves, the instantaneous rate of isotopic change was calculated as the slope of the line between the respective mean isotopic values of two months within each year.

To determine whether correction of fish tissue isotopic values was necessary, the absolute values of the instantaneous growth rate of the sampled fish and the instantaneous isotopic change rate of the baseline bivalves were compared. I assumed that if the instantaneous rate of change was greater in fish tissue than in the environment (as represented by bivalves), then changes in the environment would occur too slowly to bias the results of isotopic analyses of bay anchovy and weakfish. A model simulation supported this assumption for periods up to 30 days (see Appendix).

Prior to conducting statistical analyses, values for individual fish were averaged within each haul to avoid pseudoreplication. Overall contrasts of $\delta^{13}C$ between years, seasons, habitat types, and tissues were conducted using Student's t-tests where significant spatial trends were not detected. An ANCOVA with a distance-from-inlet covariate was used where a significant spatial trend was detected. The significance level was corrected for multiple tests using the Bonferroni method (Sokal and Rohlf 1995).

Results

Abundance Trends

The spatial distribution of bay anchovy varied across both season (summer/fall) and year (2009/2012). In summer 2009, most anchovy catch occurred within the coastal bays (Fig. 1.2). The highest catch of bay anchovy (often >1000 individuals) occurred within Isle of Wight Bay, with intermediate catch (10-25 individuals) within Assawoman Bay. Within the nearshore ocean, however, the largest catches of anchovy occurred in the sites farthest from the Ocean City Inlet. In fall 2009, the distribution of anchovy shifted to the northern Assawoman bay in the coastal bays and the most northern and southern array in the nearshore ocean. Anchovy catch in the fall was patchier than the summer, with frequent catches of both 0 and >1000 individuals. Comparing summers between 2009 and 2012, both years had relatively evenly-distributed catch throughout the bays, often exceeding 1000 individuals (Fig. 1.3). Spatial patterns of anchovy catch were consistent between years, with the highest catches found in the Isle of Wight Bay.

The highest catches of weakfish in both seasons of 2009 occurred in the nearshore ocean. While weakfish catch in summer 2009 was low and evenly-distributed throughout the coastal bays (Fig. 1.4), all but two coastal bay hauls in fall 2009 contained no weakfish. Conversely, an evenly-dispersed spatial distribution and similar numbers of weakfish were found in summer and fall of 2009 in the nearshore ocean. Weakfish catch and distribution differed between years within the summer season. Whereas catch was evenly-distributed throughout the bays in 2009, weakfish were mostly found at the extreme northern and southern ends of the bay system in 2012, with little or no weakfish catch at intervening sites (Fig. 1.5).

Isotopic Turnover

Monthly instantaneous rates of growth were greater than, or comparable to, changes in the baseline (Table 1.1). The instantaneous growth rates and baseline changes noted in Table 1.1 result in differences of less than 0.15‰ between fish and the baseline environment over the course of a 30 day simulation (see Appendix). On an extreme scale, using the lowest positive fish growth rate recorded in conjunction with the highest baseline change recorded resulted in a difference of 0.42‰. In this case, results may be biased toward earlier isotopic conditions, but this exercise indicated that tissue $\delta^{13}C$ values were unaffected by or reflective of concurrently sampled baseline bivalves.

Two instantaneous growth rates, those of weakfish in August-to-September period of 2009 and 2011, were negative, suggesting that instantaneous growth rates may be underestimated. A negative biased growth rate may have resulted of size-dependent emigration, documented for juvenile estuarine fishes, where larger individuals emigrate earlier (Able and Fahay 1998). Continued residence by smaller or slower growing individuals would cause estimated growth rates to be biased low.

The ratio of atomic carbon to nitrogen (C:N), a lipid proxy, was significantly higher in liver than in muscle tissue for each species, season, environment, and year (ANOVA, $p = 0.038$). As such, a consistent bias of approximately 2‰ $\delta^{13}C$ was observed when comparing between liver and muscle tissue of the same fish.

Overall Contrasts in $\delta^{13}C$ between Years, Seasons, Habitat Types, and Tissues

The significance of overall contrasts between $\delta^{13}C$ values across seasons and years varied according to habitat and tissue in both species. Similarly, the significance of the distance-from-inlet covariate varied between species and across season, year, habitat, and tissue. Bay anchovy muscle $\delta^{13}C$ showed a non-significant change between years and increased between seasons in the coastal bays, and increased between seasons in the nearshore ocean (Table 1.2). Liver tissue also decreased between seasons in the coastal bays and increased between seasons in the nearshore, but did not exhibit a significant change across years. Weakfish muscle $\delta^{13}C$ did not change significantly across season or year in either habitat. Similarly, weakfish liver $\delta^{13}C$ did not significantly change across year or habitat in the coastal bays. In the nearshore, however, liver $\delta^{13}C$ significantly increased between seasons.

Compared to muscle tissue, liver was depleted in the heavy carbon isotope in all seasons, environments, and years. Due to the higher prevalence of light-isotope enriched lipids in liver tissue than in muscle tissue, this is to be expected (Post et al. 2007). Liver was also more variable than muscle tissue, possibly due to the small amount of material from each sample.

Trophic Analysis- Bay Anchovy

Anchovy muscle $\delta^{13}C$ displayed an increasing trend ($p = 0.0391$) from the farthest-inland bay sites to the nearshore ocean during summer of 2009, with the exception of site CB1_2 (Fig. 1.6). Conversely, $\delta^{13}C$ values were unaffected by distance to the OCI within the nearshore ocean, remaining relatively constant throughout the sites surveyed. Unfortunately, there were not enough anchovy caught within the bays to statistically resolve spatial trends during fall. Anchovy liver $\delta^{13}C$ displayed a trend similar to anchovy muscle, with summer 2009 bay values progressively increasing as distance to the OCI decreased. Whereas an increasing trend with inlet proximity was seen in both the muscle and liver tissue of bay anchovy from the 2009 coastal bays, no such trend was evident in 2012 (Fig. 1.7). The $\delta^{13}C$ value of both anchovy muscle and liver tissue remained between -20.0‰ and -20.5‰ as distance from the OCI decreased, with liver tissue slightly depleted when compared to muscle.

The inclusion rule for bay anchovy diet resulted in five groups of prey items: decapod larvae, copepods, bivalve larvae, miscellaneous zooplankton, and miscellaneous other items (most often amphipods, *Nereis* worms, or mysid shrimp). Copepods were the numerically dominant prey item in all strata, seasons, and years except for the coastal bays in the summer of 2009, when decapod larvae were the most dominant (Fig. 1.8). Decapod larvae were the second-most numerically dominant prey item in all other seasons and strata. With the exception of summer 2009 coastal bay sample, the numerical makeup of diet across habitat and season within 2009 was rather similar. The 2012 coastal bay samples differed from summer and fall 2009 samples, in that they displayed an increased numerical dominance of bivalve larvae (32.8%) in comparison to 2009 strata which showed <5% contribution to diets.

By weight, prey items ordered differently within bay anchovy diets. Decapod larvae were the dominant prey item by weight in all seasons, strata, and years except for summer 2009 nearshore samples (Fig. 1.9). Here, the weight of highly-digested crustacean biomass (as determined by degraded carapaces) and other prey items (namely, the incidence of a single preyed-upon fish) accounted for 80% of prey by weight. While other-category items accounted for the second-most weight, copepods and unidentified crustaceans made small but ubiquitous contributions to diets according to weight.

Trophic Analysis -Weakfish

Weakfish muscle and liver $\delta^{13}C$ in summer 2009 did not show the same increasing pattern with decreasing distance to the ocean found in anchovy tissue; $\delta^{13}C$ values were relatively constant within the bays, but became progressively more enriched with increasing distance into the nearshore ocean (Fig. 1.10; Table 1.2). Fall 2009 coastal bay samples had more depleted values than nearshore samples, but similar to the bay anchovy, not enough weakfish were captured to resolve spatial trends in $\delta^{13}C$. Spatial patterns were similar between 2009 and 2012 within the coastal bays for both tissues, as both series lacked a significant spatial trend (Fig. 1.11).

Weakfish diet was more diverse than that of bay anchovy, with amphipods, decapod larvae, mysid shrimp, *Nereis* worms, juvenile fish, miscellaneous zooplankton, and miscellaneous items passing the inclusion rule. In summer 2009 coastal bay samples, decapod larvae were numerically dominant, while a few large juvenile fish dominated weight (Fig. 1.12, 1.13). Mysid shrimp were the numerically dominant species in summer 2009 nearshore samples, as well as both environments in fall 2009. Juvenile fish, more specifically bay anchovy, were the dominant prey items by weight in summer 2009 nearshore and fall 2009 coastal bay samples, whereas mysid shrimp dominated the majority (>97%) of prey weight in fall 2009 nearshore samples. In 2012, amphipods were the most numerically abundant prey items, while, similar to coastal bay samples in fall 2009, juvenile anchovy were the highest by weight.

Discussion

This study aimed to characterize the trophic dynamics of a coastal lagoon complex, hypothesizing that with the recent loss of structure through seagrasses, juvenile fish diets would be more homogenous in 2012 than in 2009 and an overall shift to more pelagic, phytoplankton-based food web would occur. I found no change in the homogeneity of diet items or a shift to more pelagic diet items in 2012 when compared to 2009. Spatial diet homogeneity in bay anchovy as determined by carbon isotopes, however, did increase between 2009 and 2012 following the loss of a spatial isotopic gradient, suggesting a more-pelagic carbon source in 2012.

Whereas summer 2009 anchovy δ^{13}C values changed in the predicted serial fashion from inner to outer bay sites, summer 2012 values were homogeneous with respect to distance from the inlet. In 2012, all summer $\delta^{13}C$ values centered at -20‰, similar to values observed closest to the inlet in 2009. This effect suggests that a more-pelagic carbon source was present throughout the northern bays in 2012. Unlike anchovy, weakfish tissue showed no apparent trend across coastal bay sites in 2009, although $\delta^{13}C$ values were slightly higher at sites closest to the Ocean City inlet. Similarly, 2012 weakfish samples showed no spatial trend in $\delta^{13}C$ throughout the bays. However, unlike 2009, there was no small increase in $\delta^{13}C$ values at sites closest to the OCI. The higher degree of homogeneity in weakfish isotope values for both years could indicate that (1) the weakfish had fed recently in a different habitat, or (2) weakfish were more mobile than anchovy and these movements caused widespread feeding, which integrated isotopic values of forage distributed across the northern bays.

Interestingly, $\delta^{13}C$ values for both species were less variable on a per-site basis in 2012 than in 2009, although 2012 diet, as determined by gut content analysis, was more variable. As introduced above, more mobile predators (bay anchovy or weakfish) or prey in one year versus the other could result in more homogenous $\delta^{13}C$ values. If the predator or prey move over days and weeks between environments of differing isotopic values, then the $\delta^{13}C$ values of predator tissue will integrate isotopic values of captured prey items, resulting in a relatively constant, intermediate isotopic value across the system. Specifically, weakfish may show less spatial trends in $\delta^{13}C$ than anchovy as the piscine and mysid prey they depend upon are more mobile than the zooplankton and decapod prey of bay anchovy. Second, the system, itself, could have become more isotopically uniform. This would allow the anchovy to approach equilibrium with its food, regardless of where the fish or its prey was located within the system. Major changes to the surrounding environment, including the collapse of seagrass and dredging of the Ocean City inlet, may have resulted in a more transient homogenous food web with uniform isotopic values throughout the bays due to increased flushing, flows and sediment exchange within the bays (Duck and da Silva 2012).

At odds with the inference of greater spatial uniformity in forage in 2012 was increased diversity of gut contents for that year for both species and lack of increased dependency on pelagic resources in weakfish. In 2012, bay anchovy were more catholic in their diets, with a comparatively even distribution of prey items when evaluated by either percent number or weight. Diets were dominated by decapod larvae in 2009 but more evenly distributed across prey items in 2012. This broader diet was accompanied by an increase in both the number and weight of pediveliger-stage bivalve larvae. As these late-stage larvae spend time in both benthic and pelagic environments in search of suitable settlement habitat (Pechenik 2005), increased levels of bivalve larvae are not necessarily indicative of pelagic or benthic trophic shifts between 2009 and 2012.

Similar to bay anchovy, weakfish direct diet analysis did not suggest a shift to a more-pelagic food web between the summers of 2009 and 2012. Weakfish increased the proportion of benthic amphipods in the diet in 2012, with benthic amphipods replacing decapod larvae as the most numerically dominant (Fig. 1.12). The proportion of weight accounted for by benthic amphipods also increased across years, but the few instances of small fish in the diet, namely anchovy, caused fish to be the most important diet item by weight in both years, perhaps becoming increasingly important in 2012.

The summer diet of bay anchovy described in this study resembled those found in the literature, which for the mid-Atlantic region show copepods to be the most common prey. In both the Chesapeake Bay (Klebasko 1991) and the Hudson River (Hartman et al. 2004), copepods are listed as the major diet item of age-0 bay anchovy. Bivalve larvae were the next-most prominent prey item of anchovy in the Chesapeake Bay, whereas mysid shrimp or bivalve larvae were next-most dominant in the Hudson depending on diet metric. Conversely, decapod larvae were the dominant prey item in this study. As decapod larvae tend to be more common in coastal environments, this discrepancy is most likely due to habitat and ecosystem differences in prey availability.

Bay anchovy have been shown to increase their ingestion of larger prey items between summer and fall seasons (Klebasko 1991, Hartman et al. 2004). Frequently, an increase in both the percent number and percent weight of larger *Acartia* copepods at the expense of smaller calanoid copepods occurred between summer and fall. In addition, Klebasko (1991) showed a switch in the second-most prevalent bay anchovy prey item in the Chesapeake Bay, from bivalve pediveliger larvae in the summer to barnacle cyprid larvae in the fall. In this study, decapod larvae were the most dominant prey item by weight between seasons in coastal bay anchovy. Copepods did increase in percent number between seasons within the bays, albeit their contribution by weight was relatively small. The consistent increase of 1-2‰ in anchovy muscle and liver $\delta^{13}C$ between seasons in 2009 nearshore samples may reflect this seasonal shift to larger prey items, as decapod larvae, especially those in the megalopae stage found more commonly in the fall, feed at a higher tropic level than copepods. Enrichment of 1-2‰ in $\delta^{13}C$ values with increasing trophic levels is common, and can exceed 4‰ in some cases (Pinnegar and Polunin 1999). Coastal bay anchovy increased decapod larvae consumption at the expense of copepods across seasons, as exhibited by an increase in percent weight of decapod larvae in anchovy guts (Fig. 1.9).

As opposed to anchovy, weakfish diets did not resemble those previously reported in the literature. Whereas this study found fish, decapod larvae, and epibenthic amphipods to be the dominant prey items of age-0 weakfish in the summer, previous studies consistently list mysid shrimp as most dominant (Merriner 1975, Stickney et al. 1975, Chao and Musick 1977). Further, these studies showed that weakfish consistently relied almost entirely on mysid shrimp until they were approximately 130mm in length, the maximum size of weakfish in my study. In contrast to northern Coastal Bay samples, mysid shrimp were found to be an important prey item by number and weight in summer and fall 2009 nearshore samples, as well as by percent number in fall 2009 coastal bay samples. However, in summer coastal bay samples across years, the influence of mysid shrimp was minimal by both percent number and weight. Similarly, amphipods and decapod larvae made up the bulk of summer diet in the coastal bays by percent number. However, when analyzing diet by percent weight, juvenile fish was the predominant prey item of age-0 weakfish. As such, weakfish in this system seem to be switching to piscivory at a smaller size than previously reported. As weakfish have more pelagic-oriented diets than other scieanids (Chao and Musick 1977), the shallow waters of the coastal bays could improve forage efficiency on pelagic prey at smaller sizes.

Mysid shrimp was the most dominant prey item of weakfish by number across seasons in 2009, with the exception of summer coastal bay diets which were characterized by decapod larvae. As mysid shrimp are larger prey items, the shift away from decapod larvae may be a consequence of the increased size and age of sampled weakfish. There was also slight $\delta^{13}C$ enrichment in the nearshore ocean between seasons, most likely due to a diet shift toward higher trophic levels, evidenced by shift from a diet mainly composed of fish and decapod larvae to that of fish and mysid shrimp.

Inferences on the influence of nearshore ocean on coastal bay diets and isotopes depended on only nearshore samples taken in 2009. Due to logistic constraints, the nearshore ocean was not sampled in 2012. In this study, stable isotopes, diet, and target fish distribution were found to be relatively homogeneous across nearshore ocean sites (as defined by distance to the OCI). In addition, overall fish assemblage was similarly homogeneous in this environment (see Chapter 2). As such, it was assumed that the nearshore ocean was unaffected by the Ocean City Inlet and that changes in isotopic values, diet, and fish distribution would occur consistently throughout the environment and without respect to this point.

The nearshore fish assemblage adjacent to Ocean City is likely influenced by several proximal nursery environments. The Virginia and Delaware coastal lagoon systems, with inlets 50-150 km south and 30 km north, respectively, would likely provide negligible species input to the nearshore ocean, similar to the Maryland coastal bays investigated here. However the Delaware Bay, approximately 55 km to the north, harbors extensive nursery habitat for many different marine and estuarine species. Larval and juvenile stage fishes are known to migrate southward from the Delaware Bay using the southward-flowing currents (Tilburg et al. 2007). In addition, Thorrold et al. (2001) described Delaware Bay juvenile weakfish as straying as far south as the Chesapeake Bay and as far north as Long Island, NY in the first 3 – 5 months of life. As such, fish sampled within the nearshore ocean adjacent to the OCI may represent production from other nurseries, namely Delaware Bay. Further isotopic analyses could help to determine the nursery of origin in the nearshore-collected fish.

Coastal lagoons and the biological, chemical, and physical process that occur within them are characterized by the rapid transitions at their boundaries. Changes to these transitions due to natural and anthropogenic forcing can be manifested in trophic interactions between the lagoon and nearshore ocean ecosystems. Here we examined how the Ocean City Inlet boundary influenced the diet and carbon source of both forage fish (bay anchovy) and piscivorous predators (weakfish), and observed that coastal bay food web dependency on marine environments varied between years in accord with expectations for one dominant species, bay anchovy, but not for the other, weakfish. Thus, trophic interactions between habitat types can be specific or ubiquitous depending on the current state of the respective environments, and suggest that proper management of coastal lagoon systems necessitates consideration of the adjacent marine environment and food web.

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Tables

Table 1.1. Instantaneous growth rates (bay anchovy and weakfish, month^{-1}) and instantaneous isotopic turnover rates (blue and ribbed mussels, month^{-1}). Blue mussel values reflect pelagic isotopic turnover of the nearshore ocean, while ribbed mussel values reflect pelagic isotopic turnover in the center of the coastal bay system.

	Bay Anchovy			Weakfish			Blue Mussel		Ribbed Mussel	
Month	2009	2011	2012	2009	2011	2012	2011	2012	2011	2012
Jul-Aug	0.658	1.08	0.594	1.22	0.939	1.17	0.145	0.384	-0.547	0.183
Aug-Sept	0.395	0.304	0.506	-0.029	-0.314	0.259	0.281		0.04	
Jul-Sept	0.526	0.676	0.55	0.597	0.312	0.716	0.247		-0.107	

Table 1.2. Contrasts between $\delta^{13}C$ values across years within the coastal bays (CB) in the summer season, across season within the coastal bays in 2009, and across season within the nearshore ocean (NS) in 2009. Student's t-tests were used except in instances with a significant distance-from-inlet covariate (†), where ANCOVA was used. Contrasts significant at α = 0.008 (Bonferroni correction for multiple tests) are emboldened.

		Bay Anchovy				Weakfish			
		Muscle		Liver		Muscle		Liver	
Contrast		Mean (SD)	P-value	Mean (SD)	P-value	Mean (SD)	P-value	Mean (SD)	P-value
CB Summer	2009	-19.87 (0.68)	0.009†	-20.87 (0.71)	0.141	-19.11 (0.74)	0.67	-20.13 (0.45)	0.911†
	2012	-20.61 (0.36)		-21.31 (0.32)		-19.26 (0.20)		-20.15 (0.42)	
CB 2009	Summer	-19.87 (0.68)	**0.005**	-20.87 (0.71)	**0.007**	-19.11 (0.74)	0.202	-20.13 (0.45)	0.175
	Fall	-21.73 (0.27)		-22.85 (0.28)		-20.08 (0.95)		-20.88 (0.70)	
NS 2009	Summer	-18.74 (0.17)	**0.0001**	-19.48 (0.34)	**0.002**	-17.80 (0.86)	0.587	-18.94 (0.89)	0.009†
	Fall	-17.12 (0.47)		-17.83 (0.56)		-16.38 (0.80)		-17.17 (0.65)	

Figures

Figure 1.1. Summer and Fall 2009, Summer 2012 sampling sites. The grid from which sites were chosen is indicated in the first panel. Sub-embayments used in the analysis (Assawoman Bay (AW), Isle of Wight Bay (IW), and the Ocean City Inlet (INL)) are labeled.

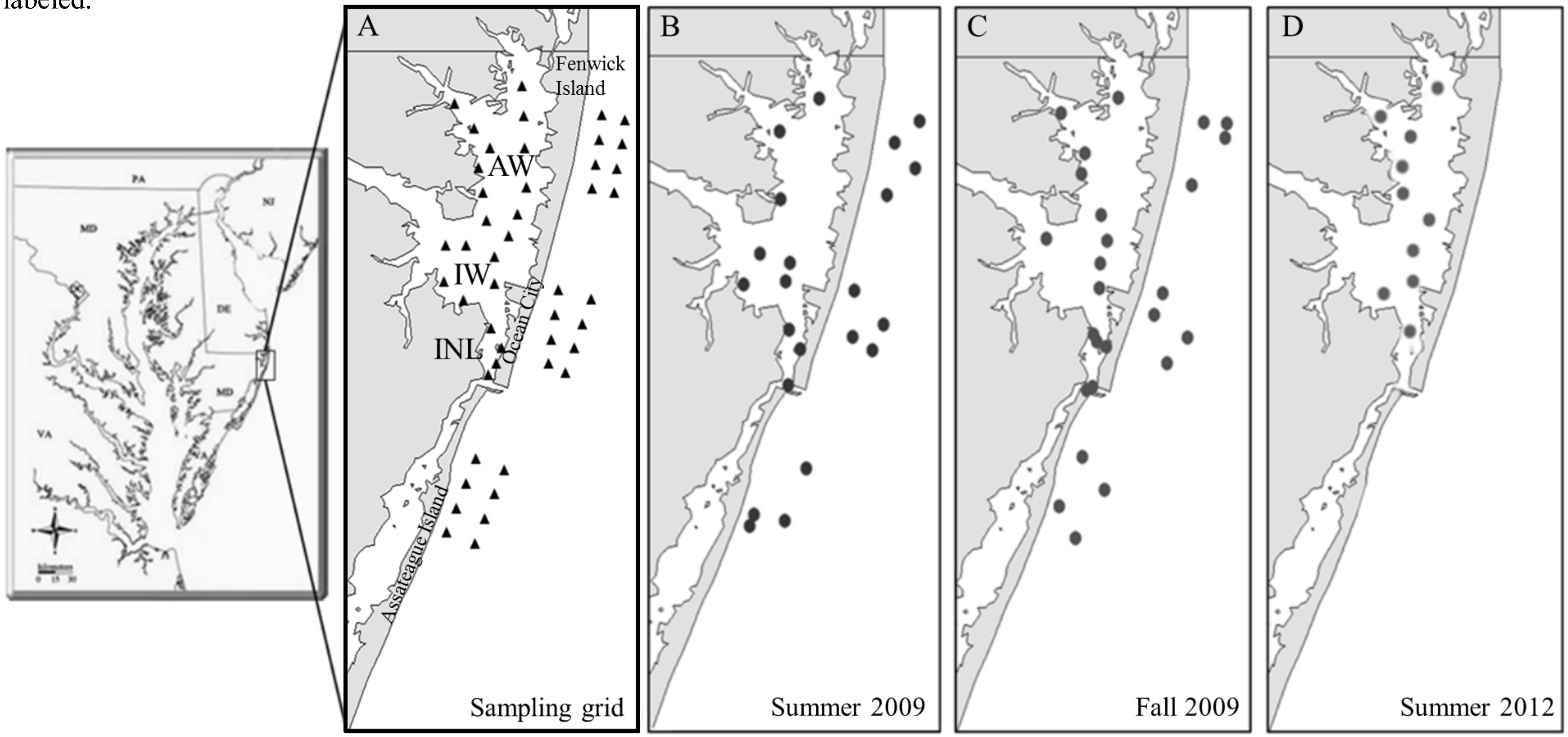


Figure 1.2. Bay anchovy (*Anchoa mitchilli*) catch per unit effort (CPUE) in the Maryland northern coastal bays and associated nearshore ocean. The summer (●) and fall (Δ) seasons of 2009 are shown.

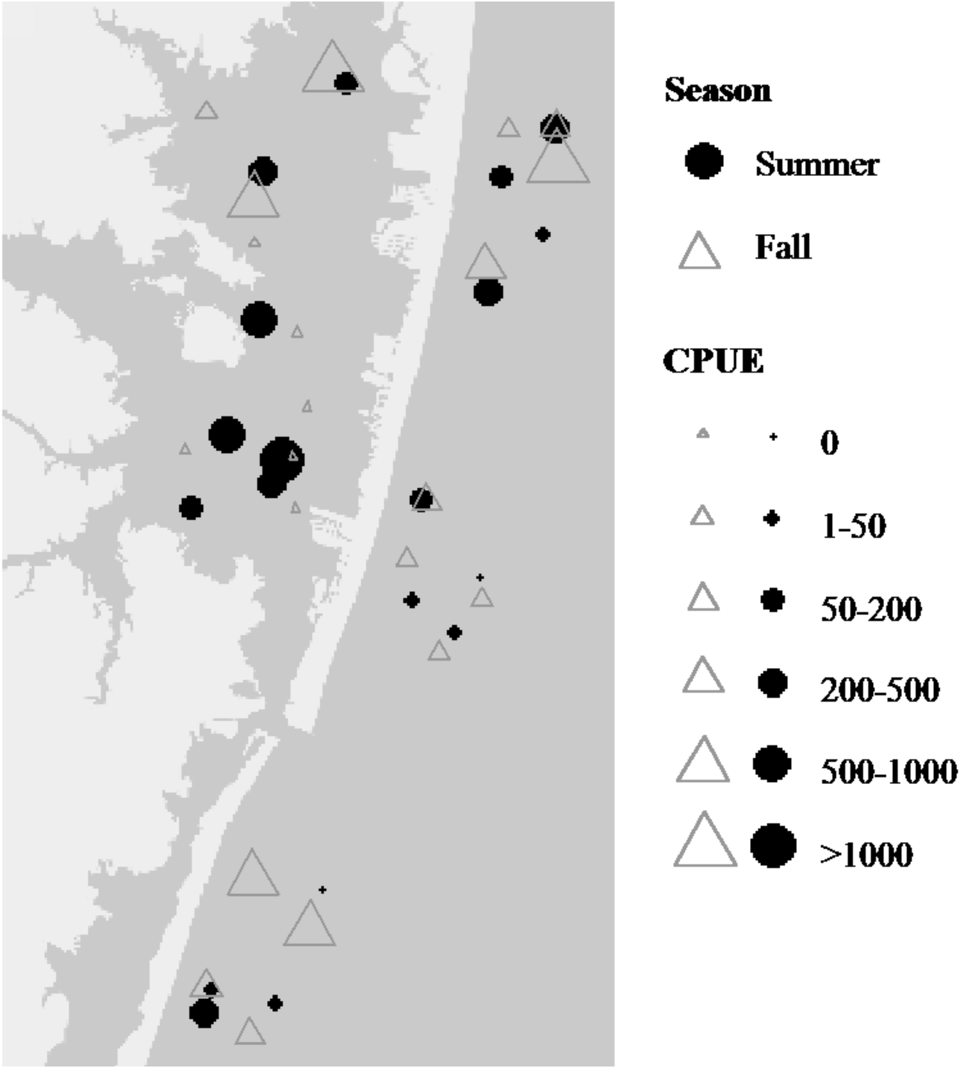


Figure 1.3. Bay anchovy (*Anchoa mitchilli*) catch per unit effort (CPUE) in the Maryland northern coastal bays. The summer seasons of 2009 (●) and 2012 (○) are shown.

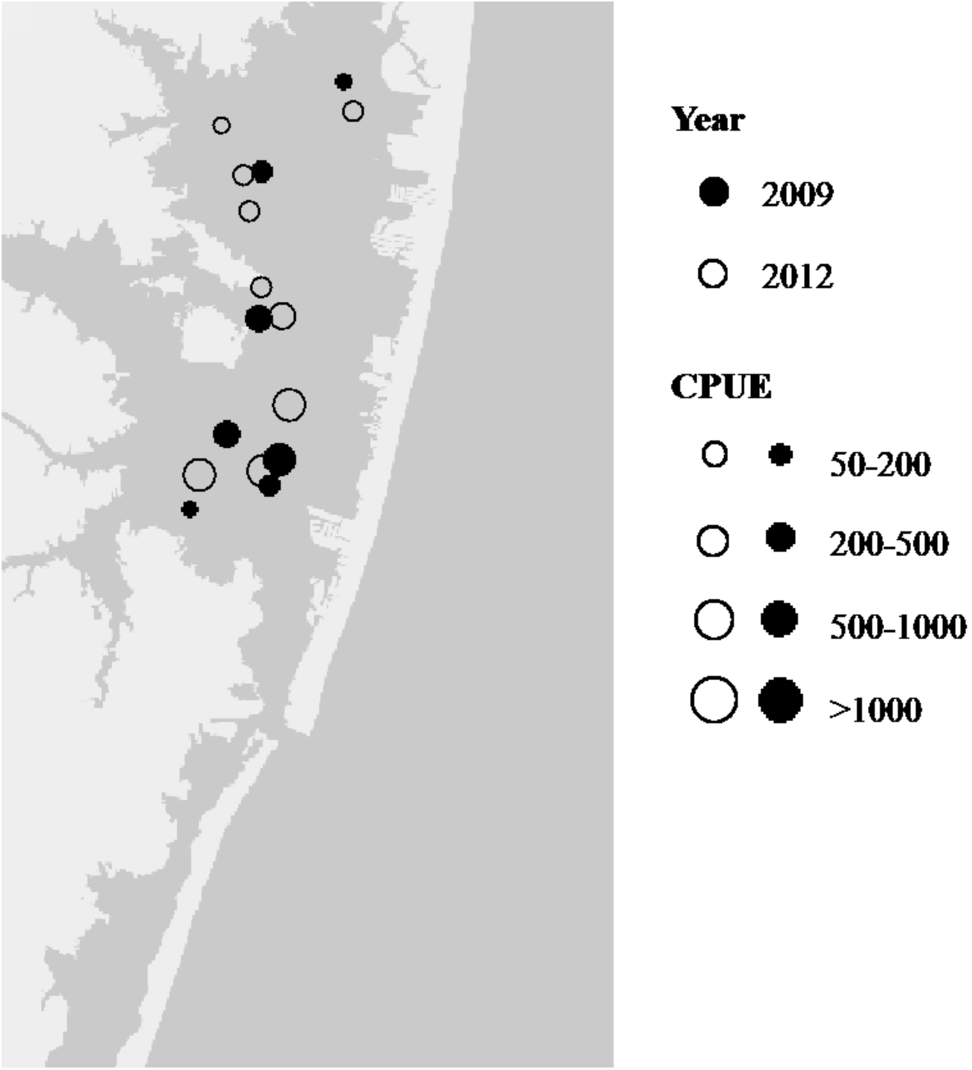


Figure 1.4. Weakfish (*Cynoscion regalis*) catch per unit effort (CPUE) in the Maryland northern coastal bays and associated nearshore ocean. The summer (●) and fall (Δ) seasons of 2009 are shown.

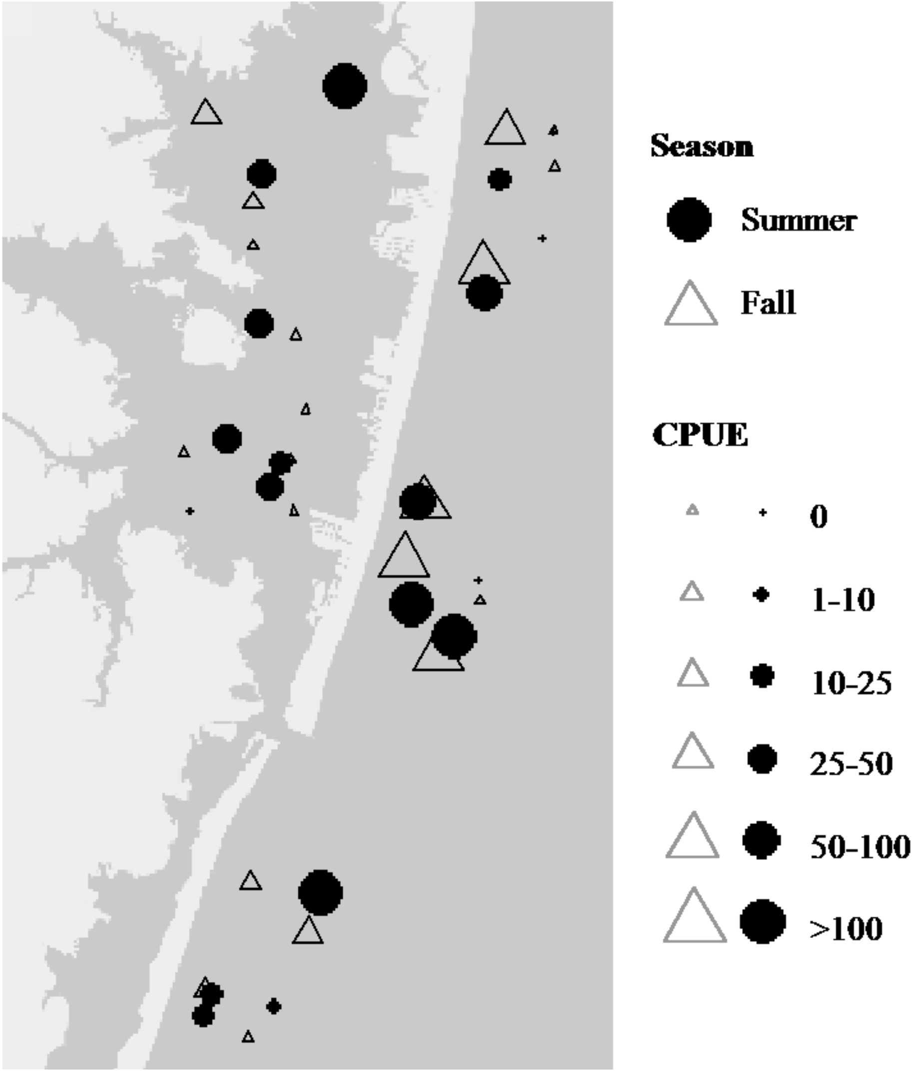


Figure 1.5. Weakfish (*Cynoscion regalis*) catch per unit effort (CPUE) in the Maryland northern coastal bays. The summer seasons of 2009 (●) and 2012 (○) are shown.

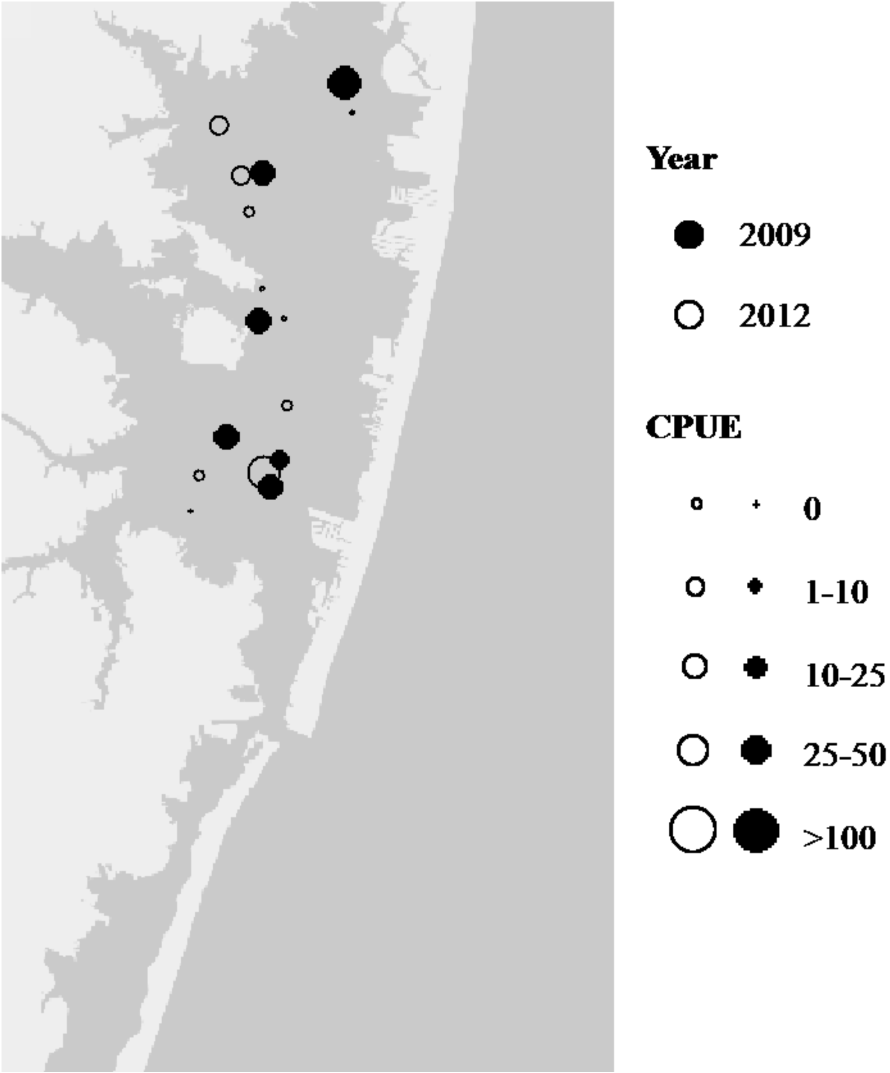


Figure 1.6. Bay anchovy $\delta^{13}C$ values for muscle and liver tissue in the summer and fall of 2009 along a gradient from the most-distal coastal bay site to the most-distal nearshore site from the Ocean City inlet. A vertical black line delineates the coastal bay from the nearshore sites. Boxes show the median (horizontal line), interquartile range (25th to 75th percentile), and range from 5th to 95th percentile (whiskers).

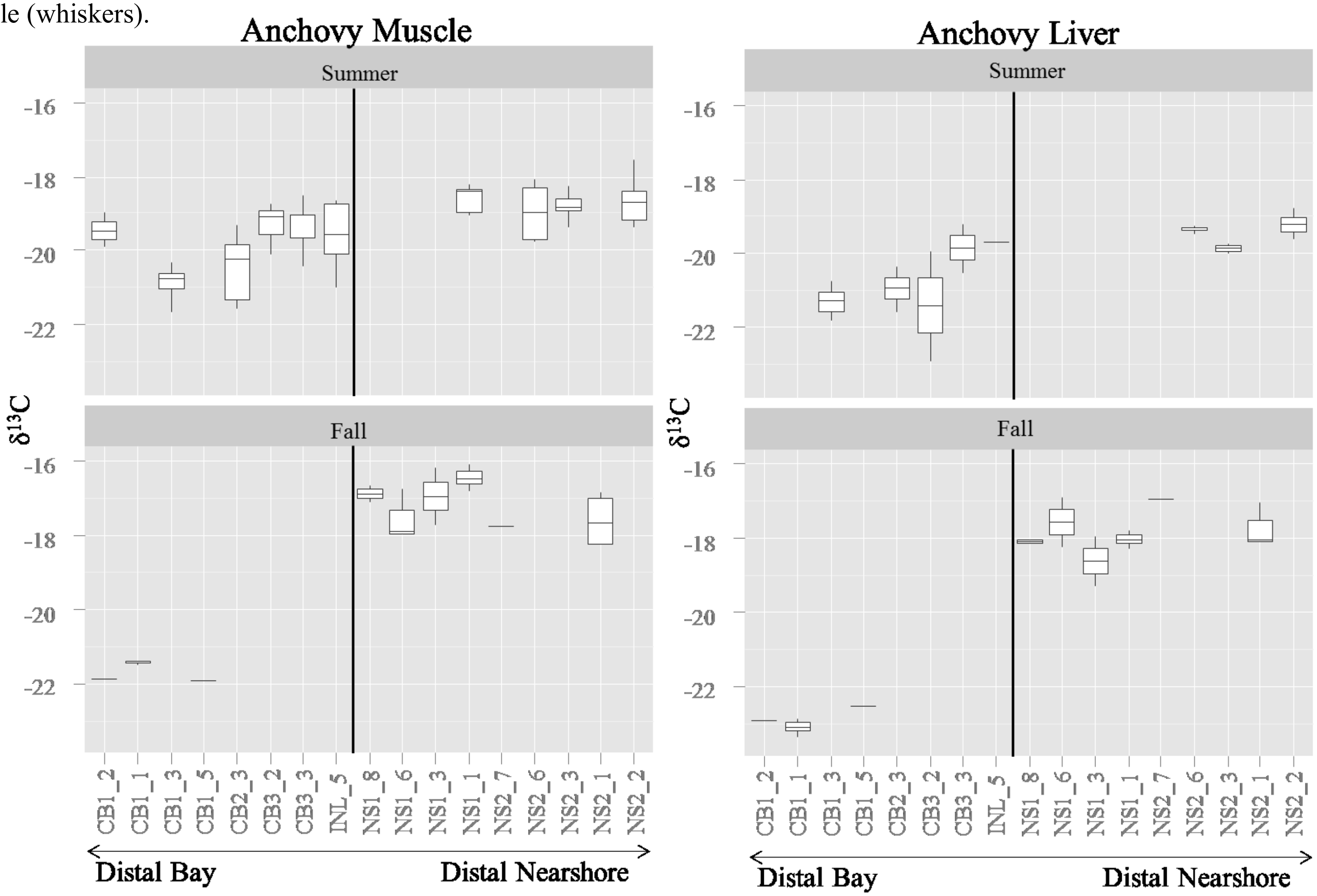


Figure 1.7. Bay anchovy $\delta^{13}C$ values for muscle and liver tissue in the summers of 2009 and 2012 along a gradient from the most-distal coastal bay site from the Ocean City inlet to the Ocean City inlet. Boxes show the median (horizontal line), interquartile range (25th to 75th percentile), range from 5th to 95th percentile (whiskers), and outliers (dots).

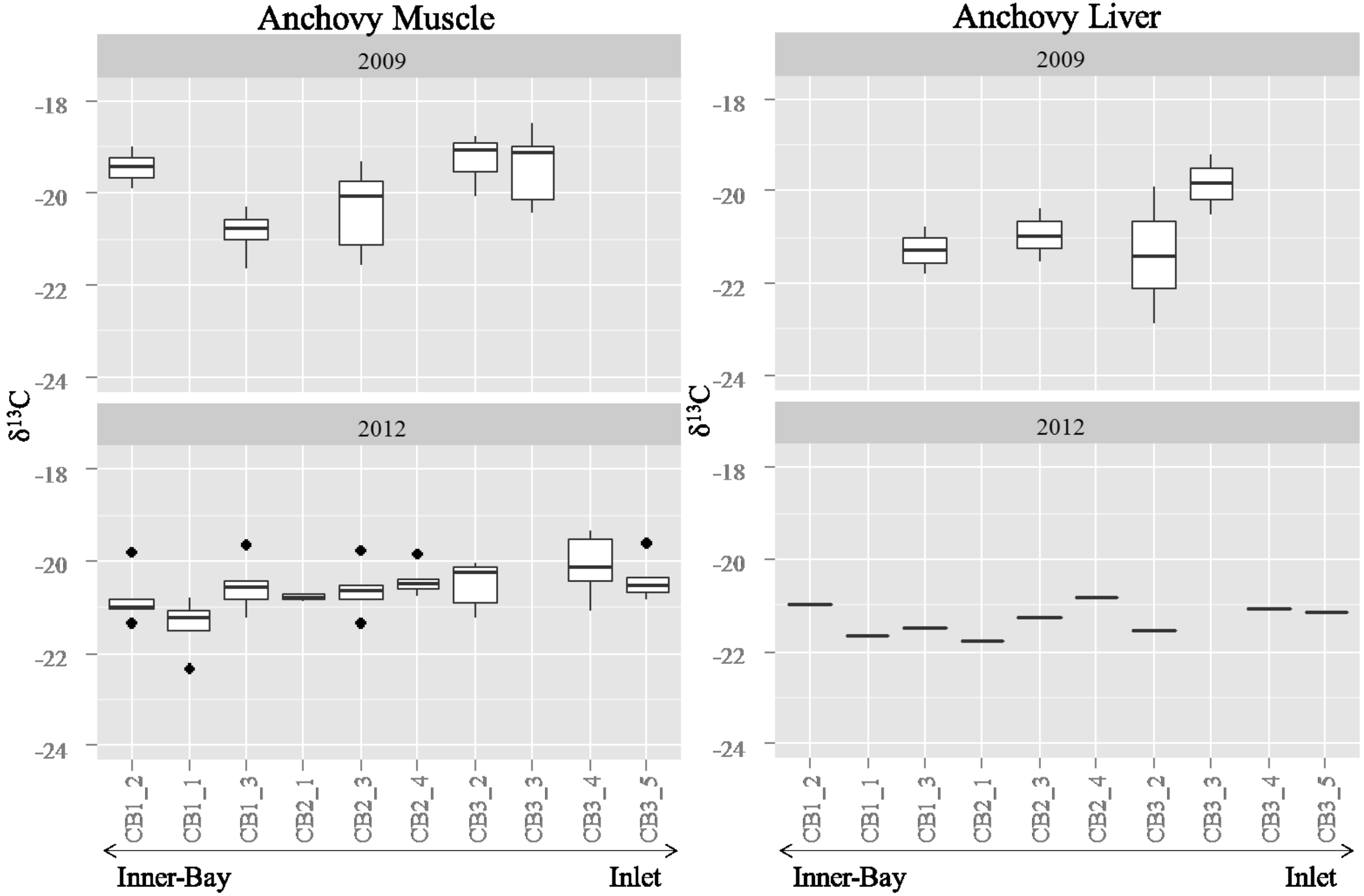


Figure 1.8. Bay anchovy diet in Maryland's northern coastal bays (Bay) and associated nearshore ocean (Nearshore) in summer and fall, 2009 (09) and 2012 (12). Diet is reported as the percent of prey items found within the gut for each habitat-season-year comination.

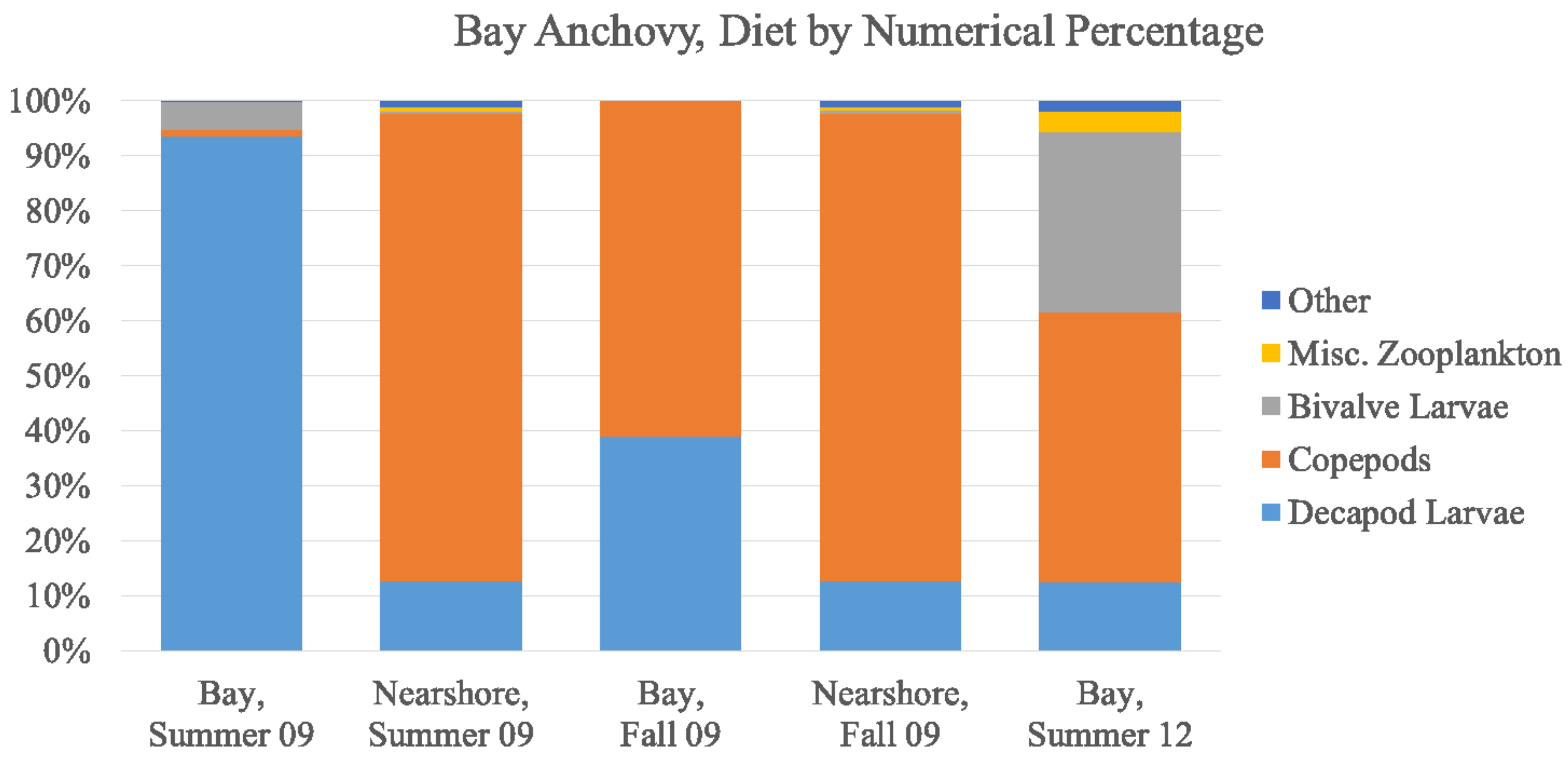


Figure 1.9. Bay anchovy diet in Maryland's northern coastal bays (Bay) and associated nearshore ocean (Nearshore) in summer and fall, 2009 (09) and 2012 (12). Diet is reported as the percent of weight accounted for by each prey item found within the gut for every habitat-season-year comination. Crustacean biomass refers to unidentifiable items that can clearly be labeled as crustacean in origin.

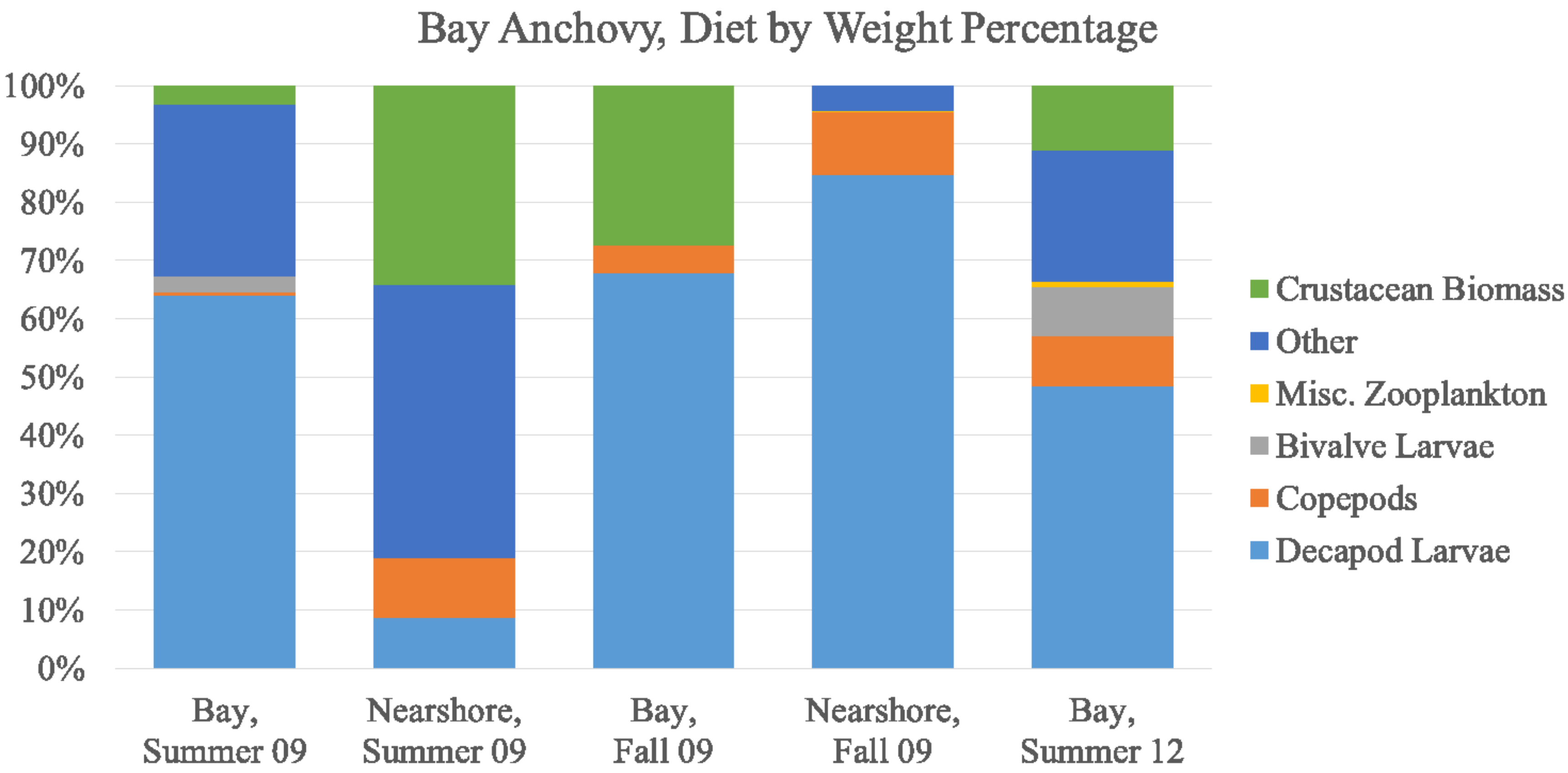


Figure 1.10. Weakfish δ^{13}C values for muscle and liver tissue in the summer and fall of 2009 along a gradient from the most-distal coastal bay site to the most-distal nearshore site from the Ocean City inlet. A vertical black line delineates the coastal bay from the nearshore sites. Boxes show the median (horizontal line), interquartile range (25th to 75th percentile), range from 5th to 95th percentile (whiskers), and outliers (dots).

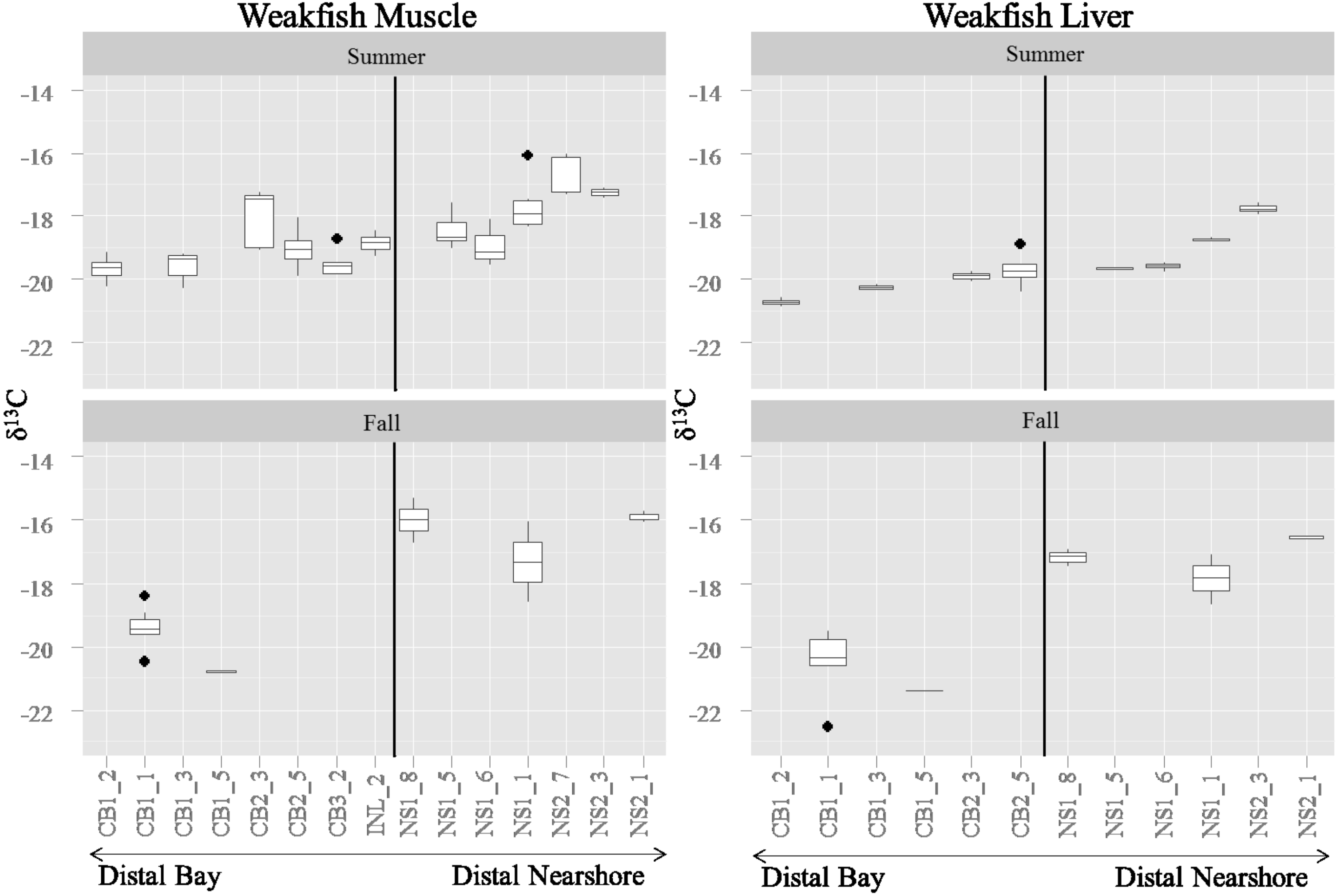


Figure 1.11. Weakfish $\delta^{13}C$ values for muscle and liver tissue in the summers of 2009 and 2012 along a gradient from the most-distal coastal bay site from the Ocean City inlet to the Ocean City inlet. Boxes show the median (horizontal line), interquartile range (25th to 75th percentile), range from 5th to 95th percentile (whiskers), and outliers (dots).

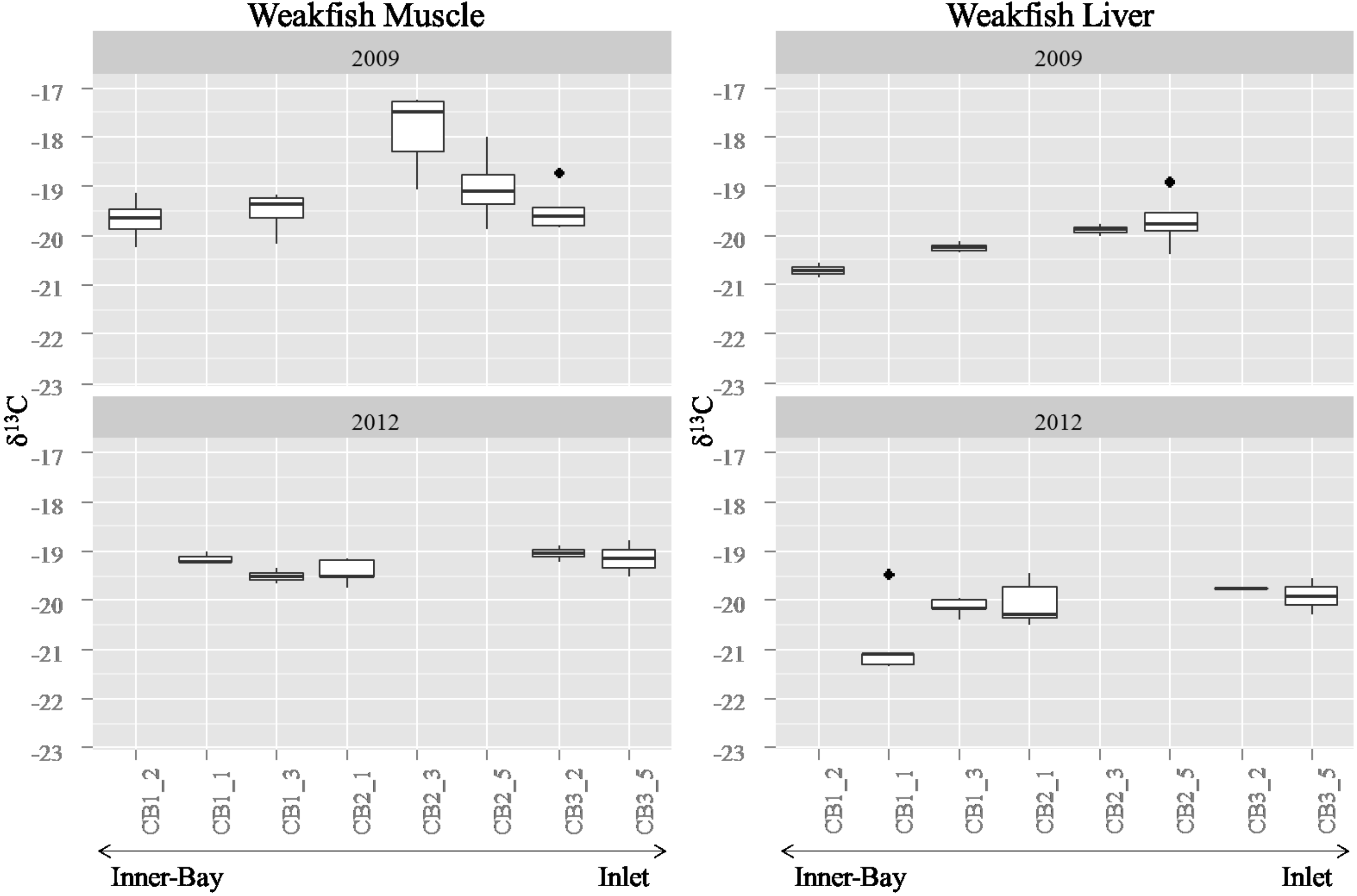


Figure 1.12. Weakfish diet in Maryland's northern coastal bays (Bay) and associated nearshore ocean (Nearshore) in summer and fall, 2009 (09) and 2012 (12). Diet is reported as the percent of prey items found within the gut for each habitat-season-year comination.

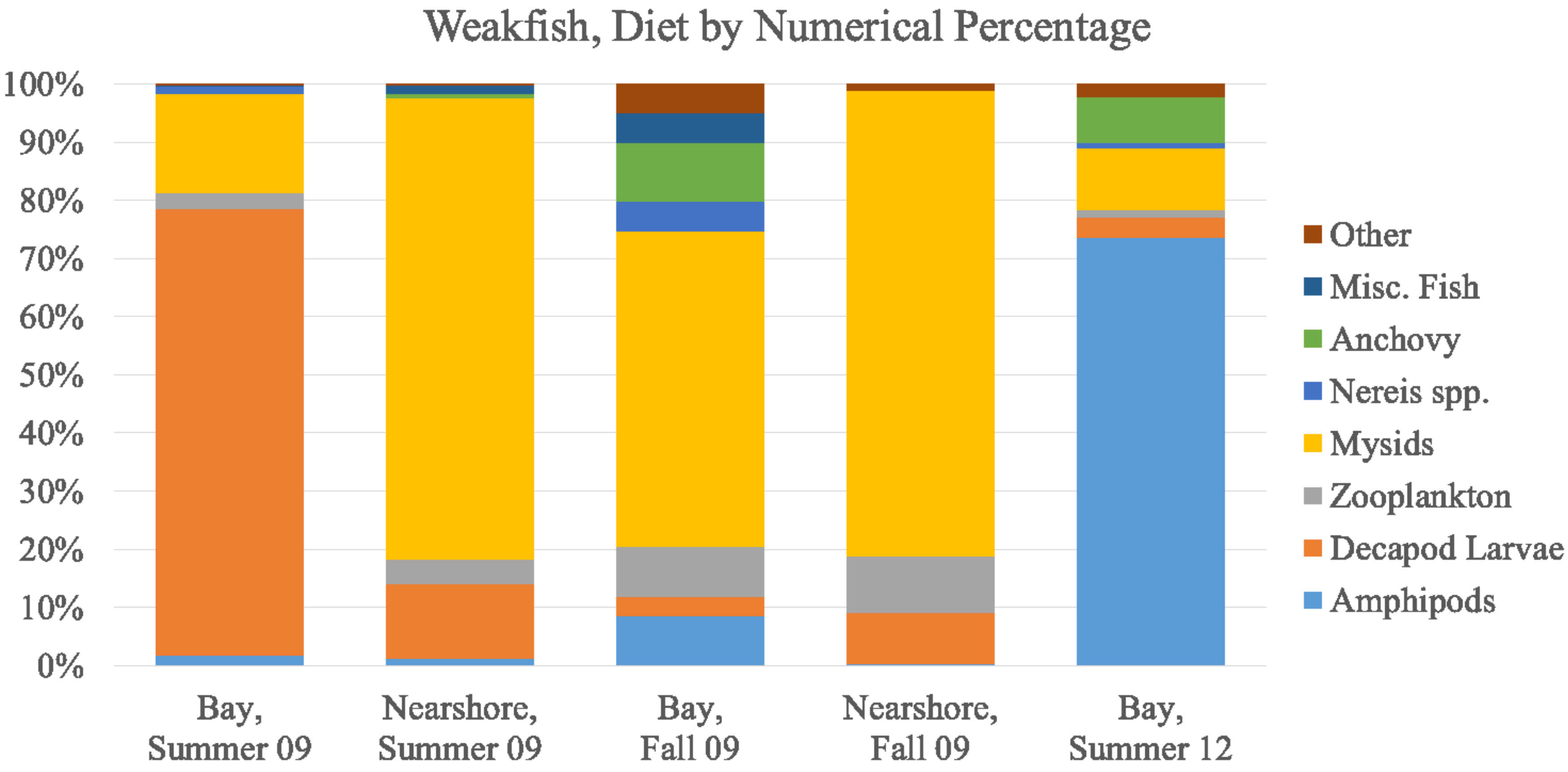
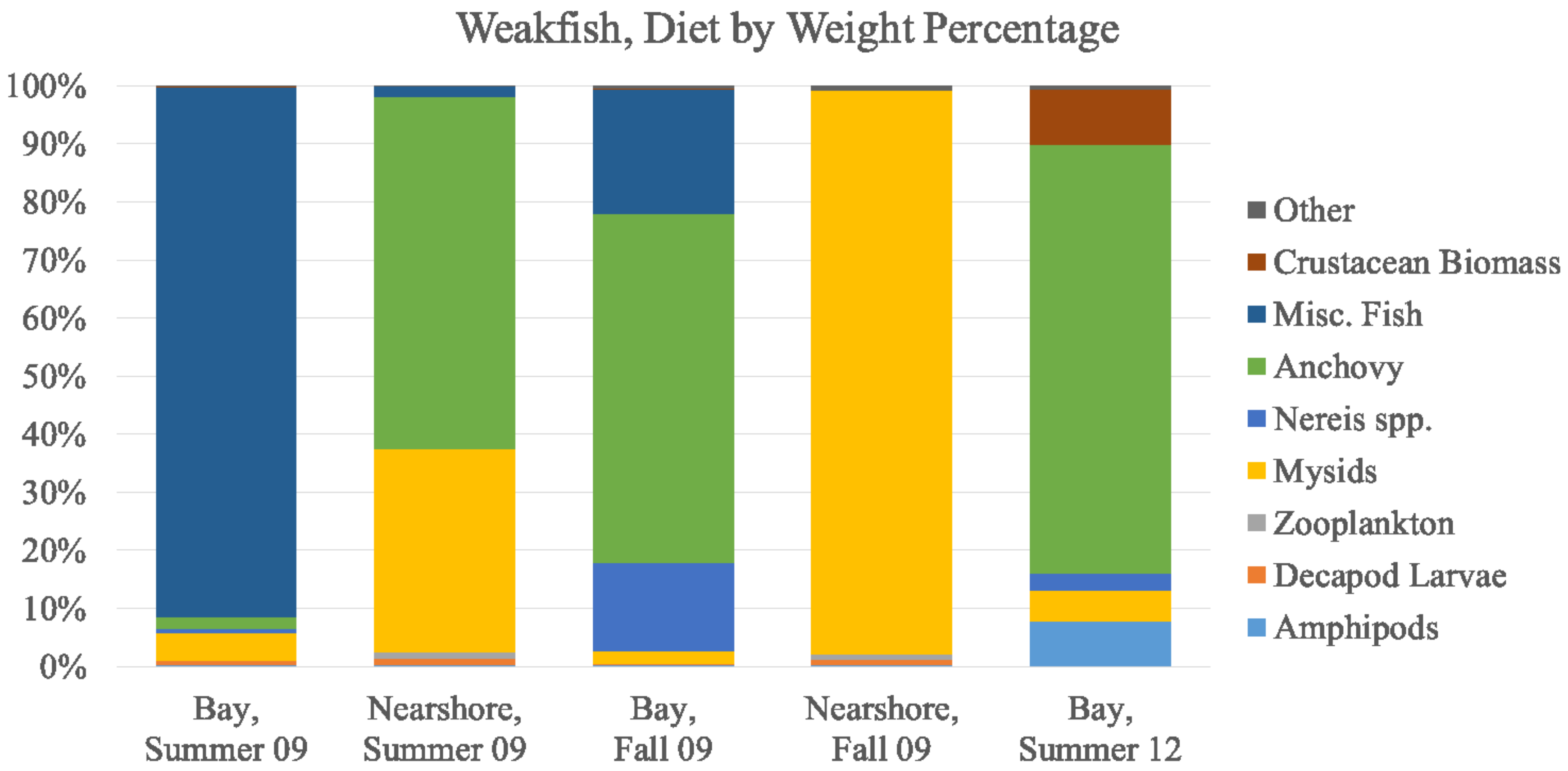


Figure 1.13. Weakfish diet in Maryland's northern coastal bays (Bay) and associated nearshore ocean (Nearshore) in summer and fall, 2009 (09) and 2012 (12). Diet is reported as the percent of weight accounted for by each prey item found within the gut for every habitat-season-year comination. Crustacean biomass refers to unidentifiable items that can clearly be labeled as crustacean in origin.



Chapter 2: Multi-scale environmental forcing on juvenile fish assemblage in Maryland's northern coastal bays

Introduction

Coastal lagoons, as a class of marine ecosystems, support diverse and productive fish communities, which are influenced by the steep transitions that define their boundaries (Tagliapietra et al. 2009). Due to their location and geomorphology, coastal lagoons possess multiple ecosystem interfaces within a relatively small area. Located at the confluence of land and sea, these shallow systems (<2 m) possess dynamic land-lagoon, lagoon-sea, sediment-water column, and water column-atmospheric exchanges (Nixon et al. 2001, McGlathery et al. 2007). Nutrient availability is often high in these environments: nutrients are delivered from the land, sea, and wind-driven resuspension of sediments. In non-impacted lagoons, the nutrient-rich, euphotic waters of coastal lagoons often increase biotic habitat structuring by promoting seagrass and macroalgae growth. High primary and secondary productivity together with biogenic structure provide quality nursery habitat for many fish species, which in turn contributes to fisheries, tourism, and other socioeconomic services (Parker et al. 2001, McGlathery et al. 2007, Brito et al. 2012, Pérez-Ruzafa and Marcos 2012).

Oceanic forcing through the lagoon-sea boundary is well documented and has been shown to exert dominant control on tidal lagoon fish assemblages (Mariani 2001, Murphy and Secor 2006). In larger, river-influenced lagoon systems and estuaries, fish assemblages grade according to changes in salinity due to a marine-freshwater gradient (Weinstein et al. 1980, Bulger et al. 1993). As such, the influence of marine species is restricted to the mouth of the estuary, freshwater species are restricted to headwaters, and more typical (i.e., euryhaline) estuarine species are dispersed throughout the system (Wagner 1999). In smaller, tidal lagoon systems, particularly those with small watersheds, the influence of ocean processes can become so great that the lagoon is relatively homogeneous with respect to the environmental variables that typically structure fish assemblages. This environmental homogeneity leads to assemblages differentially composed of resident, estuarine species and mobile, marine species (Pérez-Ruzafa et al. 2007).

Marine influence is often exacerbated by anthropogenic intervention in the natural geophysical progression of tidal lagoons. Connections to the marine environment in natural coastal lagoons are geologically ephemeral, existing anywhere from days to decades. Natural inlets are opened by high-energy events in the surrounding coastal ocean, and then close over time via persistent along-shore sediment transport. Human intervention to conserve barrier islands and the lagoon environment often emphasizes maintenance of inlets through shoreline reinforcement and removal of sediment through dredging (Duck and da Silva 2012). As such, many maintained lagoons have permanent connections to the marine environment rather than transient connections characteristic of pristine systems. Perennial connections intensify marine influence within the lagoons, as tidal height, sandy sediments, and marine species increase in the years following inlet creation and reinforcement. Through these mechanisms, artificially maintained inlets increase the influence of oceanic forcing on the geomorphology and biota within coastal lagoons (Duck and da Silva 2012).

Lagoons characterized by high exchange with the surrounding marine environment possess assemblages similar to adjacent marine ones, while lagoons with reduced marine influence have assemblages typical of estuarine communities (Pérez-Ruzafa et al. 2011). Estuarine-resident communities are influenced by internal lagoon dynamics, such as creation and availability of habitat (Pérez-Ruzafa et al. 2006), wind forcing (Sampey et al. 2004), and watershed inputs (Sosa-Lopez et al. 2007), while marine-like communities are maintained by species input through connections with the ocean. Thus, proximity to and degree of marine exchange has been hypothesized to play a role in the spatial structuring of fish assemblages, with interspecific competition between motile marine fishes and resident lagoon species resulting in spatial community grading from inlet to distal lagoon areas (Mariani 2001).

In small coastal lagoons, seasonal and inter-annual changes in marine forcing can result in dynamic and unstable assemblage dynamics. I hypothesize that the gradient from pelagic, marine-oriented to demersal, structure-oriented species assemblages will be more pronounced when marine influence is low, while a homogenous pool of marine species will be present when marine influence is high. Pulses of strong oceanic forcing can cause coastal lagoons to periodically shift from communities dictated by internal processes (benthic structuring) to those dictated by external processes (oceanic forcing) through changes in dispersal, water quality, or overall lagoon geomorphology (Panda et al. 2013). Periods of increased marine influence, exacerbated by anthropogenic reinforcement of marine exchange, should cause lagoon assemblages to be increasingly dominated by mobile marine species. Alternatively, during periods of increased internal stability, structural agencies may moderate oceanic forcing, resulting in a gradient from marine to resident-dominated assemblages.

The northern bays of the Maryland coastal lagoon complex were used as a model system to investigate the interplay of external and internal forcing on a lagoon fish assemblage (Fig. 2.1). Isle of Wight and Assawoman Bay are polyhaline, receiving limited freshwater influence from relatively small watersheds (Table 2.1). Of more importance to this study, the lagoons have been connected to the nearshore ocean through an artificially-maintained inlet since 1933, and have a history of variable internal structure due to the decline and resurgence of seagrass cover in recent decades (Orth et al. 2006).

This study investigated spatial gradients and long term changes in assemblage structure using (1) directed field surveys in 2009 and 2012 designed to detect the influence of inlet proximity on fish assemblage structure, and (2) analysis of a long-term trawl survey, conducted by the Maryland Department of Natural Resources, to evaluate yearly and decadal changes in the relative importance of internal and external forcing on fish assemblage structure. Ancillary indices of ocean forcing and internal structuring used in the analysis were mean tidal height and seagrass cover. Multivariate statistical tests examined associations between marine forcing and internal structuring on lagoon assemblage.

Methods

Directed survey: Field methods

Field sampling was conducted on August 18-19 (summer) and September 21-22, 2009 (fall), as well as August 8, 2012 (summer). Although separated by only a month, sampling was designated as occurring during separate seasons, as August represents the summer period of lagoon residence and growth, and fall (beginning in September) represents a period of species turnover when many juveniles initiate a fall egress from lagoon nursery habitats (Able and Fahay 1998). A 7-m benthic balloon trawl (3.8 cm body mesh, 0.64 cm mesh cod-end liner) was towed for 6 minutes (approx. 0.5 km) in north-south transects at each site. The coastal bays and associated nearshore ocean were sampled according to a stratified random sampling design, with sites randomly selected from a pre-established grid of sampling sites within discrete strata (Fig. 2.1). The lagoon strata were separated on a north-south transect, with the southernmost stratum proximal to the bays' confluence with the ocean within Isle of Wight Bay, the middle stratum including sites influenced by the St. Martin's River within Isle of Wight and Assawoman Bay, and the northern stratum distal to the Ocean City Inlet (OCI) and north of the mouth of the St. Martin's River within Assawoman Bay. The nearshore strata were also separated on a north-south transect, with the southern stratum south of the OCI, the middle stratum just north of the inlet, and the northernmost stratum farthest from the inlet.

Twelve sites were sampled in the nearshore marine zone (8-15 m depth) during each season in 2009. Due to logistic constraints, the nearshore assemblage was not sampled in 2012. Multivariate analyses (described below) showed significant differences between the coastal bays and nearshore ocean assemblage in both summer and fall seasons. Further, analysis of the 2009 assemblage (described in Results) indicated that the nearshore assemblage structure was unaffected by proximity to the coastal bays. Following these results, the nearshore ocean assemblage was assumed to be consistently homogeneous and different from the coastal bays.

Seven sites were sampled in MD northern coastal bays (<2 m depth) in summer 2009, with nine sites sampled in fall 2009 and summer 2012. Three sampling sites were randomly selected from three pre-determined lagoonal strata. Due to shallow waters (<1.5 m), sampling was restricted to those sites on the east side or southern channel of Isle of Wight Bay and the west side of Assawoman Bay (Fig. 2.1). Sites within the highly-trafficked Ocean City Inlet were also sampled in all seasons and years. Inlet samples were characterized by very low fish density and diversity; preliminary multivariate analyses also showed a very different assemblage structure here than in adjacent coastal bay and nearshore ocean sampling regions. Inlet samples were therefore considered unrepresentative of the local juvenile fish assemblage and not included in further analyses.

All juvenile fish species were identified to the species level, counted, and measured (total length) to 1.0 mm. Surface and bottom dissolved oxygen (mg L^{-1}), temperature (°C), and salinity were recorded using a conductivity, temperature, and depth profiler prior to each trawl deployment.

Directed survey: Assemblage analysis

To remove the influence of rare fish species, an inclusion rule was enforced. Those species that appeared in less than 5% of samples and represented less than 5% of individuals across all samples were removed from the analysis. Species selection was conducted separately for system-wide and intra-strata comparisons. In addition, invertebrate species were not considered. Species catch-per-unit-effort from each trawl was fourth-root transformed to prevent numerically dominant species from controlling the calculated similarity between site assemblages, while allowing for the influence of species that appear somewhat infrequently (Clarke 1993). Sites that contained no species were removed from further analysis.

Species abundances were compared across and within seasons, habitats, and years using an analysis of similarity (ANOSIM) procedure (Clarke 1993). To investigate the pattern of assemblage structure within the coastal bays with increasing distance from the ocean, a RELATE test by seriation (Clarke 1993) was used. For this test, each site is coded by its distance from the inlet, with a distance of "0" representing the inlet site closest to the ocean, decreasing negative numbers representing increasing distance into the ocean, and increasing positive numbers representing increasing distance into the bays. Bray-Curtis similarities between sites are then ranked from most- to least-correlated. The degree to which the order of ranked correlations corresponds to the order of site distances reflects the degree of serial spatial structure of the fish assemblage. The RELATE test was conducted across all environments, and then separately for coastal bay and nearshore sites. Summer and fall seasons in 2009 were considered separately.

Similarities between site assemblages and the species that drive them were depicted using correspondence analysis (CA) in the vegan library (Oksanen et al. 2013) of the R statistical software (R Core Team 2013). As species collected during sampling may respond in a modal fashion to underlying environmental gradients, a reciprocal averaging approach that assumes modal response is better suited to visualize the data than a method that assumes linear response (i.e., principal components analysis). In addition, the influence of season was removed prior to analysis in order to avoid the skewing of ordination results due to species turnover. Environmental vectors (depth, distance to

OCI, surface temperature, and salinity) were fitted to the ordination *post hoc*. Because surface and bottom environmental variables were highly correlated, only surface values were used. Environmental vectors that were significantly associated with the CA were used to explain variation in assemblage structure.

Long-term survey: Data sources

Data from a multi-decadal fishery survey undertaken by the Maryland Department of Natural Resources' Coastal Bays Fisheries Investigation (CBFI) were used to investigate long-term trends in juvenile fish assemblage (Murphy and Secor 2006). The CBFI has been conducted on a monthly basis between May/June and October since 1989, with seven sites within the northern coastal bays (Isle of Wight and Assawoman bays) and tributaries surveyed using a 5 m semi-balloon trawl (3.2 cm body mesh, 1.3 cm mesh cod-end liner). Data from June 1989 to October 2012 were used in this analysis. To follow system-wide changes in lagoon fish assemblage, fish catch was averaged by species across four of seven surveyed CBFI sites within the northern coastal bays (Fig. 2.1). Three CBFI sites were not selected for the analysis because they were within bay tributaries (i.e., salinity 5-10 units lower than bay sites), and thus not representative of lagoon assemblage. Monthly trawl catches were averaged by species and season: spring (May, June), summer (July, August), and fall (September, October). Rare species (< 5% threshold in abundance or incidence) were excluded and species catch-per-unit effort was fourth-root transformed. River and Atlantic herrings were excluded from the analysis because CBFI sampling did not fully capture the spring-time period of occurrence for these species. Surface temperature and salinity were recorded by the CBFI prior to each trawl deployment, and were averaged by season for use in assemblage structure analysis.

External ocean forcing of assemblage structure was represented by the North Atlantic Oscillation Index (NAO), the difference of atmospheric pressure between the Icelandic low and Azores high (Hurrell and Deser 2009). NAO alters patterns of precipitation, temperature, and wind forcing and has been associated with shifts in productivity and marine assemblage in the northern Atlantic, including that of estuarine fishes (Attrill and Power 2002), zooplankton (Fromentin and Planque 1996), and marine fish stocks (Parsons and Lear 2001). Monthly average NAO index was downloaded from the National Weather Service's Climate Prediction Center (Climate Prediction Center Internet Team 2013). Months were averaged over seasons to align the NAO Index with the CBFI dataset.

Mean tide level (MTL), the arithmetic mean of low and high tides, is likely a local manifestation of NAO forcing as MTL and NAO were significantly and negatively correlated for the analyzed time period (Fig. 2.2). Due to the low level of freshwater input into the bays, changes in MTL are due to water inflow from the nearshore ocean through the Ocean City inlet. Because of this, MTL was used as an additional proxy for external environmental forcing. MTL records from the Ocean City Inlet Station (#8570283) of the NOAA tides and currents system was incomplete, so data from the highly-correlated (Fig. 2.3, $r^2 = 0.966$, $p < 0.001$) Lewes, DE Station (#8557380), located 51 km north of the Ocean City Inlet, were used (Center for Operational Oceanographic Products and Services 2013). MTL was averaged across season to align the sampling frequency with the CBFI dataset and reduce the influence of local tidal anomalies.

Submerged aquatic vegetation (SAV) cover within the northern coastal bays was used as a proxy of internal structural forcing, while CBFI-recorded temperature and salinity were used as proxies of internal environmental forcing. SAV cover data were collected by the Virginia Institute of Marine Science's Submerged Aquatic Vegetation Survey. Yearly SAV cover (ha) was estimated through a combination of black-and-white aerial photography (scale = 1:24,000) and ground surveys (Orth et al. 2012). As only one observation of SAV cover per region is made per year, each year's observation was used for all seasons within that year.

Long-term survey: Time series analysis

Assemblages for each season-year combination were ordinated using correspondence analysis. Periodic (i.e., seasonal) variation was removed prior to analysis because assemblage changes due to the seasonal appearance of certain species were not of interest in this study. In addition, effects that drive large amounts of species turnover, like seasonal change, can lead to the "arch effect" in CA, where the second ordination axis becomes a nonlinear function of the first. CA axis scores of season-year combinations were plotted over time to display temporal trends in species composition. Environmental and CA axis time series were analyzed for significant autocorrelative lags and periodicities. In addition, rapid changes in the mean of the environmental and CA axis time series were identified in a likelihood framework through change point analysis. Change point analyses detect the point, or points, at which the statistical properties of a series of observations change (Killick et al. 2010). Environmental variables and seasonal change in environmental variables over each time step were then correlated with CA axis score and seasonal change in CA score, respectively. Environmental variables that were significantly correlated with the CA time series or the derivative of the CA time series were visually inspected for relations with change in fish assemblage structure. Species that characterized assemblage shifts identified through CA analysis were analyzed for changes in CPUE over the time series.

Results

Directed Survey

Environmental clines were observed in the northern coastal bay but not in nearshore strata. In 2009, thermal differences between the coastal bays and nearshore ocean shifted between months, where August surface and bottom temperatures were consistently warmer within the coastal bays but September temperatures did not differ (Table 2.2). Surface and bottom salinity within the coastal bays increased with decreased distance to the inlet in all sampling months and years (Table 2.2). The cline was largest in 2009, with a gradient spanning 2.47 and 5.38 salinity units in August and September, while only spanning 1.44 in August 2012. Ocean salinity was stable with regards to distance from the inlet, remaining relatively constant across the strata within each month.

Forty-six fish and 19 invertebrate species were identified across all sites and seasons, comprising 26,959 and 322 individuals, respectively. Numerical catches varied among habitat types, seasons, and years. In summer 2009, total catch-per-unit-effort (CPUE, fish trawl^{-1}) of fish species was highest in the coastal bays, lowest in the inlet and intermediate in the nearshore ocean (Table 2.2). The pattern in total CPUE between the coastal bays and nearshore ocean was reversed in fall 2009 with the coastal bays displaying an intermediate CPUE and the nearshore ocean having the highest CPUE, while the inlet sites remained the lowest. The coastal bay sites in summer 2012 had the highest CPUE among all habitats and seasons. Much of the variation in catch was due to large schools of anchovy, which is reflected in the large standard deviation associated with high catch levels. Relative patterns in species richness across habitats were similar in both months in 2009. Average species richness was highest in summer 2009 for all three habitats and lowest in fall 2009 (declines of 28-60% from summer values), with larger declines in the coastal bays than in the nearshore sites. Summer 2012 species richness in the coastal bays was intermediate compared to the 2009 seasons.

Directed survey: Assemblage analysis

Of the 46 species identified in the survey, 33 passed the inclusion rule and were included in further assemblage analyses (Table 2.3). Species assemblage did not significantly differ among coastal bay strata in any season or year, but significantly differed between environments, seasons, and years (ANOSIM, Table 2.4). In both the summer and fall of 2009, coastal bay species assemblage varied in a serial manner with increasing distance from the inlet (RELATE, $p<0.001$). Similar to 2009, coastal bay strata were not significantly different in summer 2012 (Table 2.4). However, a significant serial progression of lagoon assemblage was not detected in the summer 2012 survey (i.e., RELATE, $p=0.18$). Serial assemblage change was also not seen in the nearshore ocean during either season (i.e., RELATE, summer: $p=0.10$; fall: $p=0.18$).

Non-significant assemblage seriation across the nearshore strata indicated that the ocean assemblage was relatively homogeneous in comparison to the coastal bays. Due to the consistent homogeneity and difference from the coastal bays, the nearshore ocean was not included when sampling was repeated in 2012.

Correspondence analysis of the coastal bay fish assemblage placed most August 2012 samples near the center of the ordination, with positive near-zero values on the first axis and negative near-zero values on the second axis (Fig. 2.4). These samples were characterized by species common across all sample locations and times. The species included bay anchovy, silver perch, hogchoker, bluefish, and spot. Two samples, one each from the northern and central arrays, were placed more negatively on the second axis. The placement of these samples seems to be due to the presence of pinfish and lookdown, respectively. With the exception of the previously mentioned samples, species composition between sites in August 2012 was more self-similar than 2009 samples. August 2009 samples were ordinated mostly in the fourth quadrant, ranging from negative values on the first axis and near-zero values on the second axis to positive values on the second axis and near-zero values on the first axis. The samples of the former cluster were associated with the presence of smooth butterfly rays, Atlantic croaker, striped anchovy, and black sea bass. The samples of the latter August 2009 cluster were associated with the presence of northern pipefish, searobin, naked gobies, harvestfish, and crevalle jack. September 2009 sites were the least self-similar of those sampled. As such, there was no discernable pattern in September species composition.

Post-hoc correlation of environmental variables to CA scores aligned samples along significant gradients of surface salinity ($r^2 = 0.458$, $p < 0.001$) and distance to the

OCI ($r^2 = 0.259$, $p = 0.036$) (Fig. 2.4, 2.5). The gradient in salinity directly opposed a gradient of increasing distance from the OCI, reflecting the trend of decreased salinity with increasing distance from oceanic influence. August 2009 sites were strongly ordinated along this salinity/distance gradient, such that assemblage may have been driven by salinity. September 2009 scores were more evenly distributed across gradients, suggesting that forcing other than the measured environmental variables may have influenced assemblage structuring in this month.

Long-term survey:

The NAO index exhibited a decreasing trend, ranging from > 0.5 to < -0.5 over the course of the time series (Fig. 2.6). MTL exhibited a corresponding increasing trend, with a range of 30 centimeters over the period investigated. The NAO time series possessed significant partial autocorrelation at a 2-year lag (i.e., greater than 2 standard errors above zero, (Cryer and Chan 2008)) throughout the time series, but increased in year-to-year variation after 2005. MTL did not seem to display a corresponding change in variance over time.

SAV increased over most of the years investigated, but exhibited a large die-off event (> 95% cover area lost) between 2010 and 2011 surveys (Fig. 2.7). Following a period of very low levels from 1989 to 1992, SAV experienced a period of rapid expansion between 1993 and 1999, increasing from 20.36 to 364.17 ha. SAV cover was relatively stable at 340 ha from 2000 to 2007, whereafter it rapidly increased to 587.90 ha in 2010. The sudden decrease in SAV cover in 2011 may have been due to an acute high-temperature event immediately following the 2010 SAV survey or increased sediment loadings due to Hurricane Irene and Tropical Storm Lee (Orth et al. 2012). Following 2010, SAV cover has remained at < 30 ha.

With the exception of a cold spring in 1990, temperature within the coastal bays remained relatively constant over the time series (Fig. 2.8). Temperature oscillated at a period of 5.5 years, longer than the observed oscillation of the NAO index. Similarly, salinity had no observable trend over time. However, salinity did exhibit two long-term excursions from typical values: a high-salinity period between 1990 and 1993, and a low-salinity period between 2003 and 2007. These periods were characterized by rapid shift towards more extreme values at onset and an equally rapid shift towards more typical values at the conclusion of the excursion.

Long-term survey: Assemblage analysis

Of the 81 fish species recorded, 50 fulfilled the inclusion rule (Table 2.5). After averaging CPUE within each season, bay anchovy had the highest catch and the second-highest incidence across seasons. While summer flounder had the sixth-highest catch, it was the most common, occurring in every season of the time series. Spot had the second-highest catch and was present in 83% of seasons, while weakfish had the third-highest catch and was present in 69% of seasons. Structure-oriented species, such as American eel, oyster toadfish, and tautog were increasingly prevalent in the most recent decade (Fig. 2.9). Conversely, marine species tended to have their highest catch prior to 2005 (Fig. 2.10).

Correspondence analysis suggested a gradient on the first CA axis from more marine species associated with negative values (harvestfish, Spanish mackerel, blue cornetfish, crevalle jack) to more structure-oriented species associated with positive values (American eel, naked goby, striped blenny) (Fig. 2.11, ecological characterizations following Able and Fahay (2010)). Ordination on the second axis was driven mostly by the presence of pinfish, scup, or pigfish and was not associated with environmental gradients (see below). CA scores on the first axis showed a slight increasing trend from 1989 until 2003, after which the scores dropped to a low level until 2006 (Fig. 2.6-2.8). A significant change point ($p < 0.05$) occurred in 2007, after which the first axis CA scores shifted to much higher levels than seen previously. The scores of the first axis remained here through the rest of the time series. The second axis showed no discernable trend until after 2000, where shifts between positive and negative scores became more prevalent than in the preceding decade.

Significant gradients of MTL ($r^2 = 0.30$, $p < 0.001$), NAO ($r^2 = 0.15$, $p = 0.009$), and SAV ($r^2 = 0.177$, $p = 0.009$) were found between season-year combinations in *post-hoc* analyses (Fig. 2.12). All environmental vectors were more strongly correlated with the first correspondence analysis axis than the second, with SAV and MTL being positively correlated and NAO being negatively correlated. NAO, however, was the environmental vector most associated with the second axis. The residuals of the environmental trends were not significantly associated with either CA axis. Therefore, vectors for MTL, SAV, and NAO most likely reflect the temporal trends represented by the first CA axis.

The first CA axis oscillated in-phase with the NAO index for the first half of the series (Fig. 2.6). Following the low CA1 values observed for the 2003-2007 period, the two series lost correspondence. As NAO and MTL are negatively correlated, CA1 scores oscillated antiphasically with MTL early in the series (Fig. 2.6). Synchrony between MTL and CA1, however, was not as strong as that observed between CA1 and NAO. CA2 was unassociated with variation in both NAO and MTL.

As the SAV time series was sampled at a lower frequency than the correspondence axes, comparisons between the two are more tenuous. Both CA1 and the SAV series increased over time, although the 2011 collapse in SAV was not reflected in a shift to less-structure-oriented-species in the first correspondence axis (Fig. 2.7). Changes in temperature within the coastal bays showed little correspondence with assemblage changes on the first correspondence analysis axis (Fig. 2.8). Conversely, changes in salinity were coincident with the downward shift in CA1 during the period 2003-3007. The wholesale shift to higher CA1 values after 2007 corresponded to the recent period of higher salinities.

Discussion

Comparative analysis of short-term, fine-spatial-scale assemblages in conjunction with long-term, coarse-scale spatial assemblage changes showed that the relative influence of external (NAO, MTL) and internal (SAV, temperature, salinity) environmental forcing on the juvenile fish community of the Maryland coastal lagoon system is spatiotemporally dynamic. As revealed in the short-term survey, spatial structure of the juvenile fish community and distribution of fish catch within Maryland's northern coastal bays varied between study months in a single year, a temporal scale over which the environment external to the lagoon was relatively constant, but the internal environment changed substantially in temperature. The role of external and internal forcing on the spatial structure of the lagoon fish community varied across years: the 2009 summer assemblage changed sequentially with increasing distance from the Ocean City inlet while the 2012 assemblage was spatially homogeneous and lacked significant serial changes. For the long-term survey, external dynamics seemed to be the major driver of the overall lagoon assemblage over the first two decades of the analyzed time series, with a shift to a more internally-structured assemblage in the last six years.

The coastal bay assemblage occurred over a gradual gradient in salinity (change of 1.4 – 5.4 units). Although salinity gradients are often cited as a cause of species assemblage changes (Weinstein et al. 1980, Wagner 1999), a gradient over the noted salinity range would not be expected to be of biological importance for the marine-estuarine species found in the Maryland lagoons (Bulger et al. 1993). Guelorget and Perthuisot (1992) noted that, in benthic invertebrate communities of microtidal Mediterranean lagoons, organization of biota often followed zonal isohaline patterns despite large differences in the range and direction of the salinity gradient across coastal lagoons. As such, they theorized that lagoonal biological zonation may occur due to the degree of interaction between internal, lagoon processes and external, marine processes that is reflected in, but not necessarily the direct result of salinity gradients.

The metacommunity framework for coastal lagoon fishes outlined by Mouillot (2007) posits that coastal lagoon assemblages are a reflection of dynamic interactions between 1) the degree of species flow into the lagoon from a homogeneous pool of marine species and 2) the degree of niche separation within the lagoon. In our study, non-significant results of the RELATE by seriation and ANOSIM tests within the nearshore habitat of 2009 supported Mouillot's concept: a homogeneous marine species source supplying a species pool to an environmentally structured coastal lagoon. These features may have been particularly prevalent in 2009. In that year, the lagoon experienced the highest MTL in 20 years, subjecting the lagoon to strong marine forcing. In addition, SAV within the northern bays was at an all-time high (second only to 2010 levels, Orth et al. 2012), such that the degree of niche structure was also fairly large in 2009. Conversely, the 2012 survey was conducted during a low-MTL, low-SAV period, which would lead to a comparatively lower-level of environmental structure. The differences in external and internal forcing conditions between years may explain why the RELATE test by seriation between coastal bay sites was significant in 2009 but not 2012. These contrasting years follow Mouillot's metacommunity framework, where the interplay between internal and external environments dictates a lagoon's spatial assemblage.

While the long-term juvenile fish survey was not as spatially intensive as the short-term survey, assemblage changes due to variation in the degree of internal and external forcing was evident. From the onset of the survey in 1989 until summer 2002, increases and decreases in the North Atlantic Oscillation Index corresponded to more structure-oriented and marine assemblages, respectively. A significant change point ($p < 0.05$) in the first correspondence analysis axis occurred after summer 2007, where the assemblage seemed to switch to internal dynamics following a return to normal salinity after a rapid and sustained drop in salinity and sustained high levels of SAV.

The North Atlantic Oscillation has been associated with changes in population dynamics, reproduction, and distribution of both terrestrial and aquatic species (Forchhammer et al. 2001, Attrill and Power 2002). The effects of the NAO are evident at population, community, and individual scales and vary greatly between regions (Parsons and Lear 2001). Otterson et al. (2001) suggest that the ecological effects of the NAO can be classified into those that are a response to variables that are directly controlled by the NAO ("direct"), those that are a response to a factor controlled by the NAO through several intermediate steps ("indirect"), and those that are a response to all of the effects of an extreme NAO event within a given time period ("integrated"). Since correspondence analysis was used to reduce the dimensionality of the catch data collected by the CBFI, information on individual responses to changes in NAO are lost. As such, this study focused on integrated community responses to extreme NAO effects. It is likely that the NAO effects operate at more subtle scale than this study can identify.

Infrequent events, such as hurricanes, droughts, and floods can often change the biological legacy of a region for years or decades after the conclusion of the disturbance (Foster et al. 1998). Large and rapid shifts in environmental forcing are often associated with changes in species composition, excluding species less tolerant of the new environmental regime (Kröncke et al. 2013). In the Maryland coastal bays during 2002, salinity dropped by more than 10 units—from full-strength seawater to salinities more typical of polyhaline estuaries—in less than a year. The relatively rapid shift to less-saline waters may have allowed for the increased presence of estuarine species at the expense of less-tolerant marine species, reflected in the noted shift to "structure-oriented" estuarine fishes following salinity recovery. Rapid changes in salinity have been shown to impact the biomass and species diversity of ecosystems (Baldwin and Mendelssohn 1998), though results are often confounded by changes in temperature and other physical variables (McKinnon et al. 2003, Buchsbaum et al. 2006).

Coastal development – tourism, residential growth, industry, agriculture and navigation – have caused increased hardening of the connections between lagoon and marine environments (Duck and da Silva 2012). Because of this, inlets are often dredged and maintained, along with shoreline reinforcement typical of coastal communities. The Ocean City inlet, for instance, has been continually maintained since a natural wash-over event opened it during a hurricane in 1934 (Carruthers et al. 2013). In many developed coastal lagoons, estuarine and freshwater influence is reduced to the point of making fully marine or hypersaline bays and restructuring the geophysical processes of the lagoon. Duck and da Saliva (2012) note, for example, that the rivers that once fed the Venice Lagoon have been completely routed away from the system, causing increased depth, wave action, and degradation of marsh area. In systems impacted to a lesser degree, sediments of lagoonal systems quickly transition from biologically-active mud to biologically-inactive sand a few years after inlet reinforcement and dredging, which results in a shift away from demersal production typical of coastal lagoons (Silva et al. 2004). With increasing coastal populations, this trend may continue and external, marine forces may overwhelm typical, internal lagoon processes.

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Tables

Table 2.1. Characteristics of the Maryland northern coastal bays (adopted from Dennison et al. 2009).

Lagoon	Surface Area (km^2)	Watershed Area (km^2)	Surface Area / Watershed Area	Av. Depth (m)	Volume (10^6 m^3)	Flushing rate (days)	Human Population
Assawoman	20.9	24.7	0.85	1.2	27	21.1	13600
Isle of Wight	21.1	51.8	0.41	1.22	22.85	9.45	18600

Table 2.2. Catch-per-unit effort of fish species, fish species richness, and environmental data collected during the targeted surveys of Aug/Sept 2009 and Aug 2012. Due to instrument malfunction, dissolved oxygen was only recorded for Aug 2012 survey.

Date	Array	Depth	CPUE (fish trawl^{-1})		Species Richness		Temperature (°C)		Salinity		Dissolved Oxygen (mg/L)	
			Mean	SD	Mean	SD	Surface	Bottom	Surface	Bottom	Surface	Bottom
Aug-09	CB N	1.4	370.7	65.3	9.5	3.5	28.4	28.4	25.7	25.8		
Aug-09	CB C	1.5	717.7	211.7	8.5	0.7	28.3	27.7	27.8	28.1		
Aug-09	CB S	1.3	843.3	954.0	8.3	2.1	28.0	27.7	28.2	28.3		
Aug-09	INL	4.9	40.0	55.2	4.3	2.1	27.4	27.2	28.8	28.9		
Aug-09	OC C	8.2	221.9	154.7	10.5	4.5	24.4	23.1	30.0	30.3		
Aug-09	OC S	9.7	206.5	123.1	10.8	2.5	23.9	22.2	30.0	30.4		
Aug-09	OC N	9.6	385.2	242.1	8.5	3.1	23.9	23.0	29.9	30.2		
Sep-09	CB N	1.2	203.2	310.0	6.3	0.6	21.9	21.8	23.8	23.8		
Sep-09	CB C	1.1	4.6	4.1	2.3	2.1	22.2	22.2	25.9	25.9		
Sep-09	CB S	1.7	3.2	2.6	3.0	1.0	22.3	22.3	29.2	29.1		
Sep-09	INL	4.7	5.6	5.9	2.0	1.2	22.2	22.1	29.3	29.3		
Sep-09	OC C	10.6	153.9	82.2	10.3	4.6	22.8	21.5	29.0	29.8		
Sep-09	OC S	10.2	544.6	437.7	9.3	2.8	22.4	21.6	29.4	29.6		
Sep-09	OC N	11.1	1397.6	2320.1	7.5	3.7	22.6	21.4	29.2	29.7		
Aug-12	CB N	1.1	466.8	161.3	9.0	2.7	28.6	27.9	26.0	26.6	5.9	4.1
Aug-12	CB C	1.5	615.2	191.1	5.7	2.1	28.5	28.4	26.7	26.8	5.4	4.5
Aug-12	CB S	1.3	2073.0	1172.4	9.3	3.1	28.0	28.1	27.5	27.3	6.6	6.4

Table 2.3. Catch-per-unit-effort (CPUE) and standard deviation (SD) of species collected during the targeted survey of Aug/Sept 2009 and Aug 2012. Species used in the assemblage analysis are indicated with an asterisk (*).

Species		CPUE Mean	CPUE SD
Bay anchovy*	*Anchoa mitchilli*	447.00	124.75
Weakfish*	*Cynoscion regalis*	28.28	6.70
Silver perch*	*Bairdiella chrysoura*	16.44	4.52
Butterfish*	*Peprilus triacanthus*	9.18	2.76
Spot*	*Leiostomus xanthurus*	9.02	2.83
Scup*	*Stenotomus chrysops*	7.88	4.72
Striped anchovy*	*Anchoa hepsetus*	6.17	1.25
Atlantic croaker*	*Micropogonias undulatus*	4.19	1.32
Blue crab	*Callinectes sapidus*	3.90	0.84
Atlantic moonfish*	*Selene setapinnis*	3.34	1.10
Longfin Inshore Squid	*Doryteuthis pealeii*	2.02	0.39
Spotted hake*	*Urophycis regia*	1.64	0.50
Summer flounder*	*Paralichthys dentatus*	1.47	0.80
Bluefish*	*Pomatomus saltatrix*	1.18	0.31
Lady crab	*Ovalipes ocellatus*	0.85	0.33
Black seabass*	*Centropristis striata*	0.59	0.22
Striped cusk eel*	*Ophidion marginatum*	0.59	0.23
Hogchoker*	*Trinectes maculatus*	0.37	0.12
Common sea star	*Asterias forbesi*	0.27	0.15
Pinfish*	*Lagodon rhomboides*	0.26	0.16
Common spider crab	*Libinia emarginata*	0.24	0.17
Black-clawed mud crab	*Panopeus herbstii*	0.23	0.14
Atlantic menhaden*	*Brevoortia tyrannus*	0.21	0.08
Windowpane flounder*	*Scophthalmus aquosus*	0.17	0.07
Bullnose ray*	*Myliobatis freminvillei*	0.14	0.06
Northern pipefish*	*Syngnathus fuscus*	0.13	0.05
Northern puffer*	*Sphoeroides maculatus*	0.12	0.07
Oyster toadfish*	*Opsanus tau*	0.11	0.06
Bluntnose ray*	*Dasyatis sayi*	0.10	0.06
Hermit crab	*Pagurus* sp.	0.10	0.10
Smooth dogfish*	*Mustelus canis*	0.10	0.04
Inshore lizardfish*	*Synodus foetens*	0.09	0.06
Keyhole sand dollar	*Mellita quinquiesperforata*	0.08	0.08

Southern kingfish*	*Menticirrhus americanus*	0.08	0.05
Atlantic jacknife clam	*Ensis directus*	0.07	0.05
Crevalle jack*	*Caranx hippos*	0.07	0.05
Naked goby*	*Gobiosoma bosc*	0.07	0.04
Northern searobin*	*Prionotus carolinus*	0.07	0.04
Blackcheek tonguefish*	*Symphurus plaguisa*	0.06	0.06
Clearnose skate*	*Raja eglanteria*	0.06	0.03
Bluerunner*	*Caranx crysos*	0.06	0.04
Striped searobin*	*Prionotus evolans*	0.05	0.04
Smooth butterfly ray	*Gymnura micrura*	0.05	0.03
Harvestfish	*Peprilus alepidotus*	0.05	0.03
Whelk species	*Busycon* sp.	0.04	0.04
Spider crab species	*Libinia* sp.	0.04	0.03
Smallmouth flounder	*Etropus microstomus*	0.03	0.03
Lookdown	*Selene vomer*	0.03	0.03
Lined seahorse	*Hippocampus erectus*	0.03	0.03
Stout razor clam	*Tagelus plebius*	0.02	0.02
Feather blenny	*Hypsoblennius hentz*	0.02	0.02
Spanish mackerel	*Chilomycterus schoepfii*	0.02	0.02
Striped burrfish	*Scomberomorus maculatus*	0.02	0.02
Tautog	*Tautoga onitis*	0.02	0.02
Brown shrimp	*Penaeus aztecus*	0.02	0.02
Atlantic moon snail	*Cancer irroratus*	0.02	0.02
Atlantic rock crab	*Neverita duplicata*	0.02	0.02
Black drum	*Pogonias cromis*	0.02	0.02
Northern kingfish	*Menticirrhus saxatilis*	0.02	0.02
Cancer crab	*Cancer* sp.	0.02	0.02
Atlantic horseshoe crab	*Limulus polyphemus*	0.02	0.02
White mullet	*Mugil curema*	0.02	0.02
Commensal crab	*Carcinus maenas*	0.02	0.02
Green crab	*Pinnixia* sp.	0.02	0.02
King mackerel	*Scomberomorus cavalla*	0.02	0.02

Table 2.4. Analysis of similarity (ANOSIM) with season and habitat as the factors of a two-way test. The *R*-statistic and p-value of the ANOSIM and resulting pair-wise contrasts are shown.

	Summer		Fall		All	
Factors	R	p	R	p	R	P
Main Effects						
Season					0.434	0.001
Habitat					0.755	0.001
Pair-wise contrasts						
CB v INL	0.798	0.008	0.517	0.003	0.627	0.005
CB v OC	0.633	0.001	0.856	0.001	0.796	0.001
INL v OC	0.765	0.004	0.934	0.001	0.778	0.001

Table 2.5. Catch-per-unit-effort (CPUE), standard deviation (SD), and percent incidence of species collected by the Coastal Bays Fisheries Investigation (CBFI) in Assawoman and Isle of Wight Bays between 1989 and 2012. Species used in the assemblage analysis are indicated with an asterisk (*).

Species		CPUE		
		Mean	SD	Incidence (%)
Bay Anchovy*	*Anchoa mitchilli*	58.48	8.85	97.22
Spot*	*Leiostomus xanthurus*	34.46	10.67	83.33
Weakfish*	*Cynoscion regalis*	13.34	3.04	69.44
Atlantic Croaker*	*Micropogonias undulatus*	5.29	1.73	72.22
Silver Perch*	*Bairdiella chrysoura*	3.07	0.62	66.67
Summer Flounder*	*Paralichthys dentatus*	3.02	0.28	100.00
Naked Goby*	*Gobiosoma bosc*	2.11	1.15	43.06
Winter Flounder*	*Pseudopleuronectes americanus*	1.32	0.22	63.89
Atlantic Menhaden*	*Brevoortia tyrannus*	1.00	0.50	37.50
Smallmouth Flounder*	*Etropus microstomus*	0.95	0.13	76.39
Black Sea Bass*	*Centropristis striata*	0.88	0.13	80.56
Pipefishes*	*Gasterosteiformes* sp.	0.83	0.14	77.78
Northern Searobin*	*Prionotus carolinus*	0.81	0.16	69.44
Spotted Hake*	*Urophycis regia*	0.72	0.25	41.67
Hogchoker*	*Trinectes maculatus*	0.70	0.18	56.94
Northern Puffer*	*Sphoeroides maculatus*	0.62	0.09	70.83
Inshore Lizardfish*	*Synodus foetens*	0.58	0.11	51.39
Atlantic Silverside*	*Menidia menidia*	0.58	0.33	30.56
Oyster Toadfish*	*Opsanus tau*	0.55	0.14	52.78
Striped Anchovy*	*Anchoa hepsetus*	0.44	0.15	45.83
Lined Seahorse*	*Hippocampus erectus*	0.40	0.06	52.78
Pigfish*	*Orthopristis chrysoptera*	0.37	0.21	18.06
Windowpane*	*Scophthalmus aquosus*	0.32	0.05	50.00
Northern Kingfish*	*Menticirrhus saxatilis*	0.30	0.06	44.44
Butterfish*	*Peprilus triacanthus*	0.29	0.07	41.67
American Eel*	*Anguilla rostrata*	0.23	0.07	26.39
Striped Searobin*	*Prionotus evolans*	0.19	0.04	40.28
Spotfin Mojarra*	*Eucinostomus argenteus*	0.16	0.08	16.67
Black Drum*	*Pogonias cromis*	0.15	0.04	20.83
Blackcheek Tonguefish*	*Symphurus plagiusa*	0.15	0.04	29.17
Bluefish*	*Pomatomus saltatrix*	0.13	0.02	37.50
Clearnose Skate*	*Raja eglanteria*	0.11	0.03	26.39
Pinfish*	*Lagodon rhomboides*	0.11	0.04	16.67
Southern Kingfish*	*Menticirrhus americanus*	0.10	0.04	11.11

Green Goby*	*Microgobius thalassinus*	0.08	0.03	18.06
Crevalle Jack*	*Caranx hippos*	0.07	0.02	22.22
Feather Blenny*	*Hypsoblennius hentz*	0.06	0.02	15.28
Striped Burrfish*	*Chilomycterus schoepfii*	0.06	0.02	18.06
Tautog*	*Tautoga onitis*	0.06	0.02	15.28
Mummichog*	*Fundulus heteroclitus*	0.04	0.02	8.33
Fourspine Stickleback	*Apeltes quadracus*	0.03	0.02	4.17
Striped Blenny*	*Chasmodes bosquianus*	0.02	0.01	6.94
Lookdown*	*Selene vomer*	0.02	0.01	8.33
Scup*	*Stenotomus chrysops*	0.02	0.01	6.94
Smooth Butterfly Ray*	*Gymnura micrura*	0.02	0.01	8.33
Planehead Filefish*	*Stephanolepis hispida*	0.02	0.01	6.94
Harvestfish*	*Peprilus paru*	0.02	0.01	5.56
Southern Stingray*	*Dasyatis americana*	0.02	0.01	8.33
Bluespotted Cornetfish*	*Fistularia tabacaria*	0.02	0.01	8.33
Smooth dogfish	*Mustelus canis*	0.02	0.01	2.78
Skilletfish	*Gobiesox strumosus*	0.02	0.01	4.17
Rainwater Killifish	*Lucania parva*	0.01	0.01	1.39
Red Snapper	*Lutjanus campechanus*	0.01	0.01	2.78
Striped Killifish	*Fundulus majalis*	0.01	0.01	1.39
Atlantic Moonfish*	*Selene setapinnis*	0.01	0.01	5.56
Spanish Mackerel*	*Scomberomorus maculatus*	0.01	0.01	5.56
Cobia	*Rachycentron canadum*	0.01	0.01	2.78
Atlantic Spadefish	*Chaetodipterus faber*	0.01	0.01	4.17
Gray Triggerfish	*Balistes capriscus*	0.01	0.01	2.78
Striped Cusk-eel	*Ophidion marginatum*	0.01	0.01	4.17
Pollock	*Pollachius virens*	0.01	0.01	2.78
Sheepshead Minnow	*Cyprinodon variegatus*	0.01	0.01	2.78
Conger Eel	*Conger oceanicus*	0.01	0.01	2.78
White Perch	*Morone americana*	0.01	0.01	1.39
Sheepshead	*Archosargus probatocephalus*	0.01	0.00	2.78
Gizzard Shad	*Dorosoma cepedianum*	0.00	0.00	1.39
Gray Snapper	*Lutjanus griseus*	0.00	0.00	1.39
Atlantic Cutlassfish	*Trichiurus lepturus*	0.00	0.00	1.39
Northern Sennet	*Sphyraena borealis*	0.00	0.00	1.39
Silver Hake	*Merluccius bilinearis*	0.00	0.00	1.39
Slashcheek Goby	*Ctenogobius pseudofasciatus*	0.00	0.00	1.39
Northern Stargazer	*Astroscopus guttatus*	0.00	0.00	1.39
Gag	*Mycteroperca microlepis*	0.00	0.00	1.39

Orange Filefish	*Aluterus schoepfii*	0.00	0.00	1.39
Spotfin Butterflyfish	*Chaetodon ocellatus*	0.00	0.00	1.39
Dwarf Goatfish	*Upeneus parvus*	0.00	0.00	1.39
White Mullet	*Mugil curema*	0.00	0.00	1.39
Cunner	*Tautogolabrus adspersus*	0.00	0.00	1.39
Short Bigeye	*Pristigenys alta*	0.00	0.00	1.39
Spottail Pinfish	*Diplodus holbrooki*	0.00	0.00	1.39
King Mackerel	*Scomberomorus cavalla*	0.00	0.00	1.39

Figures

Figure 2.1. Sampling sites for targeted survey (Summer and Fall 2009, Summer 2012) and Coastal Bays Fisheries Investigation (CBFI) sites. Open squares represent unused CBFI sites within the northern coastal bays. The northern (N), central (C), and southern (S) arrays used in the direct survey are labeled. Similarly, the sub-embayments used in the CBFI (Assawoman Bay (AW), Isle of Wight Bay (IW), St. Martin's River (SM), and the Ocean City Inlet (INL)) are labeled.

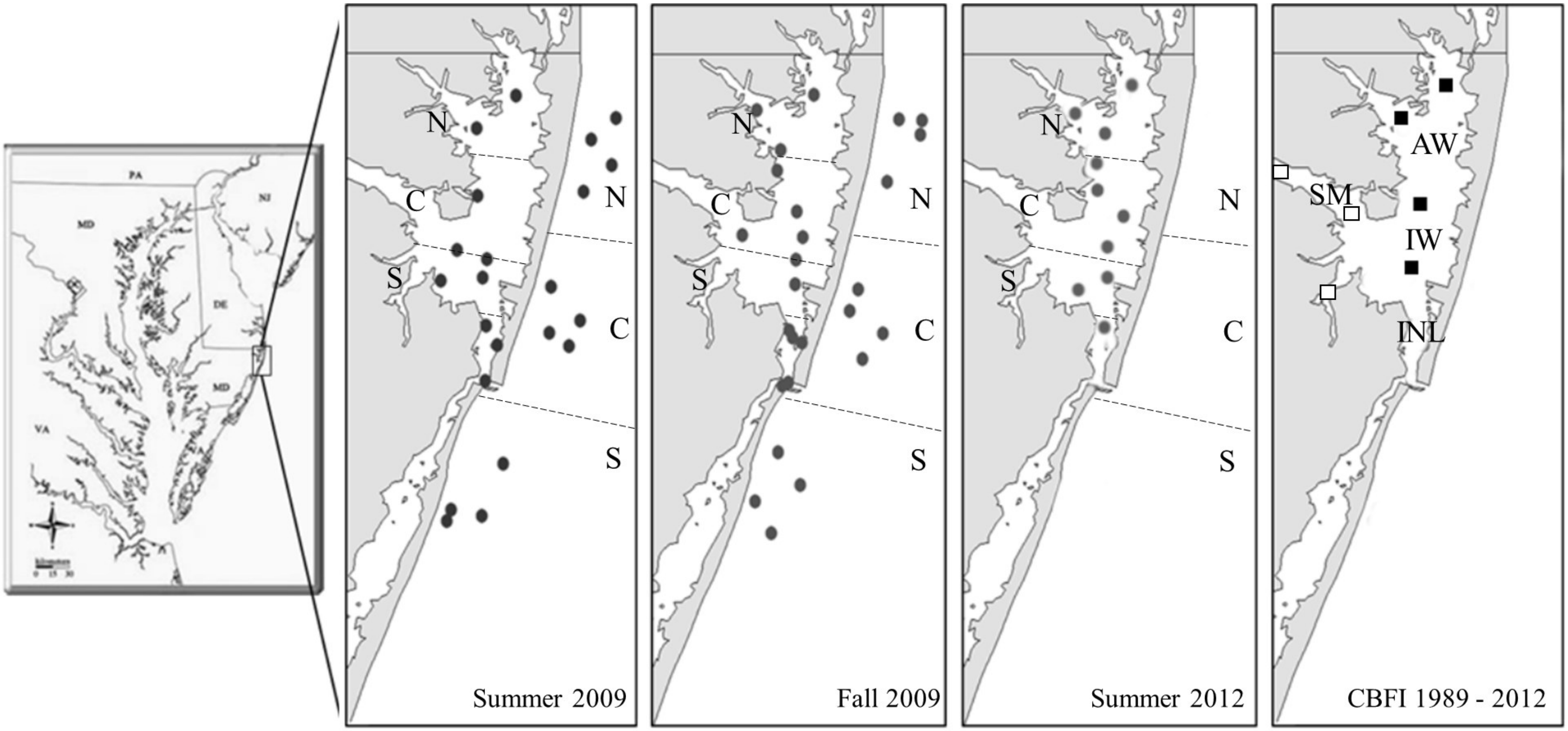


Figure 2.2. A) North Atlantic Oscillation (NAO) vs. Mean Tide Level (MTL) and (B) seasonal change in NAO vs. seasonal change in MTL for all points in the time series. Series are significantly correlated (A: $r = -0.558$, $p < 0.001$; B: $r = -0.431$, $p < 0.001$).

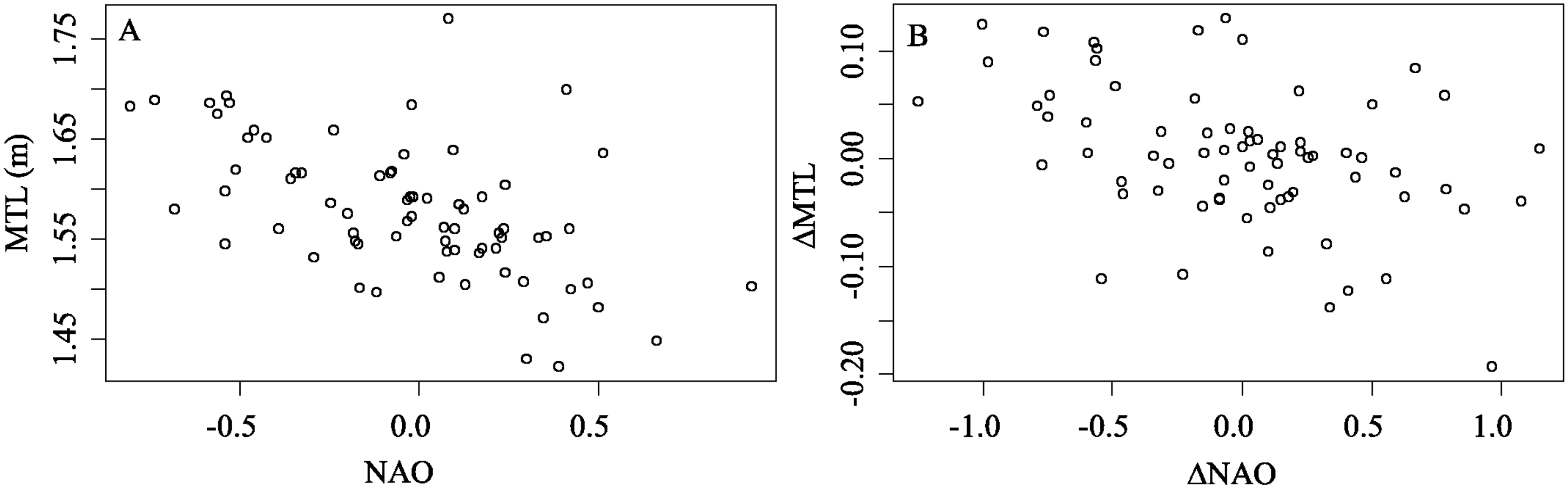


Figure 2.3. Time series of Lewes, DE, Ocean City fishing pier, and Ocean City inlet mean tidal height (MTL). MTL and rate of MTL change were significantly correlated between sites (Pearson's *r* = 0.985 and 0.990, respectively, p < 0.001).

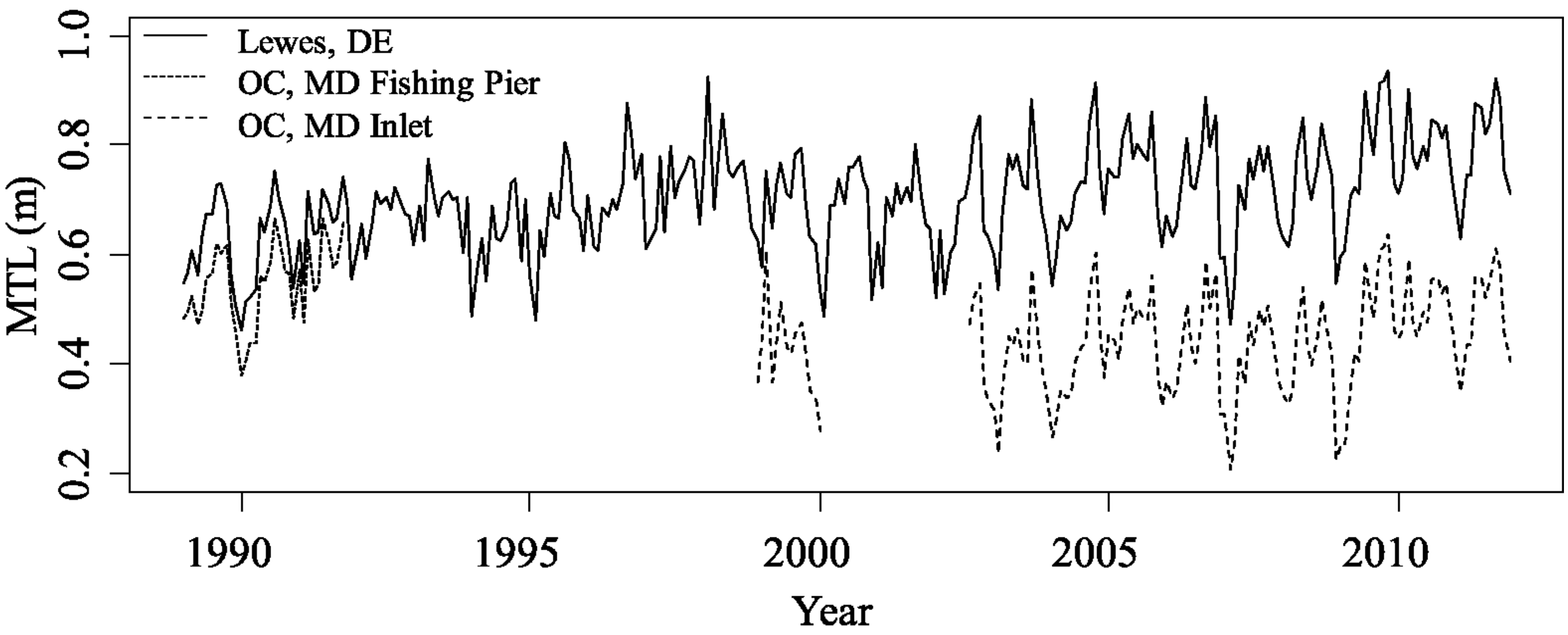


Figure 2.4. Correspondence analysis of Aug 2009 (○), Sept (◎) 2009, and Aug 2012 (O) directed surveys. Dashed lines show significant environmental gradients found in *post-hoc* analyses. "Dist." represents distance to Ocean City Inlet. The true location of species names displaced to prevent over-plotting are represented with a plus sign (+).

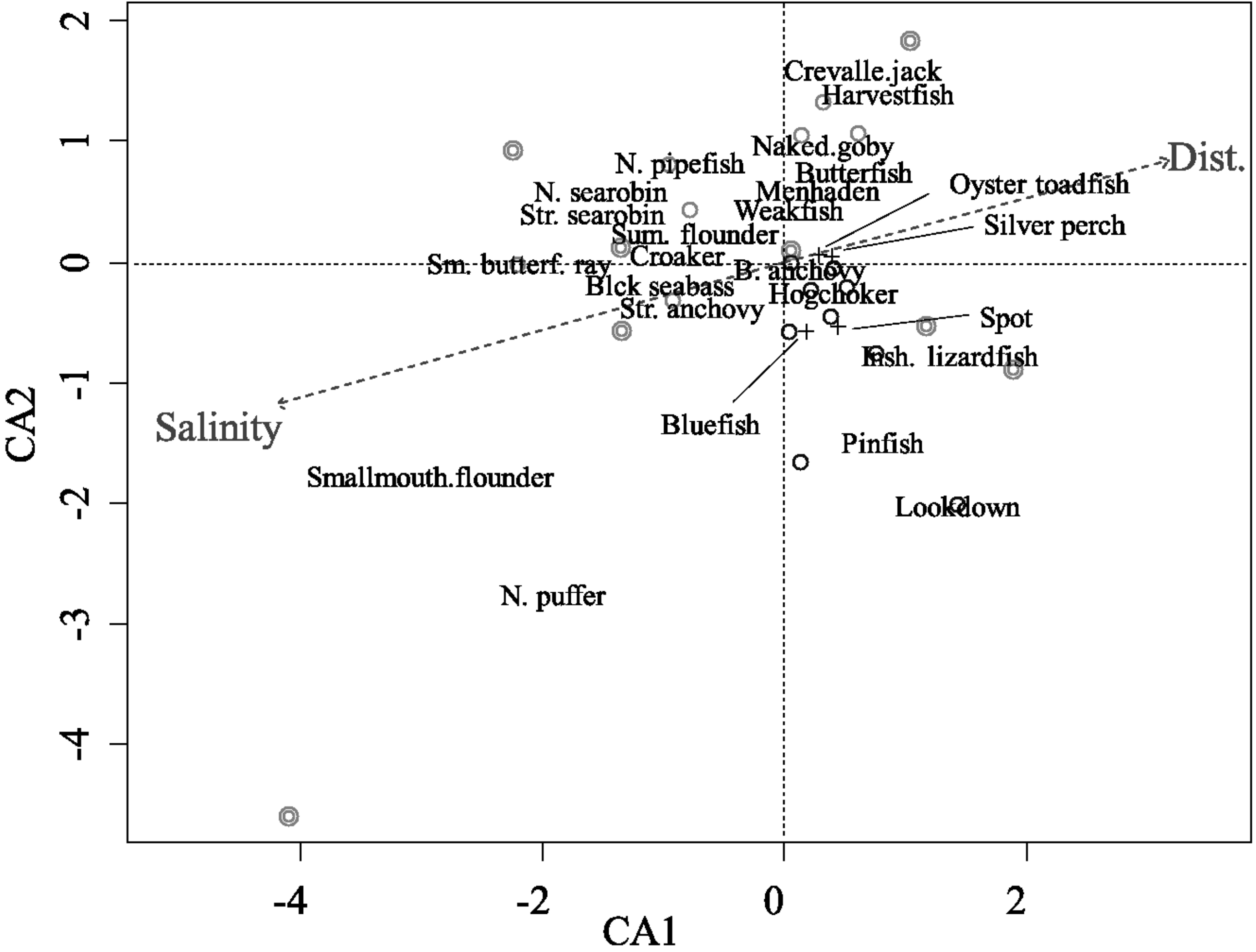


Figure 2.5. Ordination of samples from correspondence analysis with significant environmental gradients from *post-hoc* analyses (salinity and distance ["Dist."] from Ocean City inlet) overlain. Trawls from northern (N), central (C), and southern (S) portions of the coastal bays from August 2009 (grey, unboxed), September 2009 (grey, boxed), and August 2012 (black, unboxed) sampling are shown.

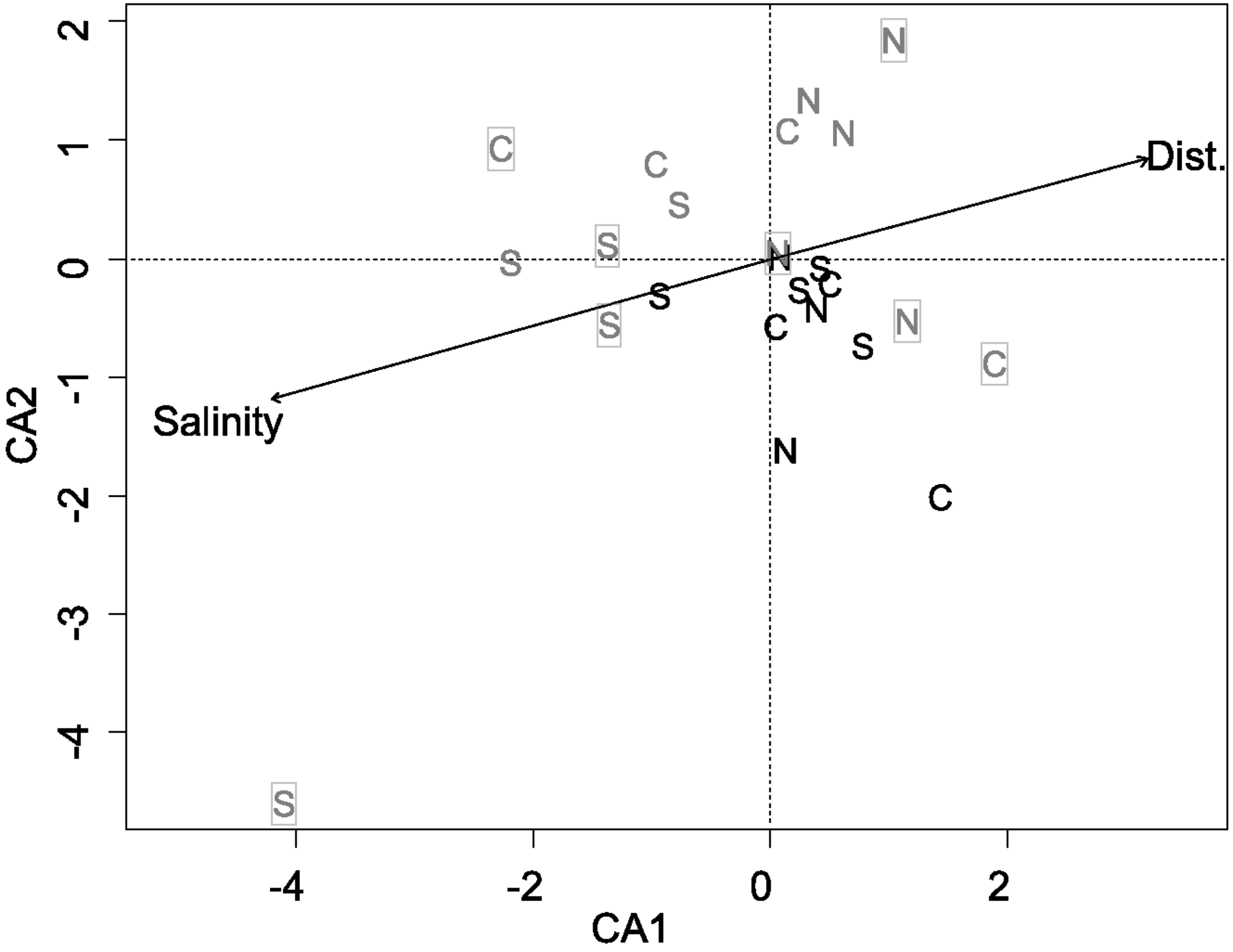


Figure 2.6. Seasonal North Atlantic Oscillation index (NAO, Climate and Prediction Center Internet Team 2013) and mean tide level (MTL, Center for Operational Oceanographic Products and Services 2013) from 1989-2012. Raw values are overlain with a loess-smoothed curve using a 5-season window.

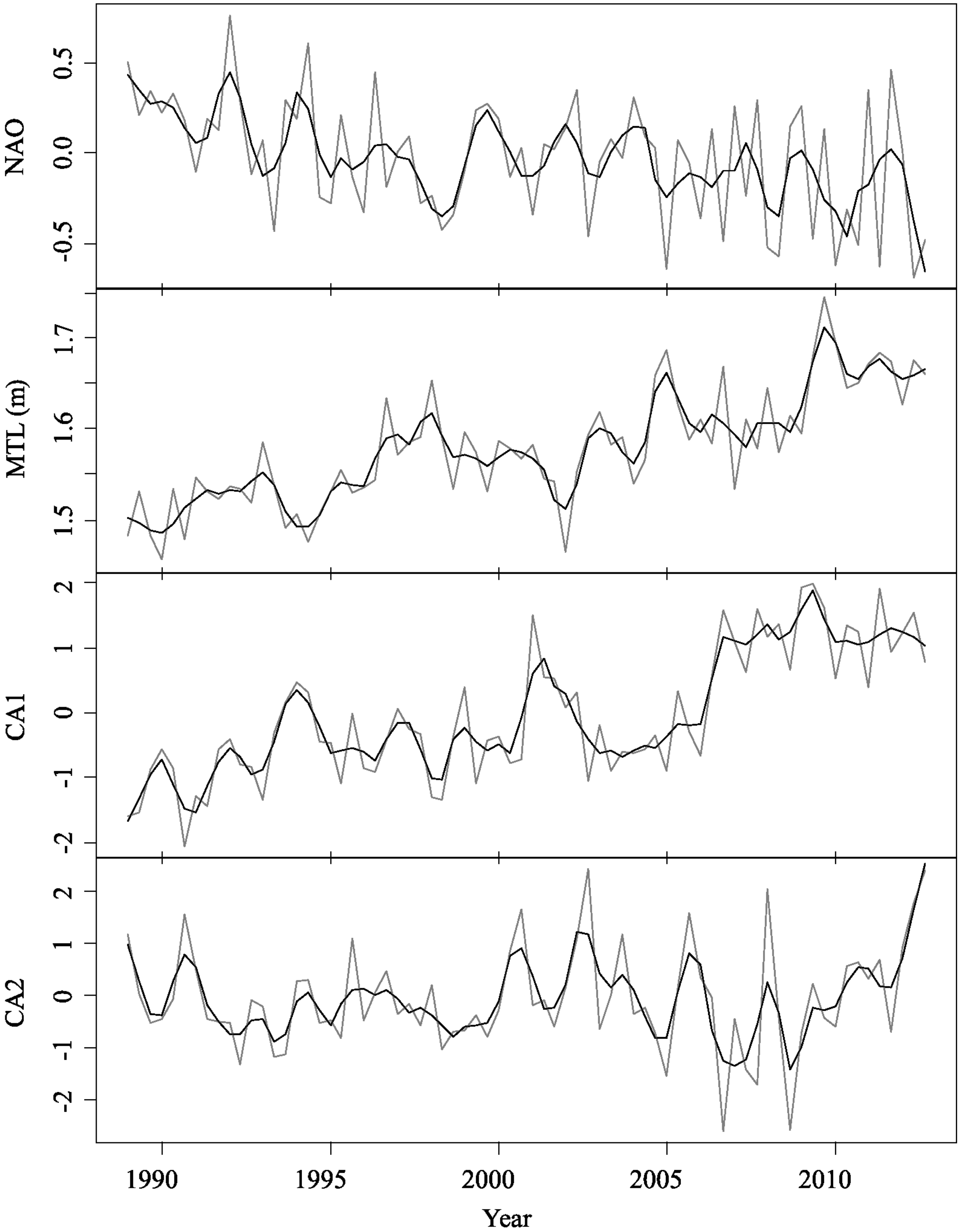


Figure 2.7. Yearly submerged aquatic vegetation cover (SAV, Orth et al. 2012) in hectares between 1989 and 2012.

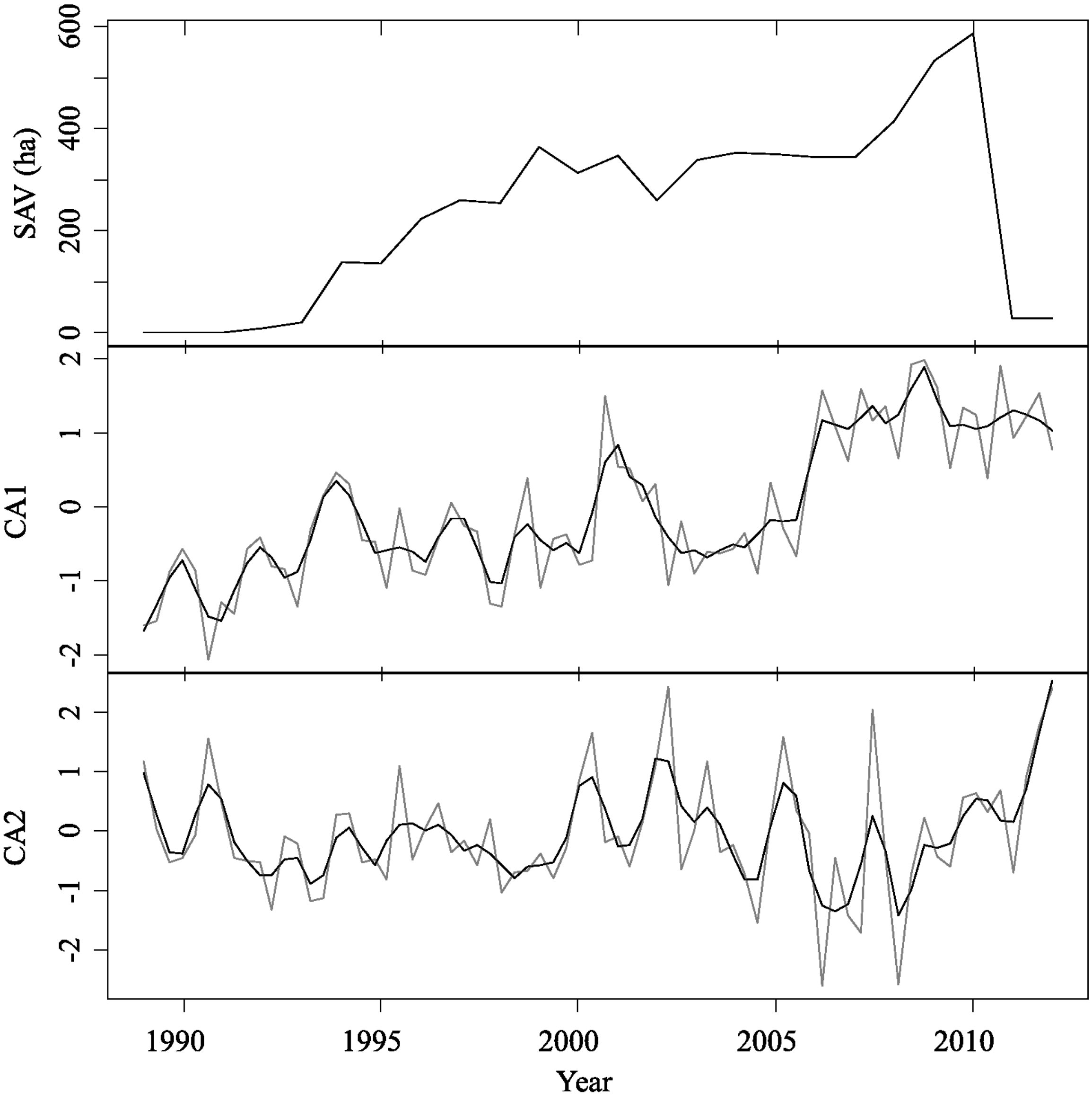


Figure 2.8. Temperature (°C) and salinity as recorded by the Coastal Bays Fisheries Investigation within the northern coastal bays from 1989-2012. Raw values are overlain with a loess-smoothed curve using a 5-season window.

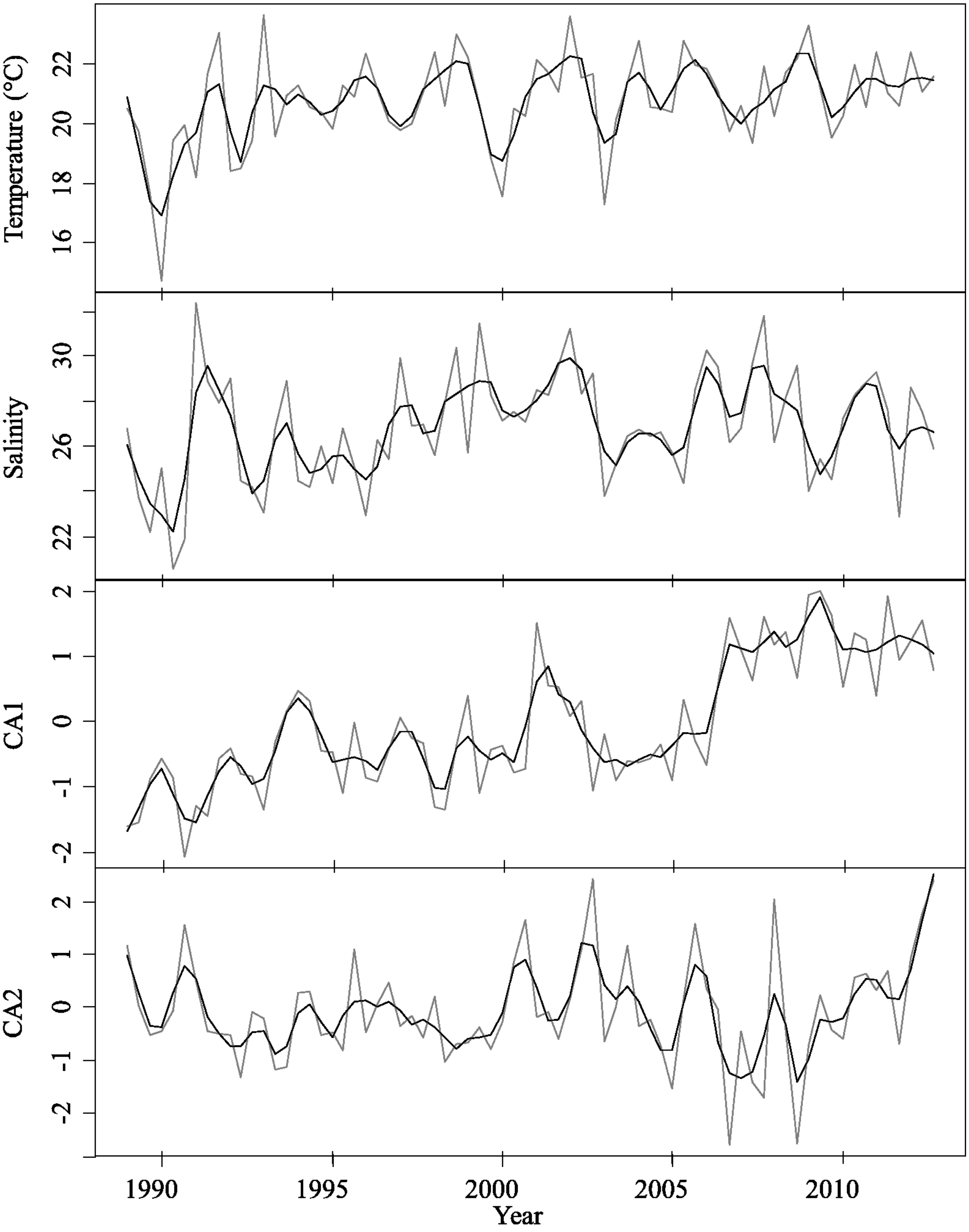


Figure 2.9. Catch-per-unit-effort (CPUE, fish trawl^{-1}) of tautog (*Tautoga onitis*), oyster toadfish (*Opsanus tau*), and American eel (*Anguilla rostrata*), common structure-oriented species, within the northern coastal bays between 1989 and 2012.

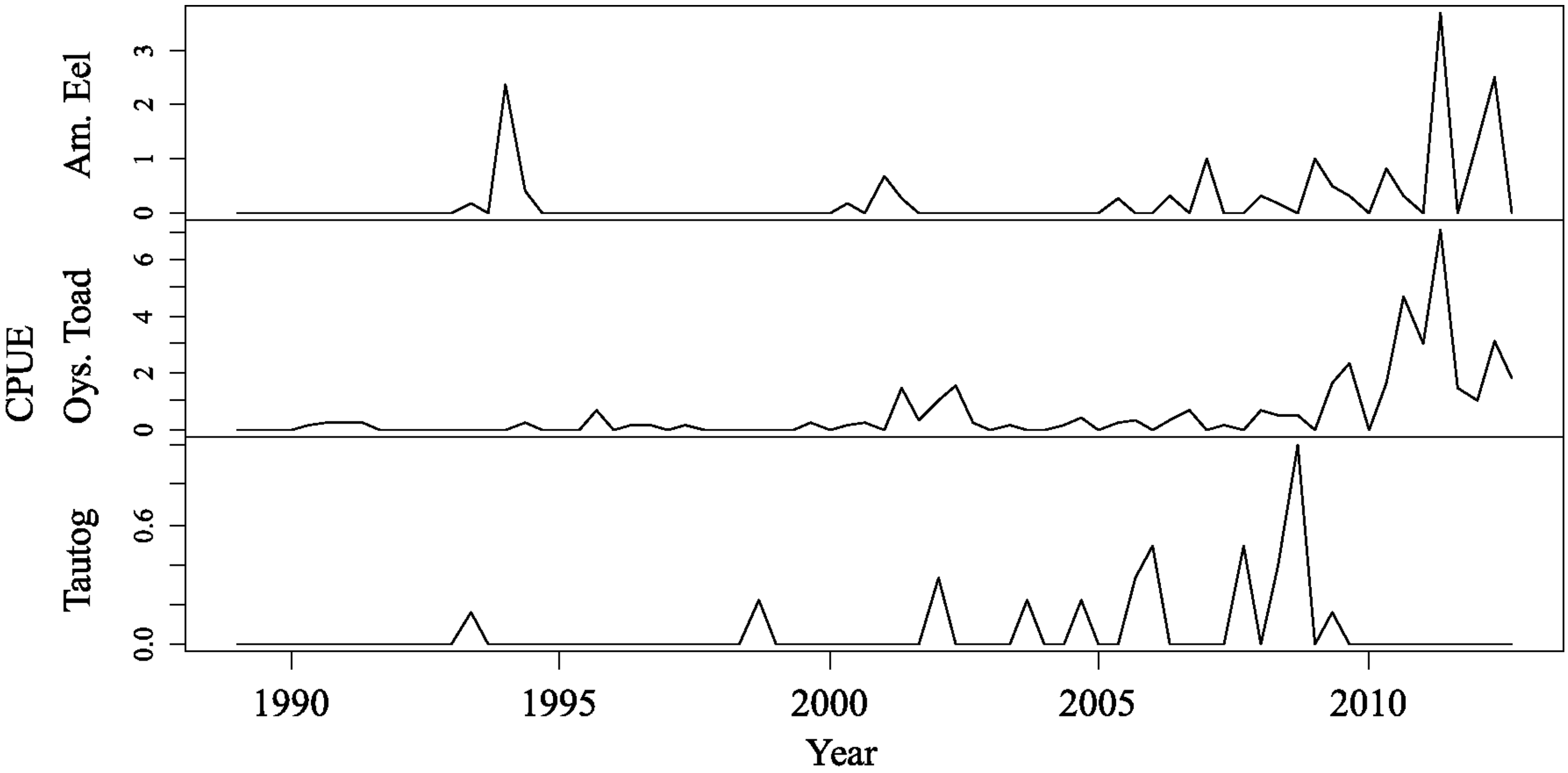


Figure 2.10. Catch-per-unit-effort (CPUE, fish trawl^{-1}) of inshore lizardfish (*Synodus foetens*) and crevalle jack (*Caranx hippos*), common marine species, within the northern coastal bays between 1989 and 2012.

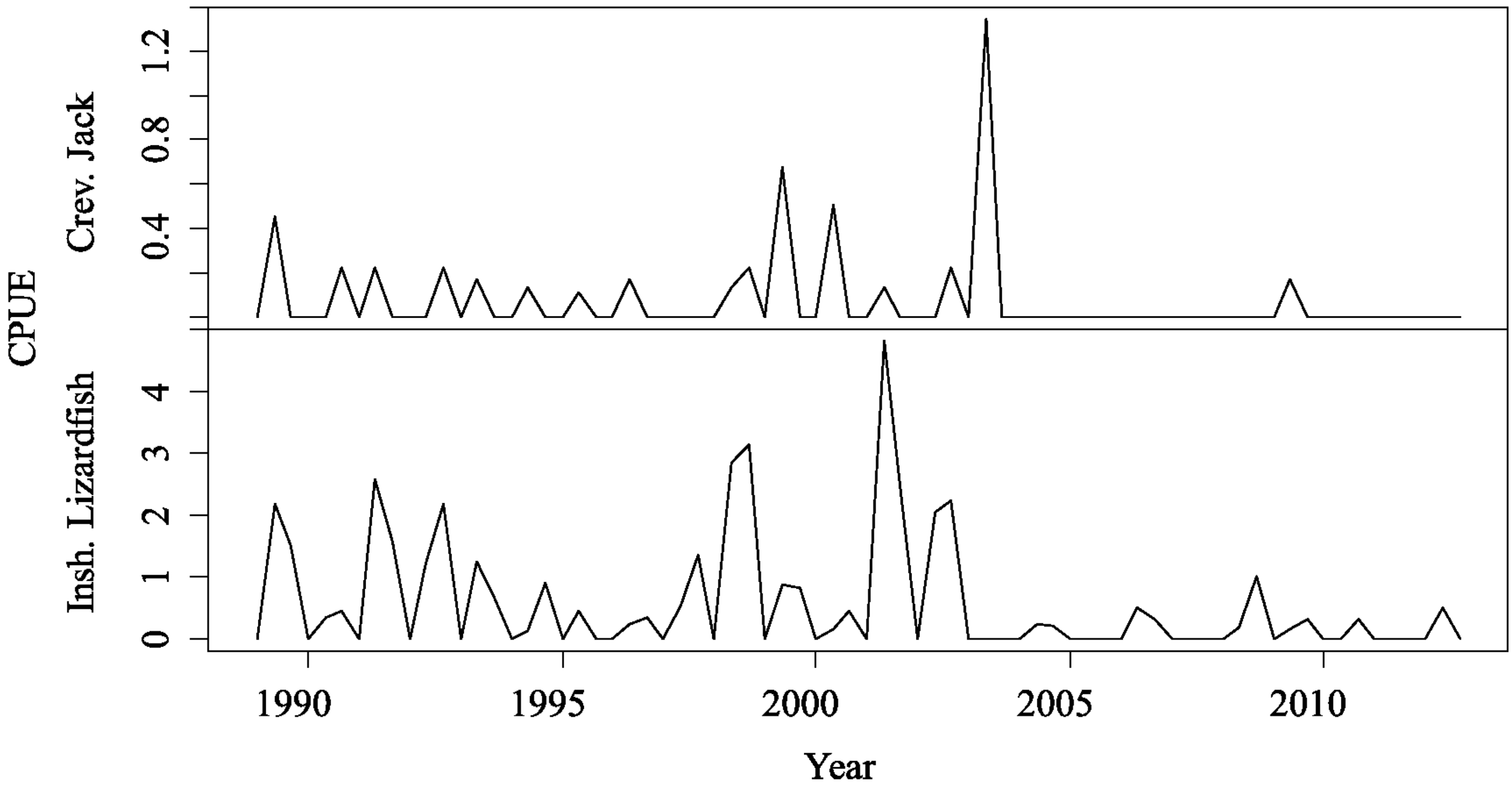


Figure 2.11. Correspondence analysis of juvenile fish species sampled seasonally by the Coastal Bays Fisheries Investigation (CBFI) between 1989 and 2012. Gradients in the North Atlantic Oscillation (NAO), submerged aquatic vegetation cover (SAV), and mean tide level (MTL) are overlain with dashed arrows. The names of infrequent species (+) were removed to prevent over-plotting.

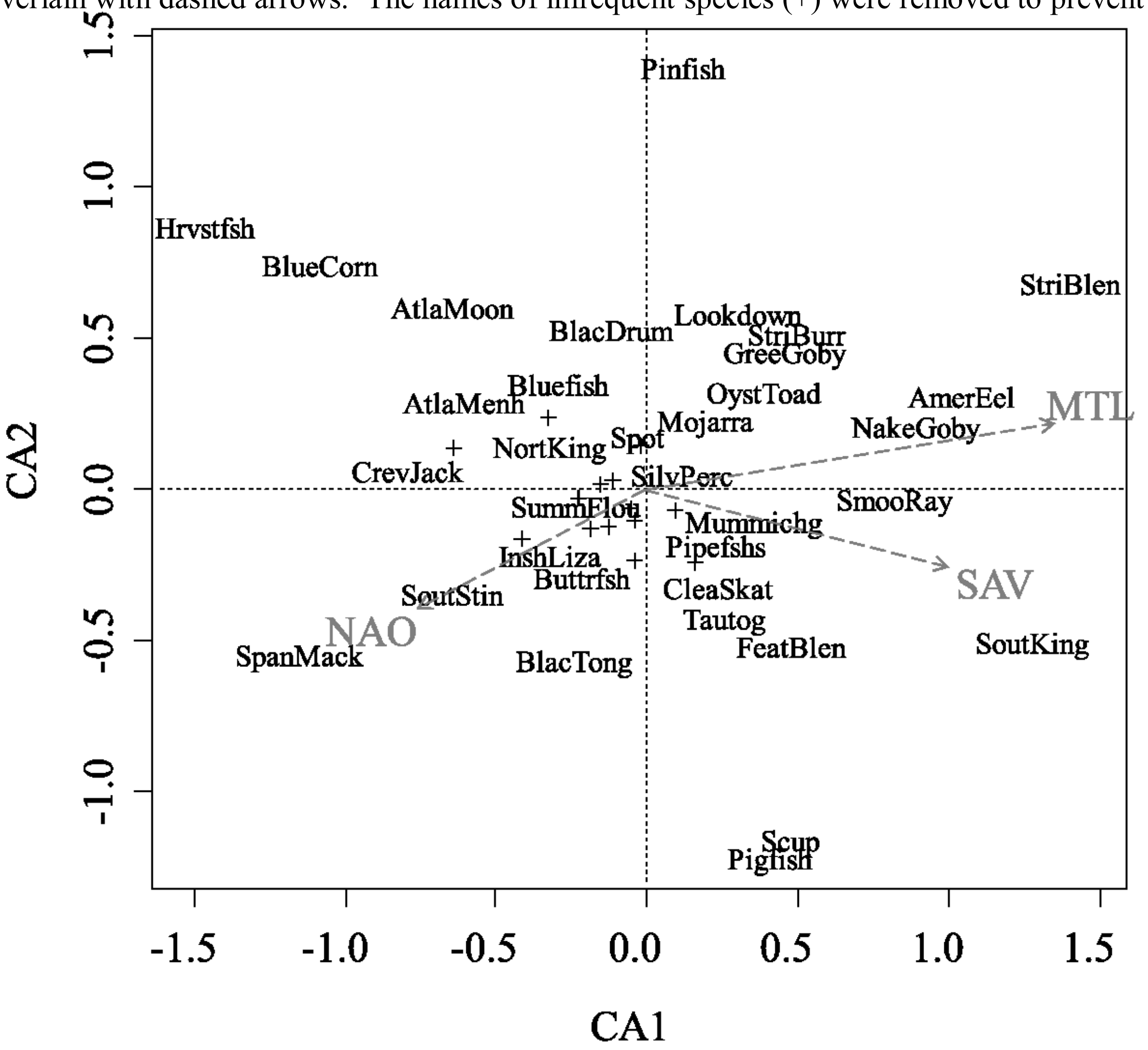
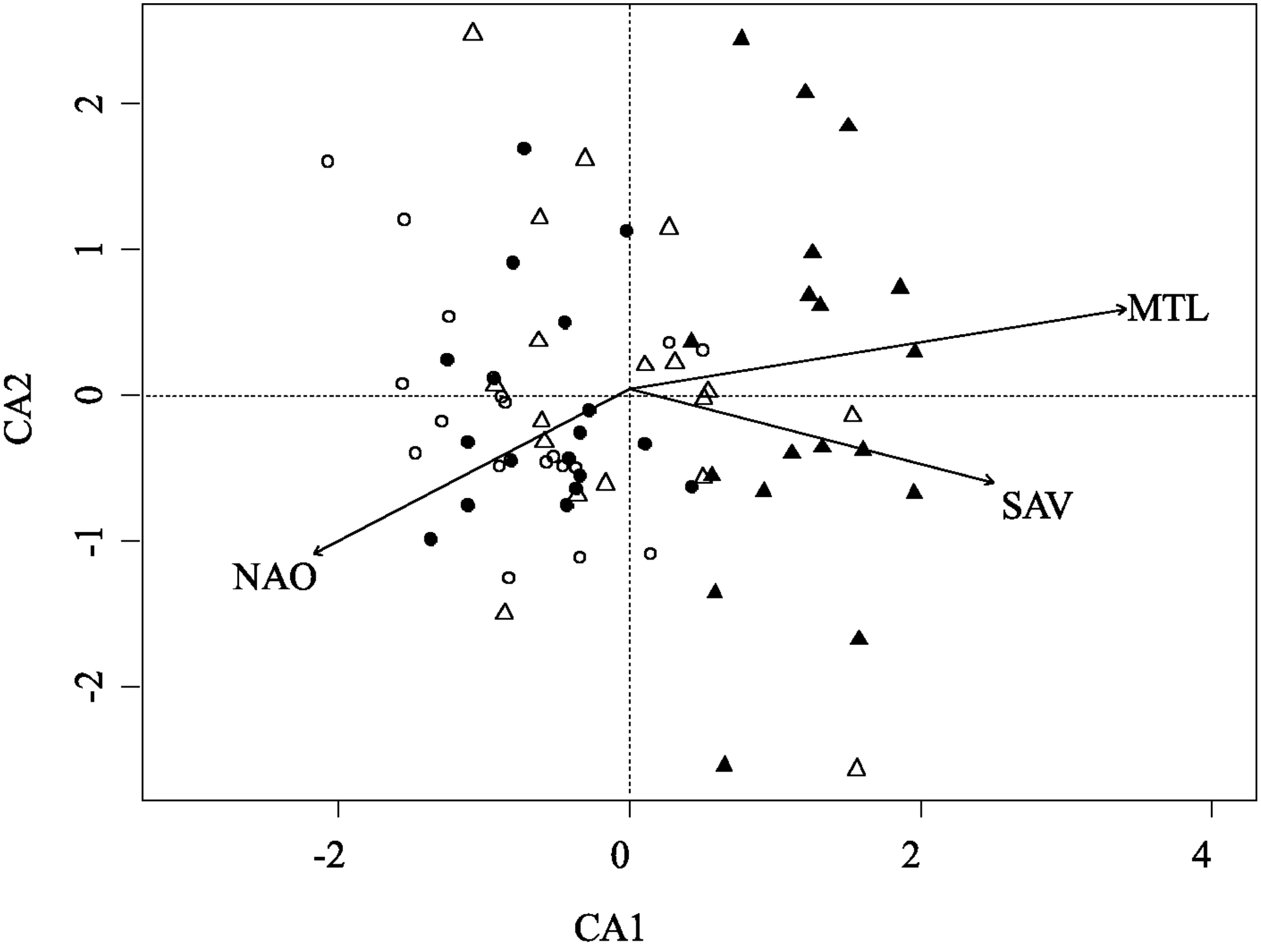


Figure 2.12. Ordination of samples from correspondence analysis with significant environmental gradients overlain. Samples from 1989-2004 (○), 1995-2000 (●), 2001-2006 (△), and 2007-2012 (▲) were significantly associated with gradients in the North Atlantic Oscillation (NAO), submerged aquatic vegetation cover (SAV), and mean tide level (MTL).



Appendix: Temporally-Dynamic Isotopic Mixing Model

Temporal trajectory of environmental baseline

Baseline isotopic values were assumed to increase linearly with time:

$$\delta^{13}C_B(t) = Rt + \delta^{13}C_B(t_0)$$

where R is the instantaneous isotopic rate of change, $\delta^{13}C_B(t_0)$ is the initial isotopic value of the baseline and $\delta^{13}C_B(t)$ is the isotopic value of the baseline at time *t*.

Temporal trajectory of fish tissue

Fish tissue was modeled as a one-endmember simplification of the dynamic baseline mixing model described in Woodland et al. (2012b):

$$\delta^{13}C_F(t) = \delta^{13}C_F(t_0)\, e^{-k(t-t_0)} + \left(1 - e^{-k(t-t_0)}\right)\delta^{13}C_B(t)$$

Here, the isotopic value of an organism at time *t*, $\delta^{13}C_F(t)$, is a function of dilution of initial isotopic value, $\delta^{13}C_F(t_0)$, and the proportion of mass accumulated after commencement of the simulation from the baseline, $\delta^{13}C_B(t)$. Here, *k* represents the instantaneous growth rate of the fish and t_0 represents initial time.

Model Simulation

The same value of -20‰ was used as the starting isotopic value of both the baseline and fish tissue. The model was simulated over 30 days with varying combinations of baseline change and fish growth rate extracted from Table 1.1, including averaging values within species. Results are reported in Table A.1.

Tables

Table A.1. Difference between a temporally-dynamic baseline and fish tissue isotopic values after a 30 day simulation under varying combinations of observed rates of change. Rates are reported as the absolute value of corresponding rates in Table 1.1.

Fish Growth Rate		Baseline Rate of Change		
Type	Rate (month^{-1})	Type	Rate (month^{-1})	30 Day Difference
Mean Anchovy	0.588	Mean Blue Mussel	0.264	0.147
Mean Anchovy	0.588	Mean Ribbed Mussel	0.219	0.122
Lowest Anchovy	0.108	Lowest Blue Mussel	0.145	0.130
Lowest Anchovy	0.108	Highest Blue Mussel	0.384	0.345
Lowest Anchovy	0.108	Lowest Ribbed Mussel	0.040	0.036
Lowest Anchovy	0.108	Highest Ribbed Mussel	0.547	0.491
Highest Anchovy	0.676	Lowest Blue Mussel	0.145	0.074
Highest Anchovy	0.676	Highest Blue Mussel	0.384	0.195
Highest Anchovy	0.676	Lowest Ribbed Mussel	0.040	0.020
Highest Anchovy	0.676	Highest Ribbed Mussel	0.547	0.278
Mean Weakfish	0.617	Mean Blue Mussel	0.264	0.143
Mean Weakfish	0.617	Mean Ribbed Mussel	0.219	0.118
Lowest Weakfish	0.029	Lowest Blue Mussel	0.145	0.141
Lowest Weakfish	0.029	Highest Blue Mussel	0.384	0.373
Lowest Weakfish	0.029	Lowest Ribbed Mussel	0.040	0.039
Lowest Weakfish	0.029	Highest Ribbed Mussel	0.547	0.531
Highest Weakfish	1.220	Lowest Blue Mussel	0.145	0.043
Highest Weakfish	1.220	Highest Blue Mussel	0.384	0.113
Highest Weakfish	1.220	Lowest Ribbed Mussel	0.040	0.012
Highest Weakfish	1.220	Highest Ribbed Mussel	0.547	0.161

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