ABSTRACT

Title: PATTERNS IN THE DISTRIBUTION, DIET AND TROPHIC DEMAND OF THE HOGCHOKER, *TRINECTES MACULATUS*, IN THE CHESAPEAKE BAY, USA.

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The hogchoker, *Trinectes maculatus* (Achiridae), is a small estuarine flatfish that, due to its ubiquitous distribution and substantial biomass, is an important component of the Chesapeake Bay ecosystem. I quantified the abundance, distribution and diet of hogchoker in the Bay based on samples from a fishery-independent survey. Hogchoker abundance varied inter-annually and spatially. A generalized additive model (GAM) explained 14.8% of the variability in the distribution of hogchoker abundance. Depth, salinity, temperature and year were significant determinants of hogchoker presence, whereas salinity and temperature determined relative abundance. Hogchoker diet primarily comprised polychaetes, however, amphipods, isopods and bivalve siphons also represented important dietary components. Graphical analyses and nonmetric multidimensional scaling indicated seasonal, spatial and ontogenetic variation in diet within the Bay. Estimates of summer trophic demand indicated that hogchoker consumed up to 0.1% of the standing stock biomass of particular macrobenthic taxa in the mainstem of the Chesapeake Bay.

PATTERNS IN THE DISTRIBUTION, DIET AND TROPHIC DEMAND OF THE
HOGCHOKER, *TRINECTES MACULATUS*, IN THE CHESAPEAKE BAY, USA.

By

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DEDICATION

I would like to dedicate this work to my family, who has always provided unconditional

support. They had faith in my abilities even at times when I started to lose faith in

myself.

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First and foremost, I would like to thank my advisor, Tom Miller, for four years of support and guidance. He repeatedly went above and beyond the call of an advisor's duties. I would also like to thank my committee, Ed Houde and Walt Boynton, for their critical review and constructive suggestions that greatly helped to strengthen my thesis. I am fortunate to have the opportunity to write this acknowledgements section after my departure from CBL and as a consequence, I have a greater appreciation of the CBL community. I have always felt quite privileged to be part of the community, however, its unique character is now much more evident. It supports an environment that fosters both academic and personal growth and I feel like I grew an extraordinary amount during my time at CBL.

I, of course, need to thank all of the members of the Houde and Miller labs, in addition to Sarah Kolesar, for all of their help in the field. Thanks also to the Miller lab group, both past and present, for always editing my work, helping me work through ideas, and most of all making me laugh. A very special thanks is also much needed for my housemates, Lori Roth, Steve Engstrom and Josh Dixon, for three years filled with fond memories. And last, but not definitely not least, I am indebted to my family for always standing by me.

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CHAPTER 1: RATIONALE

In recent years, there has been an increased interest in ecosystem approaches to management, both in terrestrial and aquatic systems (May et al. 1979; Grumbine 1994; Christensen et al. 1996; Brodziak and Link 2002; Link 2002). In fisheries, most species have been traditionally managed through single-species approaches, where the species of interest is considered in isolation of its interactions with the surrounding ecosystem. The growing interest in multispecies management has been attributed to several factors, including the perceived shortcomings of these single-species management approaches (Link 2002; Link et al. 2002), but see Hilborn (2004) for a critical view. Limitations of single-species tactics have arisen out of the estimation of natural mortality rates without explicit consideration of predation and competition with other species, concerns over habitat alteration associated with the effects of fishing (Kaiser et al. 2002), and the uncritical adoption of equilibrium-based estimates of maximum sustainable yield (MSY) as a target reference point.

Historically, fisheries were managed with MSY as a target reference point (Larkin 1977; Mace 2001). Yet, it can be shown that MSY represents an unstable equilibrium (Haddon 2001) and given the uncertainty in parameters, it is an inappropriate target reference point (Haddon 2001; Mace 2001). Consequently, with the development of the precautionary approach MSY is now considered a limit instead of a target (Jennings et al. 2001; Mace 2001). However, regardless of whether MSY is a target or limit reference point, to fish several species within an ecosystem at their respective MSYs, it must be assumed that each species is ecologically separate, where competition and predation are

negligible (Larkin 1977; May et al. 1979). Moreover, even if this assumption generally held, it is often not possible to simultaneously obtain the individual MSYs for each species within a system because the sum of the single species maximum yields commonly exceeds that of the system (Link 2002). In other cases when species are caught together in the same fishery, an example of a technical interaction, achieving MSY for all species in the catch simultaneously is likely not possible (Houde et al. 1998).

The community dynamics of any marine system are influenced by a multitude of factors, including predator-prey interactions, fishing mortality rates, competition, environmental variability and the interactions between these factors (Rice and Gislason 1996; Collie and DeLong 1999; Hollowed et al. 2000; Tsou and Collie 2001). These interactions are complex and not necessarily intuitive (Jennings et al. 2001). Fishing, for example, can substantially impact the trophic structure of a system by either removing a predator, prey or competitor species, causing direct, indirect and unpredicted responses within the food web of the system (May et al. 1979; Rice and Gislason 1996; Gislason et al. 2000). Thus, it has been suggested that the failure to include these interactions severely limits the utility of scientific advice provided to managers (NRC 1999). For example, the majority of fish production in most marine ecosystems is removed through piscivory (Bax 1998; Collie 2001; Link and Garrison 2002). Support for this claim comes from data from several marine ecosystems, including the fish community on Georges Bank, USA, where piscivory is the largest source of mortality to pre-recruit fish (Collie and DeLong 1999). Thus, due to its ability to affect community structure, the incorporation of predation into species assessments is critical to accurately estimate natural mortality. In addition, competition also plays an important role in fish

community dynamics (Crowder 1984; Tonn et al. 1994; Fogarty and Murawski 1998). It has been hypothesized that the dramatic changes in the species composition of the Georges Bank fish community from groundfish to pelagic species and elasmobranches are linked to competition (Fogarty and Murawski 1998).

The management of each species as a separate component ignores critical interactions between species and can cause inaccuracies in the estimation of stock status (Roberts 1997). As a result of these limitations of single-species management and the growing views of an ecosystem perspective, there has been an increased interest in ecosystem-based fisheries management (NMFS 1999; NRC 1999; Mace 2001; Link et al. 2002; NOAA 2004). It is generally recognized that a multispecies perspective, which incorporates species interactions, could improve the sustainability of current fisheries management (Sissenwine and Daan 1991; NRC 1999; Hollowed et al. 2000; NOAA 2004), however, Hilborn (2004) provides a critical and contrasting view. Consequently, fisheries management in an ecosystem context has been both recommended and mandated (NMFS 1999; NRC 1999; CBP 2000). The incorporation of ecosystem considerations into fisheries management is being implemented currently in several systems including the northwest Atlantic with the Northeast Multispecies Fishery Management Plans for large (NEFMC 1986) and small (NEFMC 2000) groundfish, the North Sea with the development of the European Fisheries Ecosystem Plan (Piet et al. 2003), and the Chesapeake Bay with the Chesapeake Bay Fisheries Ecosystem Plan (NOAA 2004).

Fisheries management in the Chesapeake Bay is moving toward adopting an ecosystem-based approach (CBP 1987; Miller et al. 1996; Houde et al. 1998; CBP 2000;

NOAA 2004). The Chesapeake Bay's fishery resources are managed by the states of

Virginia and Maryland and the Potomac River Fisheries Commission. Management is

coordinated through the Chesapeake Bay Program (CBP), a multi-level entity spanning

both state and federal levels. The goals of the CBP, including the protection and

restoration of living resources, habitat and water quality (through management of runoff,

discharges and nutrient loading into the Bay) are at the ecosystem level, and it has

become apparent that the current single-species fisheries management approach does not

completely incorporate these system goals (CBP 1987; Miller et al. 1996; Houde et al.

1998; CBP 2000; NOAA 2004).

In June 2000, the signatories of the CBP signed the Chesapeake 2000 agreement,

reaffirming their commitment to the protection and restoration of the Bay (CBP 2000).

Through this agreement, the CBP formally committed to move towards ecosystem-based

fisheries management, incorporating two particular objectives into the agreement to

elucidate this goal. These objectives were to 1) "develop ecosystem-based multispecies

management plans for targeted species by 2005", and 2) "by 2007 to revise and

implement existing fisheries management plans to incorporate ecological, social, and

economic considerations, multi-species fisheries management and ecosystem

approaches" (CBP 2000). The CBP recognized that the implementation of these

multispecies management plans was dependent on a deeper understanding of key issues

in the Chesapeake Bay such as species interactions, water quality and habitat (NOAA

2004).

A principal challenge to the adoption of ecosystem-based approaches to fisheries

management in the Chesapeake Bay is the identification of appropriate boundaries

(NOAA 2004). Clear demarcation of boundaries is a critical consideration in ecosystem-based approaches that has implications both for understanding the ecology and exploitation of the ecosystem. This is particularly true for a dynamic estuary such as the Chesapeake Bay, which is used only seasonally by many species. This seasonal pattern of habitat use presents unique challenges to defining the boundaries of the ecosystem. For example, if boundaries are drawn to include all life stages of seasonal migrants that use the Chesapeake Bay, the system's boundaries may well stretch from Florida to Nova Scotia. More natural geographic boundaries, which do not span the mouth of the bay, require researchers and managers to understand the flux of seasonal migrants over the boundary. One goal of boundary delineation is defining an effective fisheries management unit. Consequently, the established boundaries must enable the protection of the ecosystem processes and habitats essential to fish and invertebrate species. The specified ecosystem-based management objectives influence boundary locations. For example, many fish species, such as striped bass, menhaden and bluefish, migrate between Chesapeake Bay and coastal waters. As a consequence, objectives to manage these migratory species would require the incorporation of both estuarine and coastal ocean waters into the management unit. An apparent tradeoff exists between the determination of boundaries that minimize management and jurisdictional complexity yet still incorporate the ecosystem processes and both physical and biological characteristics critical to the integrity of the Chesapeake Bay community (NOAA 2004).

By definition, ecosystem-based approaches to fishery management must also address both economically and ecologically important species and their interactions. As a consequence, ecosystem-based approaches to fisheries will require that data be

collected on species that are not traditionally the focus of research studies. A key

challenge is to incorporate the population dynamics and ecology of these relatively

unstudied, but ecologically important species into ecosystem-based fishery management

plans to more realistically estimate allowable harvests of exploited species. It is

imperative to have an understanding of the ecology and life history of these species in

order to add them into a multispecies framework to establish a more holistic management

approach and determine their influence on the ecosystem of interest.

The hogchoker *Trinectes maculatus*, a demersal fish species of the American sole

(Achiridae) family, is neither fished nor a dominant prey species of Chesapeake Bay

piscivores. However, it is still an important component of the Bay ecosystem due to its

substantial standing crop and the amount of energy transferred through this species. In a

study examining seasonal trends in energy flow in the Chesapeake Bay, Baird and

Ulanowicz (1989) created a representation of the annual flow of carbon between 34

principal components of the mesohaline region of the Bay (Figure 1). The upper trophic

levels, depicted on the right side of the food web are comprised of many economically

important species. However, hogchoker, an unexploited species, exhibits a standing

stock comparable or exceeding that of many fished species, including Atlantic croaker,

Micropogonias undulatus, bluefish, *Pomatomus saltatrix*, weakfish, *Cynoscion regalis*,

and striped bass, *Morone saxatilis* (Baird and Ulanowicz 1989). In a fishery-independent

survey that estimated the effects of heated-water release from a steam electric generating

station in the Patuxent River, hogchoker comprised, on average, over one-quarter of trawl

catches by number and a maximum of almost 70 percent of the total catch, demonstrating

its substantial abundance in the Bay (McErlean et al. 1969). Additionally, in a study

investigating the presence of marine fish in fresh and brackish waters of several Virginia rivers of the Chesapeake Bay, (Massman 1954) frequently collected hogchoker in 4 out of the 5 sampled rivers and up to 40 miles upriver from the boundary between fresh and brackish water. Together, these studies from both Maryland and Virginia demonstrate the widespread distribution and substantial abundance of hogchoker in the Chesapeake Bay, yet it is a relatively unstudied component of the Bay ecosystem.

Unlike many exploited species in the Chesapeake Bay, the hogchoker is a year-round resident (Murdy et al. 1997). Furthermore, hogchoker exhibits a seasonal migration pattern between saline spawning grounds and overwintering/nursery grounds near the interface of salt and freshwater. This migration pattern was first proposed for the northern subspecies of the hogchoker in the Patuxent River, a sub-estuary of the Chesapeake Bay (Dovel et al. 1969). Subsequent research in the Gulf of Mexico and Mississippi Sound has indicated that the southern subspecies also undertakes this seasonal migration (Peterson 1994; Peterson 1996). Additional studies in Georgia, New York, North Carolina and the Gulf of Mexico/Mississippi Sound have supported the proposed migration pattern (Koski 1973; Reichert and Veer 1991; Walsh et al. 1999).

Hogchoker spawns in the summer in relatively high salinity waters of approximately 15-20 and in the fall both larvae and adults move upstream to low salinity nursery and overwintering grounds (Peterson 1996). During the following spring, adults migrate from overwintering grounds to the more saline spawning habitats. Juveniles move toward the spawning area in the spring and their travel range increases each year until they reach the spawning area at approximately 4 years of age (Dovel et al. 1969; Peterson 1996). Previous work on the effects of salinity on juvenile metabolism, growth

and survival has indicated that this migration pattern is likely due to the influence of salinity on juvenile metabolism and not a salinity intolerance (Peterson-Curtis 1997). In the Chesapeake Bay, however, Dovel (1969) indicated that the observed Patuxent River hogchoker likely comprised a resident population that was relatively confined to the river. Accordingly, the seasonal distribution of hogchoker within the mainstem of the Chesapeake Bay is still unclear.

Studies of hogchoker diet have indicated that hogchoker feeds on benthic invertebrates, primarily annelids and small crustaceans, with spatial changes in diet composition along a salinity gradient (Castagna 1955; Carr and Adams 1973; Koski 1973; Smith et al. 1984; Pihl et al. 1992; Derrick and Kennedy 1997). In freshwater, oligohaline and lower mesohaline regions, amphipods, isopods and chironomids were important constituents of hogchoker diets. In upper mesohaline and polyhaline regions, however, polychaetes dominated gut contents (Derrick and Kennedy 1997). These studies, however, were either descriptive or limited in either their temporal or spatial sampling range. Thus, a comprehensive evaluation of hogchoker diets in the Chesapeake Bay is still lacking.

The primary goal of this thesis was to investigate the distribution, demographics and ultimately trophic demand of the hogchoker in the mainstem of the Chesapeake Bay to facilitate the incorporation of this ecologically important species into ecosystem-based fishery management. Data were collected through the Chesapeake Bay Fishery Independent Multispecies Survey and Trophic Interactions in Estuarine Systems programs, multispecies surveys of the bentho-pelagic fish community of the Chesapeake Bay. The particular objectives of this project were to 1) model the distribution and

abundance of the hogchoker in the mainstem of the Chesapeake Bay 2) investigate patterns in diet and 3) quantify the trophic demand of the hogchoker on the Bay ecosystem.
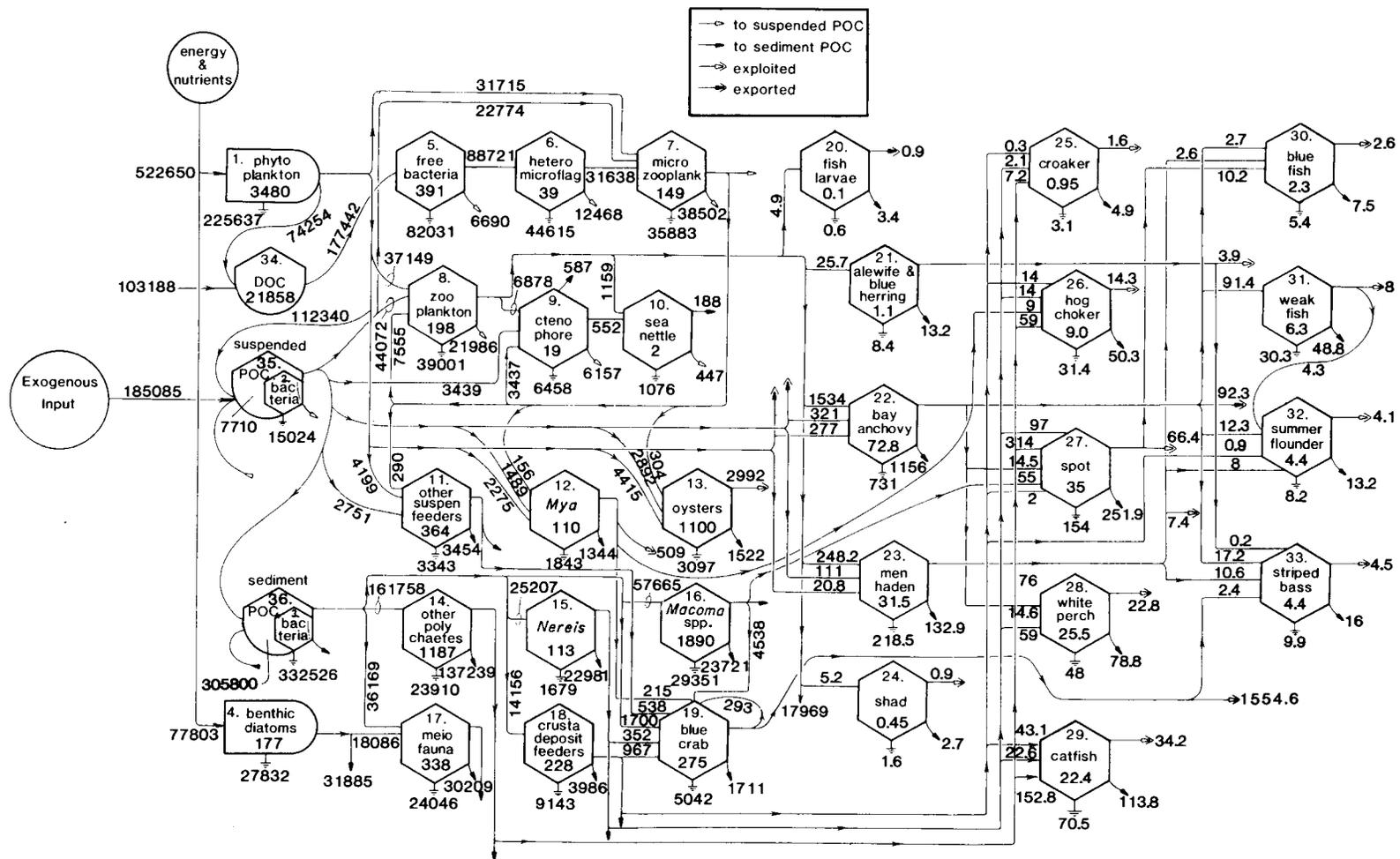
Figure 1. Representation of the annual flow of carbon ($mg*m^{-2}*yr^{-1}$) through the dominant food web components of the mesohaline Chesapeake Bay. Figure from Baird and Ulanowicz (1989).

CHAPTER 2: THE DISTRIBUTION OF HOGCHOKER IN THE CHESAPEAKE BAY: INFERENCES FROM A GENERALIZED ADDITIVE MODEL

INTRODUCTION

Abiotic factors can have a profound impact on the energy budget of a fish, ultimately influencing metabolic and growth rates (Mihursky and Kennedy 1967; Fry 1971; Elliott 1975; Wootton 1990; Jager et al. 1993; Valiela 1995; Lalli and Parsons 1999). The effects of these abiotic factors, including temperature, salinity and dissolved oxygen, on fish metabolic and growth rates result in a preference for a set of environmental variables that maximizes the performance of physiological functions, growth, fecundity and survival (Coutant 1987; Allen and Baltz 1997). Experiments have shown that fish preferentially select the most profitable habitats based on environmental parameters (Wildhaber and Crowder 1990). Accordingly, the distribution of these abiotic factors in the environment likely substantially influences the distribution of fish in the field.

The Chesapeake Bay is a partially mixed estuary that exhibits strong gradients in abiotic factors (Day et al. 1989; NOAA 2004). For example, salinity values range from less than 0.5 at the head of the bay to approximately 32 at the bay mouth. Winter water temperatures can fall to 1-4º Celsius and summer temperatures can reach as high as 28-30ºC (Murdy et al. 1997). In addition to the strong latitudinal gradients, the mainstem of the bay generally has a sharp pycnocline, resulting in strong vertical gradients of temperature and salinity (Jung and Houde 2003). Furthermore, as a result of this stratification, oxygen becomes depleted in subpycnocline waters (Breitburg 1992).

During spring and summer stratification episodes, oxygen concentrations below the pycnocline can fall near zero milligrams per liter (mg/L) (Day et al. 1989; Breitburg 1992; Murdy et al. 1997). The amount of Chesapeake Bay waters with biologically-relevant low oxygen conditions has exhibited a 15-fold increase since 1950, likely due to increased nutrient inputs (Breitburg 1992; Murdy et al. 1997). Areas affected by hypoxia are primarily located in the mainstem of the Bay, north of the Rappahannock River, in waters where depths exceed approximately 12-meters (Murdy et al. 1997).

As a consequence of the spatial and temporal variability in abiotic factors in the Chesapeake Bay, the abundance and distribution of fish stocks varies seasonally, regionally and inter-annually (Jung and Houde 2003). Many additional studies have demonstrated that temperature (Coutant 1987; Planque and Fox 1998; Zheng et al. 2002), oxygen (Pihl et al. 1991; Breitburg 1992; Wannamaker and Rice 2000; Breitburg 2002) and salinity (Powell and Schwartz 1977; Jung and Houde 2003) influence fish distributions. Temperature and salinity are often considered to have the greatest effect on distributions (Lalli and Parsons 1999; Zheng et al. 2002). However, studies have also identified water depth as an important factor influencing fish distribution (Maravelias 1999; Maravelias et al. 2000b), in particular the distribution of flatfish (Pearcy 1978; Swartzman et al. 1992; Allen and Baltz 1997; Abookire and Norcross 1998; Piet 2002). Water depth is directly associated with habitat structure and related to benthic community structure and composition (Pearcy 1978; Abookire and Norcross 1998). Since demersal fish are tightly coupled with the benthos, it is likely that they exhibit even stronger associations with particular water depths than pelagic species (Maravelias 1999).

Ontogenetic shifts in depth preferences often exist, with juvenile fish confined to shallow nursery areas (Baltus and Van Der Veer 1995).

The hogchoker (*Trinectes maculatus*: Achiridae), a demersal sole species, is an important species in the Chesapeake Bay food web (Mihursky and Kennedy 1967). It is a year round resident of the Chesapeake Bay and exhibits a standing stock comparable to or exceeding that of many fished species in the Chesapeake Bay, including Atlantic croaker, *Micropogonias undulatus*, bluefish, *Pomatomus saltatrix*, weakfish, *Cynoscion regalis*, and striped bass, *Morone saxatilis* (Baird and Ulanowicz 1989). In a fishery-independent survey conducted in the Patuxent River, a sub-estuary of the Chesapeake Bay, hogchoker was the most abundant species in shallow water collections with a beam trawl and the second most abundant species in deep water collections with an otter trawl (Mihursky 1968; McErlean et al. 1969). It is widely distributed and has been collected in the bay from the mouth to the interface of fresh and saltwater at head of the bay and throughout associated tributaries. In a study of the fish community in fresh and brackish waters of several Virginia rivers of the Chesapeake Bay, hogchoker was collected up to 40 miles upriver from the boundary between fresh and brackish water (Massman 1954). Hogchoker exhibits a seasonal migration pattern between saline spawning grounds and overwintering grounds near the interface of fresh and saltwater (Dovel et al. 1969; Peterson 1994; Peterson 1996). Previous work has indicated that hogchoker exhibit a depth range of approximately 1-75 meters (Miller et al. 1991).

The objective of this study was to investigate the relationship between the distribution of hogchoker abundance and environmental parameters in the Chesapeake Bay with the primary goal of determining the mechanisms that drive hogchoker

distribution. Previous work on the hogchoker utilized frequency distributions and linear regression analyses to investigate the relationship between distribution and abiotic factors (Dovel et al. 1969; Koski 1973; Peterson 1996), mark-recapture methods to investigate seasonal movements (Smith 1986) and laboratory approaches to determine the effect of abiotic factors on survival, behavior, growth, feeding and metabolism (Castagna 1955; Peters and Boyd 1972; Peterson-Curtis 1997). However, there are statistical concerns over the reliability of earlier analyses of the field studies, which assumed that hogchoker are distributed continuously and exhibit normally distributed responses to environmental parameters. Here I develop and apply a generalized additive model (GAM) to the analysis of hogchoker distributions that relaxes the restrictive assumptions of earlier analyses. The rationale for the use of a GAM to investigate the distribution of hogchoker is presented in Appendix 1. Hastie and Tibshirani (1990) and Venables and Dichmont (2004) provide an introduction to GAMs, and Jensen et al. (in press) provide a recent application of a GAM to the distribution of animals in the Chesapeake Bay.

METHODS

Sample Collection

Samples were collected as part of the Trophic Interactions in Estuarine Systems (TIES) and Chesapeake Bay Fishery-Independent Multispecies Survey (CHESFIMS) programs, bay-wide surveys of the bentho-pelagic fish community of the Chesapeake Bay.

The TIES program was conducted from 1995 – 2000, with the primary goal of examining the factors that control secondary production (Jung and Houde 2003). Three research cruises were conducted annually in April-May, June-August and October. Between 20 and 52 stations fixed to transects, spanning the mainstem of the bay, were occupied each cruise (Jung 2002). Fish were sampled with a midwater trawl (MWT) with an 18-m^2 opening and 3-mm mesh in the cod end. At each station, a standardized 20-minute stepped, oblique tow was conducted that fished the entire water column from surface to bottom in two minute depth intervals (Jung and Houde 2004). All fish collected were identified and subsamples were measured and weighed immediately after the tow. CTD casts were only performed at 29% of the MWT stations to obtain depth profiles of temperature, salinity and oxygen. To obtain profiles of environmental factors at the remaining MWT stations, kriged estimates were used (Jung and Houde 2003). Both night and day MWT tows were performed during TIES. Only data from those TIES stations sampled at night were used in subsequent analyses to ensure a consistent sampling protocol over both surveys.

The CHESFIMS program began in 2001 and served as an extension to the fisheries component of the TIES program. Like TIES, three research cruises were conducted each year. The spring (April/May) and summer (July) cruises overlapped with those of TIES, however, the fall survey was conducted earlier in the season (September). In 2001, all stations were allocated on fixed transects spanning the mainstem of the Bay. During the spring cruise, 31 stations were occupied based on sampling conducted within the TIES program. The sampling intensity increased to 52 stations in the summer and fall 2001. In 2002 the sampling design was modified, where the original 31 fixed TIES

stations were sampled, however, the locations of the remaining stations were randomly selected using a stratified random design proportional to strata volume (Figure 1). The 20 random stations were reselected each cruise, therefore, no random station was repeatedly occupied. Weather conditions limited sampling effort during some cruises. Consequently, sampling intensity varied between cruises. To facilitate the comparison of TIES and CHESFIMS, the station sampling protocol remained the same, with a 20-minute stepped tow with a MWT of the same dimensions and mesh size. All collected fish were identified and subsamples were measured and weighted immediately after the tow. A CTD cast was performed at each station to obtain profiles of temperature, salinity and dissolved oxygen.

As hogchoker is a demersal species, the total MWT tow time was likely not an appropriate index of sampling effort. Accordingly, the effective effort of each tow was adjusted for the time the MWT was within five meters of the station depth, a zone within which demersal hogchoker would have been vulnerable to the gear. A distance of 5-meters was utilized to coincide with the height of the net when it was fully open. The amount of time the net was within five meters of bottom, subsequently referred to as bottom time, varied among stations. Bottom time was considered a potential explanatory variable in all analyses.

For each station, bottom time was determined from a minilog, a device that was placed on the float line of the trawl and recorded depth measurements at particular time intervals. At some stations the estimated bottom time equaled zero. At these stations, however, it was unclear whether the net truly never came within five meters of the station bottom or whether the station depth decreased during the tow, allowing the net to come

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within five meters of the bottom. Due to the inability to distinguish between these alternatives, all stations where bottom time equaled zero were eliminated from the analyses. It was also possible that station depths deepened during the MWT tows. Thus, the station depth utilized to calculate bottom time was assumed to be the deeper of the station depth recorded during the beginning of the MWT tow and the deepest depth measurement from the minilog file.

Statistical Analysis

To explore hogchoker distribution, the relative abundance at each station was mapped using ArcGIS and interpolated through an inverse distance weighting procedure. Subsequently, a two-stage GAM was utilized to investigate the relationship between hogchoker catch and multiple environmental parameters. The approach used followed that developed by Jensen et al. (in press) to model blue crab distributions in the Chesapeake Bay. Briefly, the first stage of the GAM predicts presence of hogchoker at a station whereas the second stage predicts abundance of hogchoker given presence. By uncoupling the two processes, the restrictive statistical assumptions that characterized earlier analyses are relaxed. Specifically, the analysis accounts for both the large number of hauls in which no hogchoker were caught (zero-inflation) and the potentially complex, non-normal responses of hogchoker to environmental parameters.

Due to their influence on growth, metabolism and distribution, average bottom salinity, temperature, oxygen and water depth were included as covariates in the full model. For stations where CTD profiles were available, average bottom abiotic parameters were calculated as the average within five meters of bottom. For other

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stations, near-bottom environmental parameters were estimated from kriged distributions constructed from CTD profiles (Jung and Houde 2003). Bottom time was incorporated into the model as a proxy of fishing effort. To investigate if the same environmental factors influence distributions in different seasons and years, time can either be incorporated as a continuous variable into a GAM (Swartzman et al. 1992; Maravelias et al. 2000a; Rand 2002), incorporated as a factor (Piet 2002) or a separate GAM can be constructed for each year (Swartzman et al. 1992; Swartzman et al. 1995; Maravelias 1999; Maravelias et al. 2000a; Jensen et al. in press). Due to the number of observations and degrees of freedom needed for a two-stage GAM, year was included as a continuous covariate to determine if the relationship between abundance and environmental covariates changed across years. To determine if this relationship differed among seasons, day of year was included as a covariate in the model.

In the first stage of the model, hogchoker catches were transformed to a binary variable indicating presence/absence. The probability that hogchoker were present at a station was modeled as an additive function of bottom time, salinity, oxygen, temperature, year, day of year and depth. A binomial error distribution with a logit link function was used to describe the underlying distribution of the data. Each covariate was modeled with a smooth function and the smooth functions were fit with penalized regression splines using an iterative approach (Wood and Augustin 2002). The full model, without any interaction terms, was simplified through backwards elimination until all variables in the model were significant at the 5% significance level. After the full model was reduced, all two-way interaction terms between the remaining variables were added to the model. Interactions that incorporated bottom time as a covariate and the

interaction between year and depth were not included in any model because they were difficult to interpret biologically. The full model with interactions was reduced using backwards elimination. An insignificant main effect term was not eliminated from the model if it was incorporated into a significant interaction term.

The second stage of the GAM modeled only those stations where hogchoker were present. The natural log of hogchoker relative abundance was modeled as a function of the same environmental covariates utilized in the first stage of the analysis, with the exception of bottom time. Bottom time was not included as a covariate because it was incorporated into the response variable, hogchoker relative abundance, as hogchoker catch per minute of bottom time. Relative hogchoker abundance was modeled with a Gaussian distribution and an identity link function. Similar to the first stage of the model, each covariate was modeled with a smooth function, optimized using penalized regression splines, and the full model was simplified through backwards elimination. Model selection was conducted using the same protocol as the first stage.

After the completion of both stages of the GAM, predicted hogchoker abundance at a given location was calculated by multiplying together the results from each stage. To assess overall model fit, predicted hogchoker abundance was calculated and subsequently compared to observed abundances. All GAMs were constructed using the mcgv package in R.

RESULTS

Hogchoker were collected in only 21% of all hauls. The distribution of hogchoker varied both seasonally and inter-annually in the Chesapeake Bay (Table 1).

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Additionally, hogchokers were not uniformly distributed (Figure 2). Preliminary investigation of the relationships between relative hogchoker abundance and the environmental covariates did not indicate clear relationships between hogchoker relative abundance and any environmental parameter (Figure 3). Hogchoker were collected in water with bottom temperatures between 8.58 and 29.40 $^{\circ}$C, with peak catches occurring at intermediate temperatures (Figure 3a). Water salinities at which hogchoker were collected varied from 0.026 – 32.00 without apparent trend (Figure 3b). Similarly, hogchoker were caught at a depth range of 3.5 – 42.4m, with highest catches seen at intermediate depths (Figure 3c). The distribution of hogchoker catches as a function of dissolved oxygen (Figure 3d) paralleled the pattern seen with respect to temperature, reflecting the strong covariation between temperature and dissolved oxygen.

For each stage of the GAM, correlations between the covariates included in the full model were first investigated to ensure that multicollinearity was not a substantial concern (Tables 2 and 3). Several correlations were significant at the 5% significance level. The first stage of the GAM incorporated data from 731 stations at which tows were made over 10 years. For these stations, the most significant correlations were between depth and bottom time (r = -0.38), depth and oxygen (r = -0.20), salinity and oxygen (r = -0.23), temperature and oxygen (-0.56) and temperature and day of year (0.47). In the second stage of the GAM, only those stations at which hogchoker were caught were considered. This subset resulted in observed catches from 154 stations over 10 years. Within this subset of the data, the most significant correlations were between salinity and oxygen (r = -0.36), temperature and oxygen (r = -0.55), temperature and day of year (r = 0.30) and year and day of year (r = -0.38). Since all correlation coefficients

were less than 0.8, no explanatory variables were omitted from the full model as a concern of collinearity.

The first stage of the GAM predicts the probability of hogchoker occurrence, P, at any station. The reduced model, resulting from backward elimination of the full suite of parameters, modeled hogchoker occurrence as an additive combination of smooth functions of bottom time (BT), temperature (T), salinity (S), year (YR), depth (D) and the interaction of temperature with year (T*YR) given by:

$P = logit(I) = s(BT) + s(T) + s(S) + s(YR) + s(D) + (T*YR)$

where I is the binary variable indicating hogchoker presence (I=1) or absence (I=0) and each s represents a penalized regression spline smooth function for a particular environmental covariate (Table 4). The first stage of the GAM explained 16.1% of the variability in occurrence.

To investigate the importance of each individual covariate in the fitted stage 1 model, the conditional contribution of each covariate, given the inclusion of the remaining covariates in the model, was plotted. In the first stage, the GAM plot for bottom time indicated an asymptotic relationship with the probability of hogchoker occurrence (Figure 4a). The standard error bands indicated relatively low variability near the center of the plot with increasing variability towards the extremes. Due to high variability at greater bottom time values, it was difficult to determine if the relationship was truly asymptotic or a function of the observed covariate values.

The relationship between depth and occurrence was nonlinear (Figure 4b). The limited number of samples at shallow and deeper depths restricted inferences outside the 5-20m depth range. Within this range, however, hogchoker occurrence generally

increased with depth up to approximately 15 meters, beyond which the probability of occurrence slightly decreased. The GAM plot for salinity indicated that occurrence was lowest at intermediate salinities and increased as the water became more and less saline (Figure 4c). The greatest probability of occurrence occurred in oligohaline and freshwater habitats. Temperature and hogchoker occurrence exhibited a linear relationship with increasing probability of occurrence as temperature increased (Figure 4d). There was more variability in the predicted spline for temperature compared to those of other covariates, including salinity and bottom time.

The relationship between hogchoker occurrence and year was not significant ($p = 0.67$), however, year remained in the model due to its significant interaction with temperature (Figure 4e). The interaction of temperature with year generally indicated a relatively high probability of occurrence at intermediate temperatures across years (Figure 4f). This probability was greatest during early years. With the exception of the most recent years, occurrence declined as temperature progressed towards the extremes. In the most recent years, however, occurrence increased as temperature declined.

The second stage of the GAM modeled the natural log of relative hogchoker abundance, incorporating only those stations where hogchoker were present into the model. The reduced model included temperature (T) and salinity (S) as significant terms. Relative hogchoker abundance was calculated as hogchoker catch per minute of bottom time (cpue) and was given by:

$Ln(cpue) = s(T) + s(S)$

where each s represents a penalized regression spline smooth function for a particular environmental covariate (Table 5). The second stage of the analysis explained 12.5% of the variability in abundance.

The GAM plots corresponding to the second stage portray the conditional relationship of each covariate with hogchoker relative abundance (Figure 5). Relative abundance and temperature exhibited a dome-shaped relationship with an increase in abundance with increasing temperatures up to approximately 21° Celsius, beyond which hogchoker abundance declined (Figure 5a). The peak in occurrence at 21°C, however, corresponded with an area of high variability due to a small number of observed temperatures between approximately 19°C and 23°C. Variability also increased towards the low and high extreme temperature values. Salinity exhibited a negative linear relationship with abundance, where abundance declined with increasing salinities (Figure 5b).

To assess overall model fit, predicted hogchoker abundance at each original station was calculated and subsequently compared to observed abundances. This comparison resulted in a correlation coefficient of 0.383 (Figure 6). The intercept and slope of a regression model with observed relative abundance as the independent variable and predicted relative abundance as the dependent variable were 0.048 and 0.059, respectively. The intercept of the regression model was significantly different from zero ($t_{(729)} = 23.29$, $p < 0.001$) and the slope was significantly different from one ($t_{(729)} = -188.42$, $p < 0.001$).

DISCUSSION

Generalized additive modeling is a flexible approach that is capable of modeling complex and nonlinear ecological data. Through the extension of traditional GAMs into a two-stage approach, GAMs can be utilized to adequately model the variability in zero-inflated count data. In this study, however, the two-stage GAM fitted to relative hogchoker abundance data explained 15.9% of the variance in hogchoker abundance.

Abundance and distribution were significantly related to several habitat variables. The results of the GAM indicated that water depth was important in describing hogchoker distribution. The first stage of the model demonstrated that hogchoker occurrence increased as depth increased until approximately 15 meters, beyond which occurrence likely decreased. At depths greater than 20 meters, the relationship between hogchoker occurrence and depth was uncertain due to the shallow nature of the Chesapeake Bay, where average depth is just 6.4 meters and depths greater than 20 meters are relatively uncommon (Houde et al. 1998). Regardless of the relationship at depths greater than 20 meters, however, it was evident that hogchoker exhibited a preference for moderate depths. Investigation of hogchoker microhabitat use in a Louisiana estuary indicated that over the range of water depths sampled (0.7-6.1 meters), hogchokers preferred the deeper habitats (Allen and Baltz 1997). This preference was further supported by a study of the ecology of the hogchoker in the Hudson and Connecticut Rivers, where hogchoker CPUE at trawl stations greater than five meters in depth was significantly greater than that of trawl stations less than five meters (Koski 1978). This outcome is also consistent with multiple previous studies that demonstrate depth associations of particular demersal species (Pearcy 1978; Abookire and Norcross

1998; Piet 2002). Depth is generally correlated with sediment grain size, however, variability in this relationship exists (Abookire and Norcross 1998). Accordingly, the significance of water depth could potentially indicate the influence of bottom type on hogchoker distribution. Due to the potential variability between water depth and sediment grain size, it is possible that bottom substrate would also exhibit a significant relationship with hogchoker occurrence.

Temperature significantly influenced hogchoker occurrence and abundance through its interaction with year in the first stage of the GAM and as a main effect in both stages of the model. The main effect of temperature in the first stage indicated a positive linear relationship with occurrence. However, with the exception of the most recent years, the interaction of temperature with year indicated the highest probability of occurrence at intermediate temperatures. The importance of year indicated the contribution of an additional variable, not present in the model, which varied across years. As temperature progressed towards low and high extremes, the probability of occurrence declined. This relationship was further supported by the results of the second stage of the model, which indicated a dome shaped relationship between temperature and hogchoker abundance. A dome shaped relationship between hogchoker abundance and temperature was also documented in the Hudson River (Koski 1978). This relationship is likely a function of the influence of temperature on the physiology and growth rate of a fish. As temperature increases, chemical reaction rates also increase, ultimately resulting in an increase in metabolic rate (Wootton 1990; Lalli and Parsons 1999). Temperature can control growth rates of flatfish, with growth rates increasing with temperatures up to a maximum temperature, above which growth declines (Jager et al. 1993; Valiela 1995).

When temperature exceeds this maximum, it is possible that hogchokers move to more favorable habitats, resulting in a decline in abundance.

Hogchoker abundance and distribution were also significantly influenced by salinity. Salinity and occurrence exhibited a parabolic relationship with the greatest probability of occurrence at low and high salinities. The low occurrence in mesohaline conditions may be related to the low total biomass and diversity of organisms in the mesohaline region of the Chesapeake Bay (Jung and Houde 2003). Furthermore, hogchoker occurrence was greater at low than high salinities. The second stage indicated a negative linear relationship between salinity and abundance with greatest abundances in low salinity habitats. Greater occurrence and abundance in low salinity areas could be a result of differences in total abundance between saline spawning and low salinity overwintering/nursery grounds. Hogchoker exhibit a seasonal migration pattern between these spawning and overwintering grounds. This migration pattern was first proposed for the northern hogchoker in the Patuxent River, a tributary of the Chesapeake Bay (Dovel et al. 1969), but has also been observed for the southern hogchoker in the Mississippi Sound and the Gulf of Mexico (Peterson 1994; Peterson 1996). Additional studies from Georgia (Reichert and Veer 1991), North Carolina (Walsh et al. 1999) and New York (Koski 1978) have also supported this migration pattern.

Hogchokers spawn in the summer in relatively high salinity areas of approximately 15-20 (Peterson 1996). In a study examining distributional trends of ichthyoplankton, however, hogchokers were frequently caught at a sample site, which exhibited a salinity range from 28-34, from the end of May through the beginning of October (Hettler and Chester 1990). These studies indicate that the salinity of spawning

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areas may vary across systems. In the fall, larvae move upstream to low salinity nursery areas near the interface of salt and freshwater. Juveniles move toward the spawning area in the spring and their travel range increases each year until they successfully reach the spawning area at approximately 4 years of age. Adults typically reside in low salinity areas over the winter and then migrate to the spawning grounds in the spring (Dovel et al. 1969; Peterson 1996). The results from the inverse distance weighted interpolation procedure support this seasonal migration pattern. Accordingly, all age classes overwinter in habitats near the interface of fresh and saltwater, and juveniles remain close to these habitats throughout the year. It is only the adults that fully move into saline spawning grounds during the spring and summer (Dovel et al. 1969; Peterson 1996). Therefore, when averaging over all seasons, the entire population resides at some point during the year in the low salinity habitats where only a portion of the population is ever present in high salinity spawning areas, ultimately resulting in a greater overall abundance in lower salinity regions over the course of the survey.

It is important to recognize that the model left a substantial amount of the variability in hogchoker distribution unexplained. Additional abiotic factors beyond temperature, salinity, dissolved oxygen and water depth, such as bottom substrate or food availability, are potentially important in controlling hogchoker abundance. However, concerns over the resolution of coverage maps for both bottom type and prey availability precluded their incorporation into the model.

Many studies have demonstrated that bottom substrate can impact the distribution of flatfish, which often exhibit a preference to a particular substrate type (Powell and Schwartz 1977; Jager et al. 1993; Gibson 1994; Allen and Baltz 1997; Abookire and

Norcross 1998). It has been hypothesized that sediment type can define the habitat of a flatfish, with active selection by individual species of sediments according to grain size (Gibson 1994; Abookire and Norcross 1998). Previous work has indicated that the hogchoker are generally found in muddy and sandy habitats (Castagna 1955; Walsh et al. 1999). This substrate preference indicates that bottom composition may be an important abiotic variable controlling hogchoker distribution and abundance.

Substrate may be correlated with the behaviors of a particular species. Species that bury themselves for protection, for instance, may be able to more effectively cover themselves in particular habitat types (Gibson 1994; Abookire and Norcross 1998). Differences in burying ability across habitat types are primary due to differences in grain and fish size (Tanda 1990). A study of the southern hogchoker in Florida noted that the hogchoker exhibited this burying behavior (Castagna 1955), further emphasizing the potential importance of benthic substrate in modeling hogchoker abundance.

Particular substrate preferences can also be linked to prey availability (Jager et al. 1993; Gibson 1994). Together with predation vulnerability, food availability is an important factor in determining the quality of a habitat(Gibson 1994). Hogchoker diets are comprised of benthic fauna, primarily annelids, isopods, bivalve siphons, chironomids and arthropods (Koski 1973; Pihl et al. 1992; Derrick and Kennedy 1997). The incorporation of benthic community composition and abundance into the GAM could potentially enhance model fit.

Inaccuracies in the calculation of bottom time, which was included as a covariate in the first stage of the model and incorporated into the response variable (as catch per minute bottom time) in the second stage, could also influence model fit. Bottom time,

calculated for each station and used as a proxy for hogchoker fishing effort, was based on a log of each tow and the recorded station depth. The results of the first stage indicated that bottom time significantly influenced the probability of hogchoker occurrence. Bottom time and occurrence appeared to exhibit an asymptotic relationship, however, due to the high variability in the smooth function at extreme bottom time values, it was difficult to ascertain the true relationship at high bottom times. Furthermore, an underestimation of bottom time could potentially result from a decline in station depth during the length of the tow. This inaccuracy is not detectable and could influence the results of the model.

In the CHESFIMS multispecies survey, a CTD cast was performed at each station prior to the deployment of the midwater trawl to obtain depth profiles of several abiotic variables. During the TIES survey, however, CTD casts were only performed at 29% of the midwater trawl stations. At the remaining stations, bottom temperature, salinity and dissolved oxygen measurements were obtained from kriged datasets of the bay (Jung and Houde 2003). Kriged measurements were obtained from TIES CTD casts, performed primarily during the day. All MWT tows included in the GAM, however, were conducted at night. Diel fluctuations in abiotic factors due to tidal changes and the absence of photosynthesis at night often occur (D'Avanzo and Kremer 1994), which could influence fish distributions. Accordingly, the use of daytime measurements of abiotic factors to predict the abundance and distribution of hogchoker at night could have contributed to the unexplained variance of the model.

It is also possible that the development of separate GAMs for each ontogenetic stage might elucidate the relationship between abundance and salinity. Previous

laboratory studies have indicated that juvenile behavior, feeding patterns and metabolic rates vary across salinities (Peterson 1994; Peterson-Curtis 1997). This variation has been attributed to an ontogenetic shift in osmoregulatory capabilities, which is potentially correlated with maturation. Accordingly, separate GAMs constructed for juveniles and adults will likely depict varying correlations between salinity and abundance. Such analyses were not possible here because of limited sample sizes.

Due to the acute influence of oxygen on metabolic rates, it was surprising that oxygen was not significantly related to hogchoker abundance or distribution. Trawl collections in the York River, a southern tributary of the Chesapeake Bay, indicated that hogchoker were impacted by hypoxia and responded to hypoxic conditions through movements from deep to shallow strata (Pihl et al. 1991). Yet after hypoxic episodes, hogchoker returned to deep strata, even when concentrations remained below 2.6 mg/L. Laboratory studies indicated that hogchokers were able to acclimate to oxygen levels at 1.0 mg/L and survive until concentrations reached 0.3-0.4 mg/L (Pihl et al. 1991). This tolerance to low oxygen concentrations could have contributed to the absence of a significant relationship between bottom dissolved oxygen and abundance. Furthermore, dietary studies demonstrated that hogchokers were able to optimally exploit prey during and immediately after hypoxic events (Pihl et al. 1992). This optimal exploitation was due to increased availability of the benthos due to sublethal effects of hypoxic conditions (Pihl et al. 1992). Consequently, hypoxic conditions can both positively and negatively affect demersal fish. The interaction of these effects may contribute to the absence of an overall relationship between bottom dissolved oxygen levels and hogchoker abundance.

In addition to abiotic factors, biotic factors may also be important in controlling the distribution of hogchoker abundance. Biotic interactions, including predation and competition, can modify habitat selection (Sogard 1992). The hogchoker is not commercially harvested, however, it is an ecologically important species in the bay due to its substantial biomass and wide distribution (Massman 1954; Mihursky and Kennedy 1967; McErlean et al. 1969; Smith et al. 1984; Baird and Ulanowicz 1989). This large distributional range may result in competition of resources with several exploited species, including white perch, *Morone americana*, spot, *Leiostomus xanthurus*, white catfish, *Ameiurus catus*, and Atlantic croaker, which exhibit dietary overlap to varying degrees with hogchoker (Homer and Boynton 1977; Smith et al. 1984; Baird and Ulanowicz 1989; Pihl et al. 1992).

Therefore, as a consequence of the dietary overlap, it is important to determine if the hogchoker overlaps spatially with these exploited species. A study investigating nekton organization in shallow marsh habitats of the York River indicated that hogchoker were more abundant in shoal habitats where white perch were more abundant in tidal creeks, potentially indicating resource partitioning (Smith et al. 1984). The determination of the factors that control the distribution of these species will help to elucidate the extent of resource overlap or partitioning. Furthermore, the apparent dietary overlap demonstrates the need to incorporate species interactions into fisheries management policies. With the progression towards multispecies fisheries management in the Chesapeake Bay (CBP 2000), unexploited but abundant species must be incorporated into fishery management plans to more realistically estimate the harvests of commercially important species. Accordingly, the investigation of the factors controlling hogchoker

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distribution, an ecologically important species, has implications for multispecies

management policies in the Chesapeake Bay.

Table 1. The percentage of stations with zero hogchoker catch (% Zeros) and the average (Avg), standard deviation (SD), minimum (Min) and maximum (Max) hogchoker CPUE (catch per minute of bottom time) at each station within each year, season and stratum.

Year	Season	Strata	% Zeros	Avg	SD	Min	Max
				Hogchoker CPUE			
2000	Summer	Lower	63.64	0.29	0.74	0	2.49
		Middle	83.33	0.05	0.13	0	0.31
		Upper	83.33	0.15	0.36	0	0.88
	Fall	Lower	70.00	0.08	0.13	0	0.36
		Middle	62.50	0.19	0.31	0	0.80
		Upper	83.33	0.21	0.51	0	1.26
2001	Spring	Lower	86.67	0.03	0.10	0	0.37
		Middle	80.00	0.03	0.07	0	0.22
		Upper	50.00	0.99	1.80	0	4.53
	Summer	Lower	88.24	0.11	0.42	0	1.74
		Middle	80.00	0.05	0.13	0	0.50
		Upper	83.33	0.10	0.32	0	1.12
	Fall	Lower	0	0	0	0	0
		Middle	5.00	0	0	0	0
		Upper	9.00	0.72	1.40	0	3.41
2002	Spring	Lower	24.00	0.06	0.11	0	0.48
		Middle	10.00	0.01	0.02	0	0.07
		Upper	12.00	0.10	0.34	0	1.19
	Summer	Lower	24.00	0.04	0.11	0	0.55
		Middle	15.00	0.05	0.15	0	0.57
		Upper	10.00	0.04	0.12	0	0.37
	Fall	Lower	25.00	0.04	0.09	0	0.30
		Middle	17.00	0	0	0	0
		Upper	9.00	0.47	0.67	0	1.82
2003	Spring	Lower	25.00	0.03	0.08	0	0.32
		Middle	17.00	0	0	0	0
		Upper	9.00	0.09	0.19	0	0.55
	Summer	Lower	24.00	0.04	0.15	0	0.67
		Middle	16.00	0.14	0.46	0	1.84
		Upper	9.00	0	0	0	0
	Fall	Lower	10.00	0.05	0.16	0	0.51
		Middle	10.00	0	0	0	0
		Upper	9.00	0.01	0.02	0	0.05
2004	Spring	Lower	24.00	0.04	0.07	0	0.27
		Middle	16.00	0	0	0	0
		Upper	9.00	0.11	0.15	0	0.40

Table 2. Pearson correlation matrix for the environmental covariates included in the first stage of the GAM. The first row of data for each covariate is the correlation coefficient, r, and the second row of data is the corresponding p-value.

	Bottom Time	Depth	Salinity	Temperature	Oxygen	Year	Day Of Year
Bottom Time	1	-0.3765	0.0224	0.0096	0.0747	0.0357	0.0197
		<.0001	0.5448	0.7964	0.0435	0.3357	0.5957
Depth		1	0.0263	-0.0801	-0.2038	-0.0173	-0.0088
			0.4775	0.0303	<.0001	0.6411	0.8120
Salinity			1	0.1284	-0.2312	0.1301	0.1680
				0.0005	<.0001	0.0004	<.0001
Temperature				1	-0.5569	-0.0599	0.4663
					<.0001	0.1056	<.0001
Oxygen					1	-0.1489	-0.1730
						<.0001	<.0001
Year						1	-0.3165
							<.0001
Day Of Year							1

Table 3. Pearson correlation matrix for the environmental covariates included in the second stage of the GAM. The first row of data for each covariate is the correlation coefficient, r, and the second row of data is the corresponding p-value.

	Depth	Salinity	Temperature	Oxygen	Year	Day Of Year
Depth	1	0.0343	-0.1092	-0.1188	-0.1007	0.1310
		0.6731	0.1775	0.1423	0.2138	0.1054
Salinity		1	0.1872	-0.3637	0.1742	0.0731
			0.0201	<.0001	0.0307	0.3679
Temperature			1	-0.55224	-0.0785	0.2956
				<.0001	0.3333	0.0002
Oxygen				1	-0.1676	-0.1641
					0.0378	0.0420
Year					1	-0.3840
						<.0001
Day Of Year						1

Table 4. Model fitting results from the first stage of the GAM (n = 731) for significance of smooth terms. Non-significant (n.s) smooth terms were dropped from the model through backwards elimination. Model fit statistics: adjusted r^2 = 0.161, deviance explained = 16.5%.

	Degrees of Freedom	Chi Square	P-value
Bottom Time	1.763	10.937	0.0031
Temperature	1	4.847	0.0277
Salinity	2.798	34.222	<0.0001
Year	1	0.185	0.6670
Depth	4.851	20.829	0.0008
Oxygen			n.s.
Day of Year			n.s.
Temperature*Year	13.420	31.502	0.0035
Temperature*Salinity			n.s.
Temperature*Depth			n.s.
Salinity*Year			n.s.
Salinity*Depth			n.s.

Table 5. Model fitting results from the second stage of the GAM (n = 154) for significance of smooth terms. Non-significant (n.s) smooth terms were dropped from the model through backwards elimination. Model fit statistics: adjusted r^2 = 0.125, deviance explained = 15.3%.

	Degrees of Freedom	Chi Square	P-value
Temperature	3.862	13.558	0.0098
Salinity	1	12.940	0.0004
Year			n.s.
Depth			n.s.
Oxygen			n.s.
Day Of Year			n.s.
Temperature*Salinity			n.s.
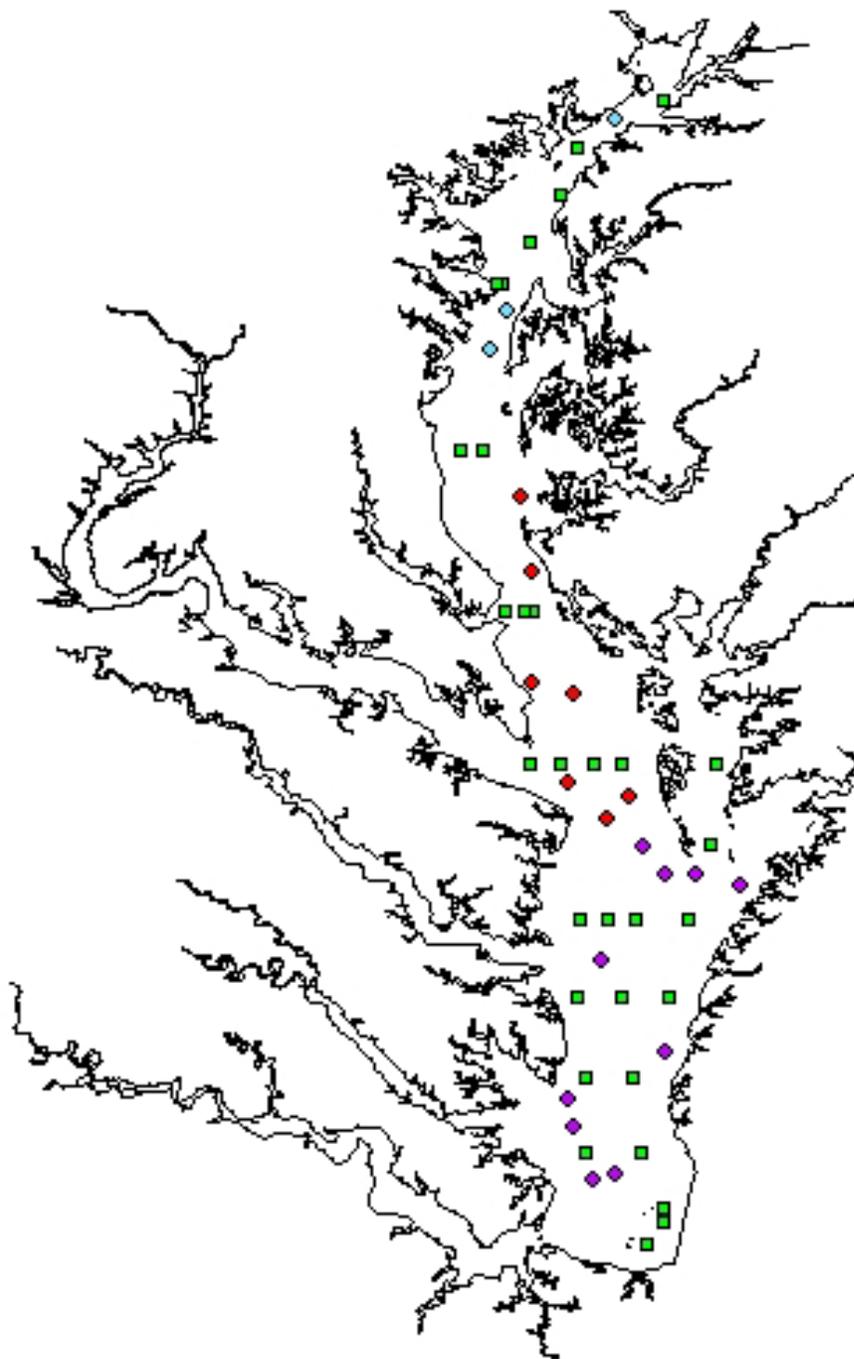
Figure 1. Sampling scheme for a CHESFIMS cruise. Green squares depict the 31 stations fixed to transects. Blue, red and purple diamonds represent the randomly selected stations for the upper, middle and lower bays, respectively.

2a)
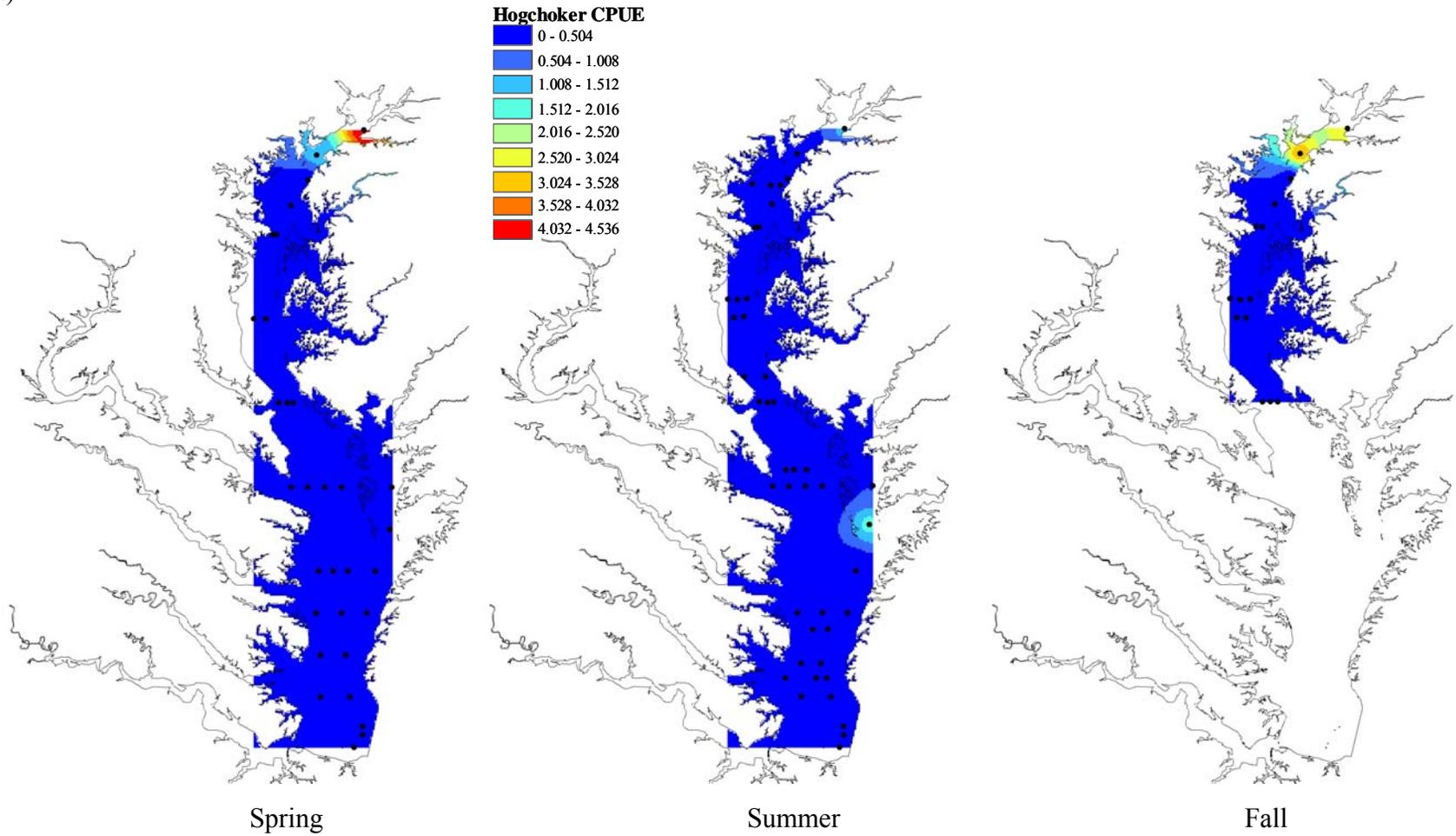
Figure 2. Relative abundance (catch per minute bottom time) of hogchoker in each season and year of CHESFIMS: 2001 (a), 2002 (b) and 2003 (c).

2b)

Hogchoker CPUE
- 0 - 0.202
- 0.202 - 0.404
- 0.404 - 0.606
- 0.606 - 0.808
- 0.808 - 1.010
- 1.010 - 1.212
- 1.212 - 1.414
- 1.414 - 1.616
- 1.616 - 1.818

Spring   Summer   Fall

2c)

Hogchoker CPUE
- 0 – 0.204
- 0.204 – 0.408
- 0.408 – 0.612
- 0.612 – 0.816
- 0.816 – 1.020
- 1.020 – 1.224
- 1.224 – 1.428
- 1.428 – 1.632
- 1.632 – 1.836

Spring   Summer   Fall
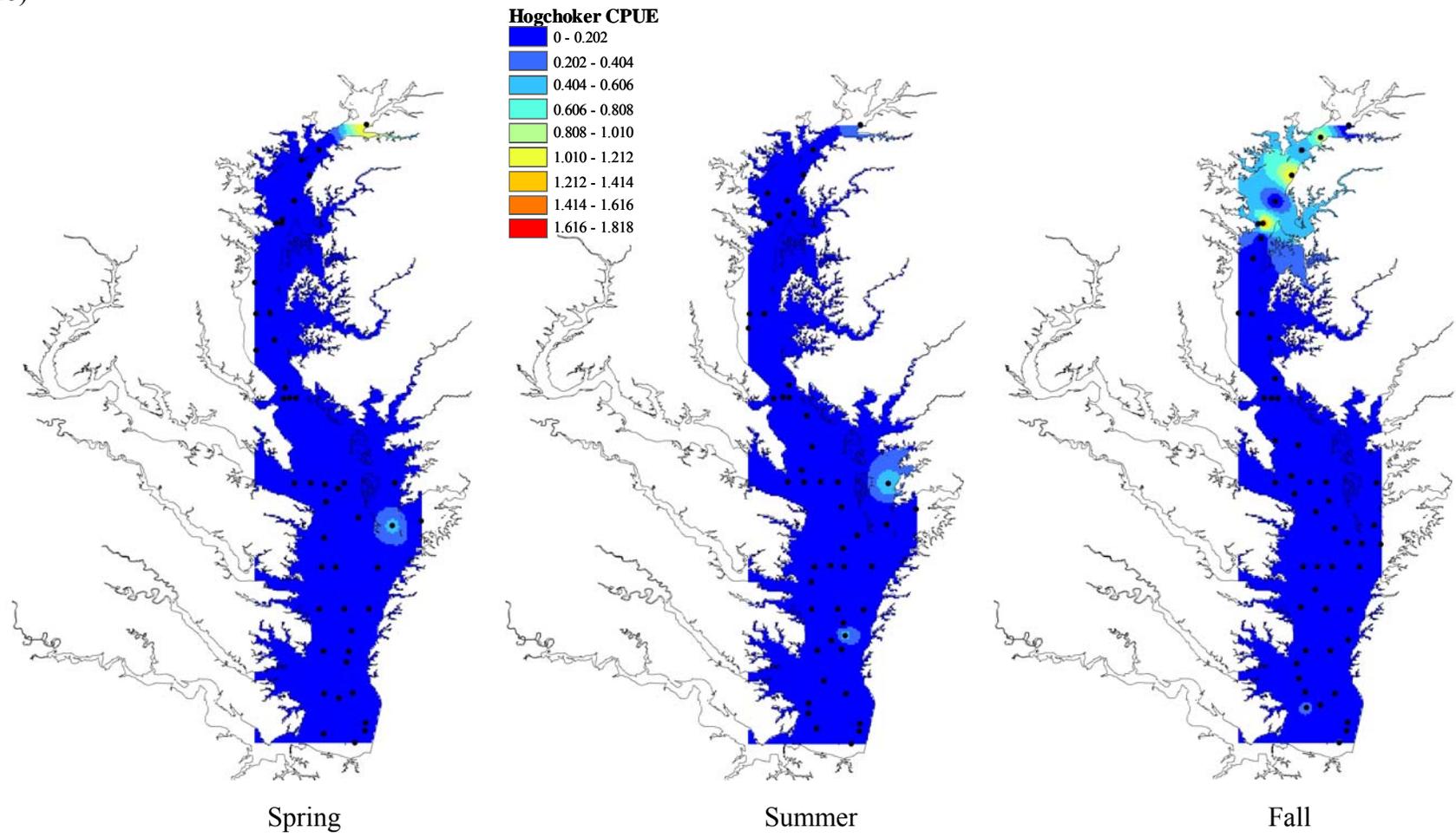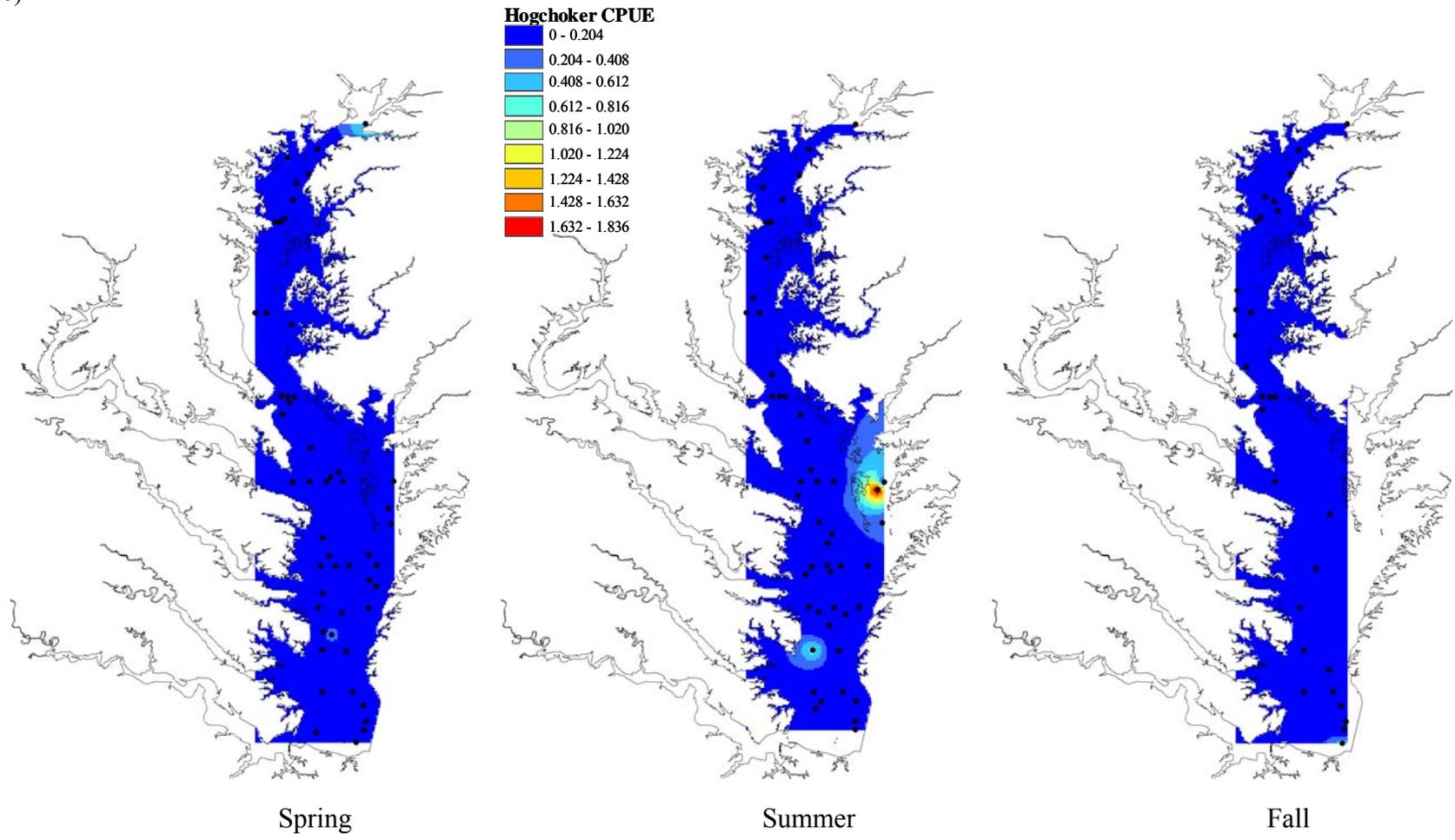
3a)
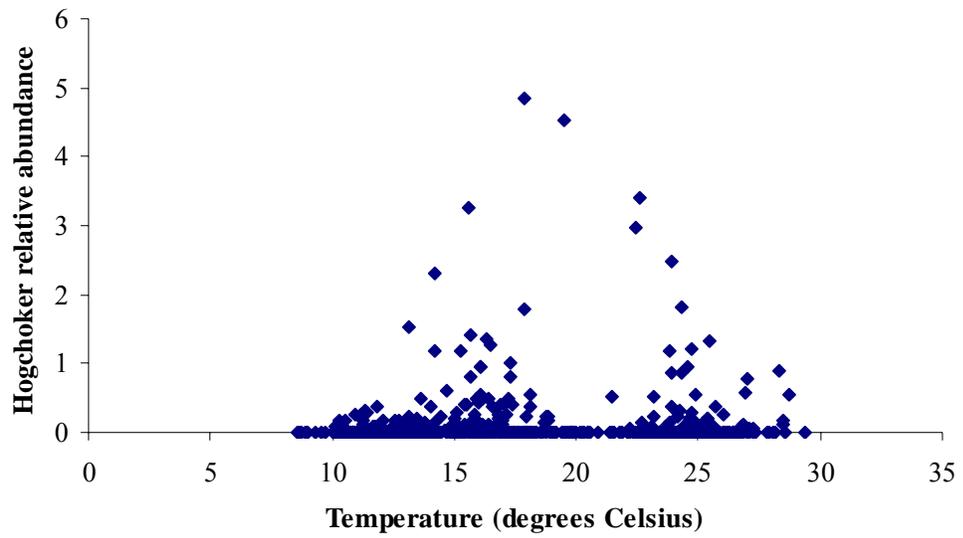
3b)
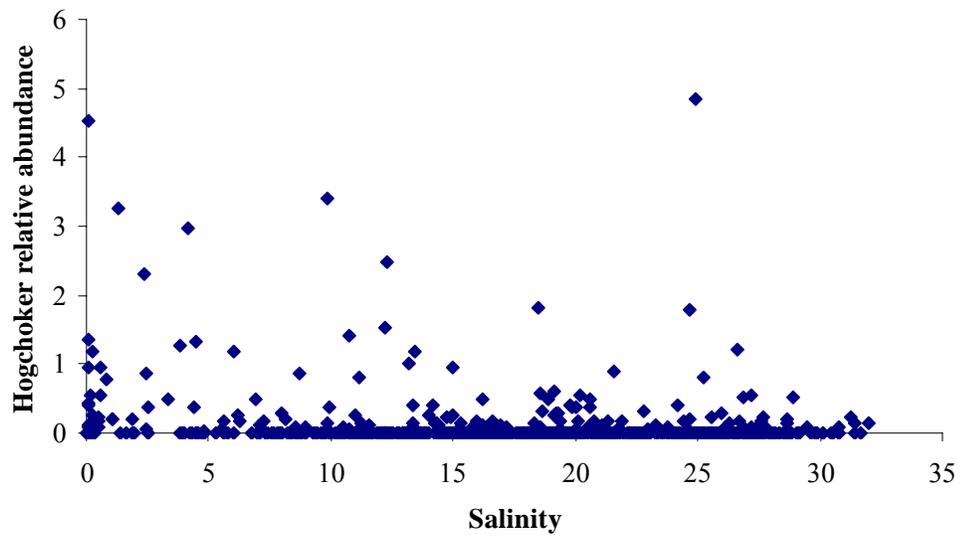
Figure 3. Relationship between hogchoker relative abundance and the environmental covariates, a) temperature b) salinity c) depth d) oxygen e) year and f) day, included in the full GAM model.

3c)
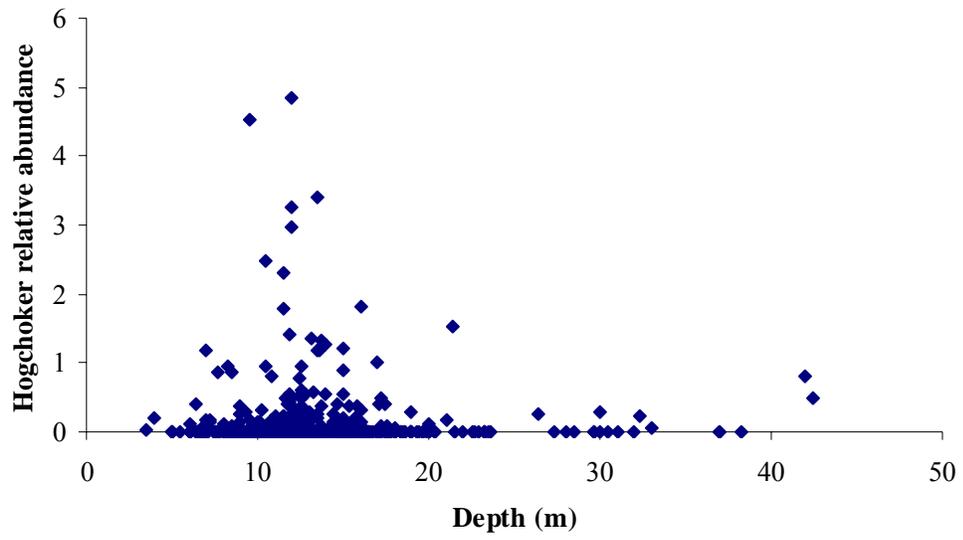
3d)
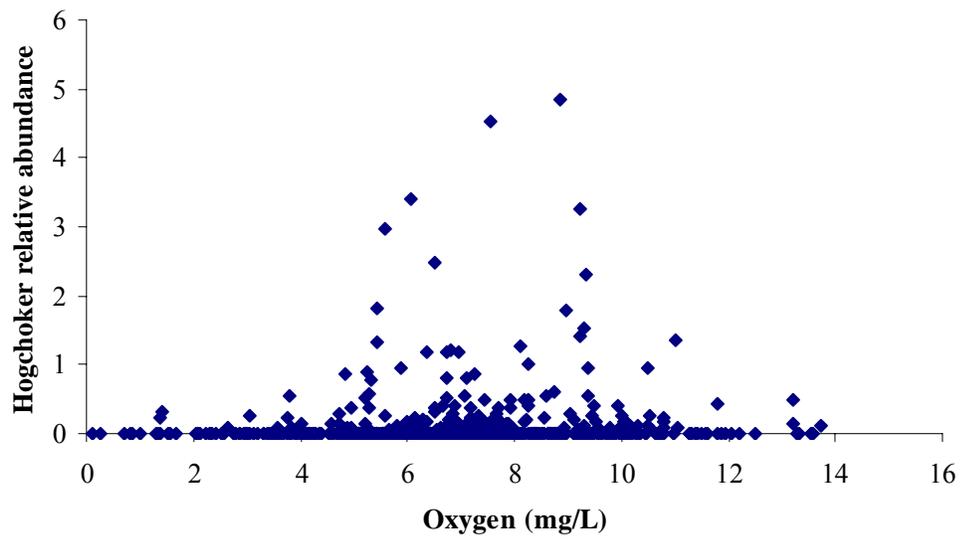
3e)
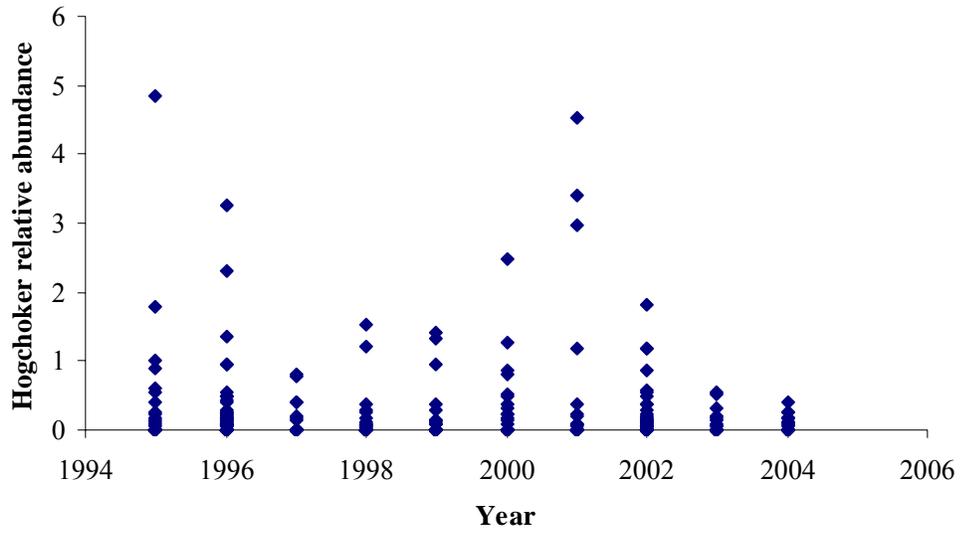
3f)
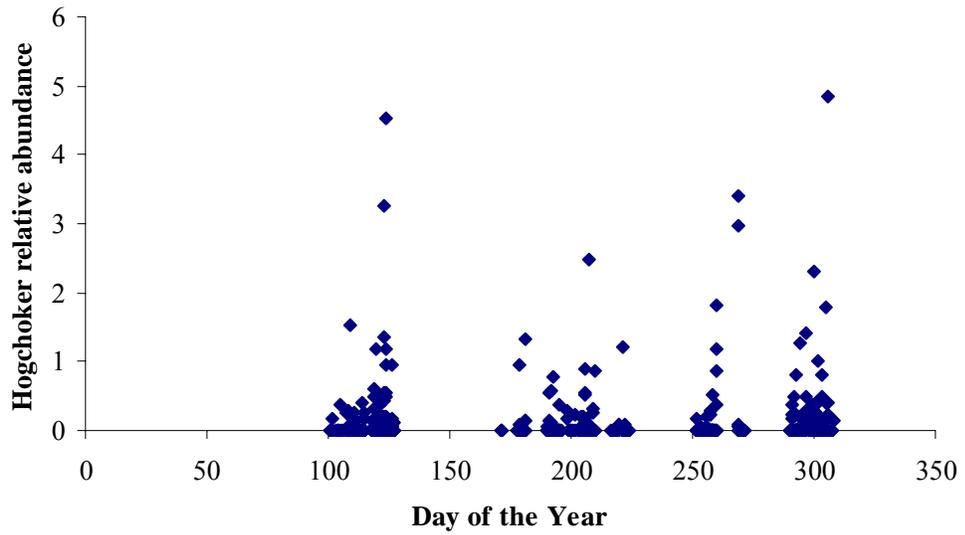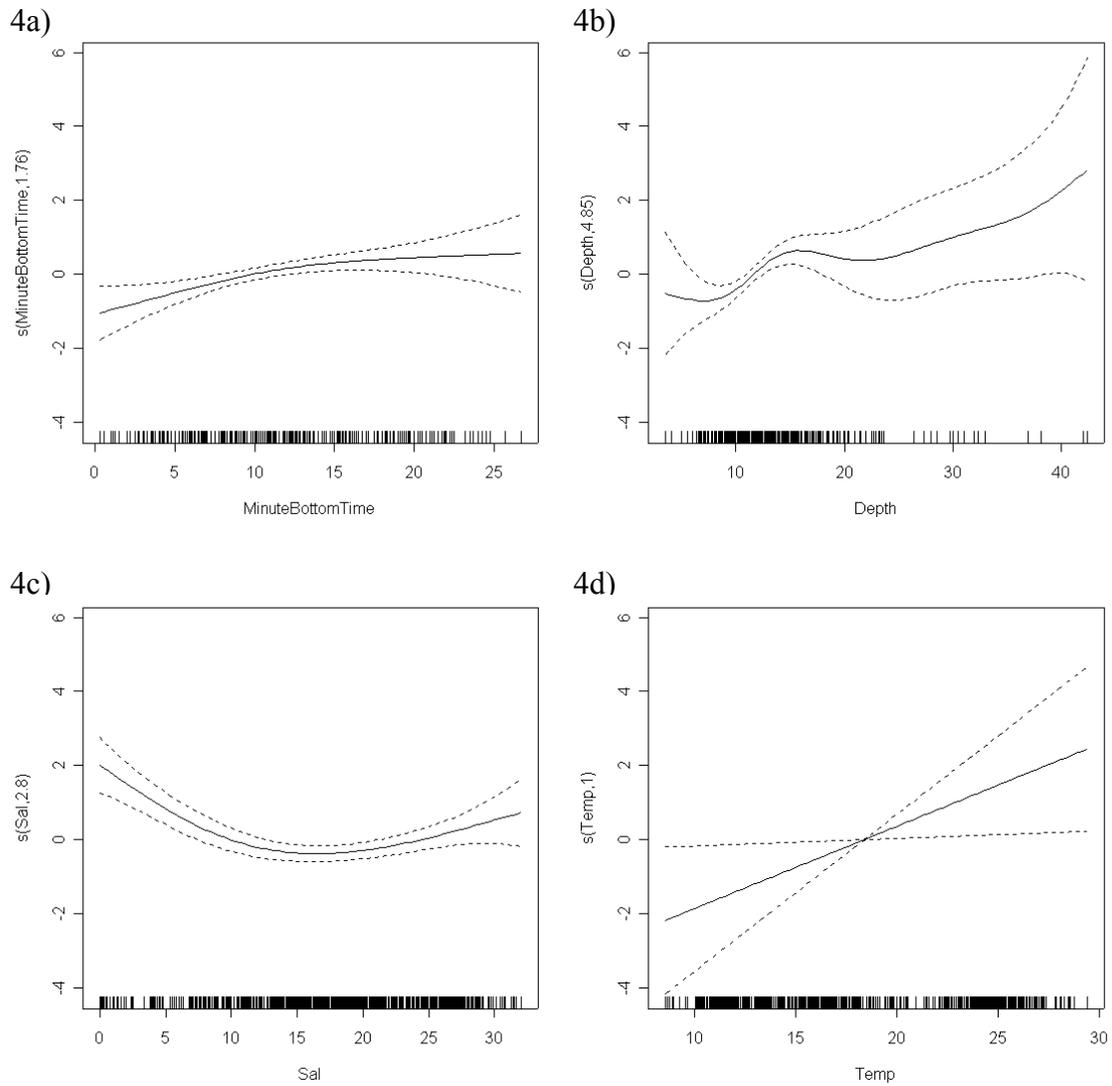
Figure 4. GAM plots for the environmental covariates, a) bottom time b) depth c) salinity d) temperature e) year and f) the interaction of temperature and year, included in the first stage of the model. The solid line represents the fitted smooth function, the dashed lines represent two standard errors above and below the smooth estimate and the rug plot on the x-axis represents the covariate values used in the model.

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4e)

4f)

5a)

5b)
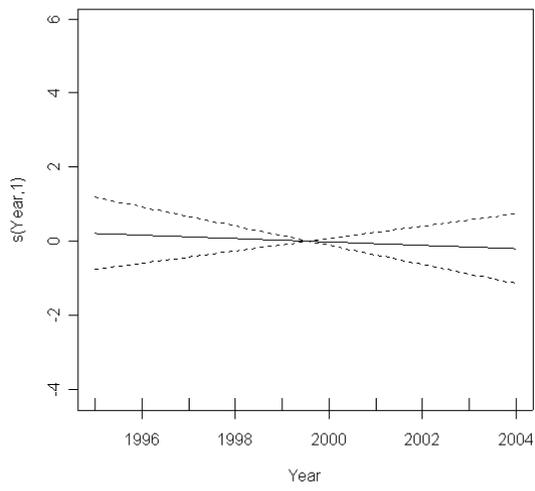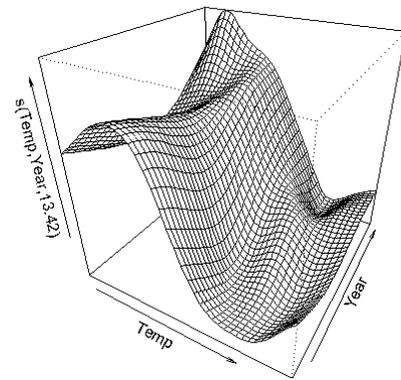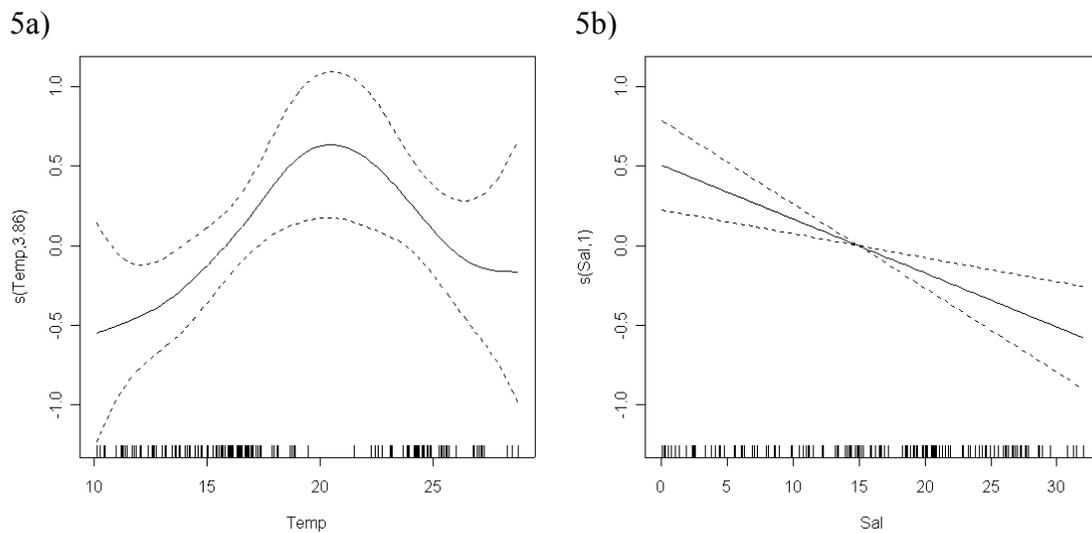
Figure 5. GAM plots for the environmental covariates, a) temperature and b) salinity, included in the second stage of the model. The solid line represents the fitted smooth function, the dashed lines represent two standard errors above and below the smooth estimate and the rug plot on the x-axis represents the covariate values used in the model.
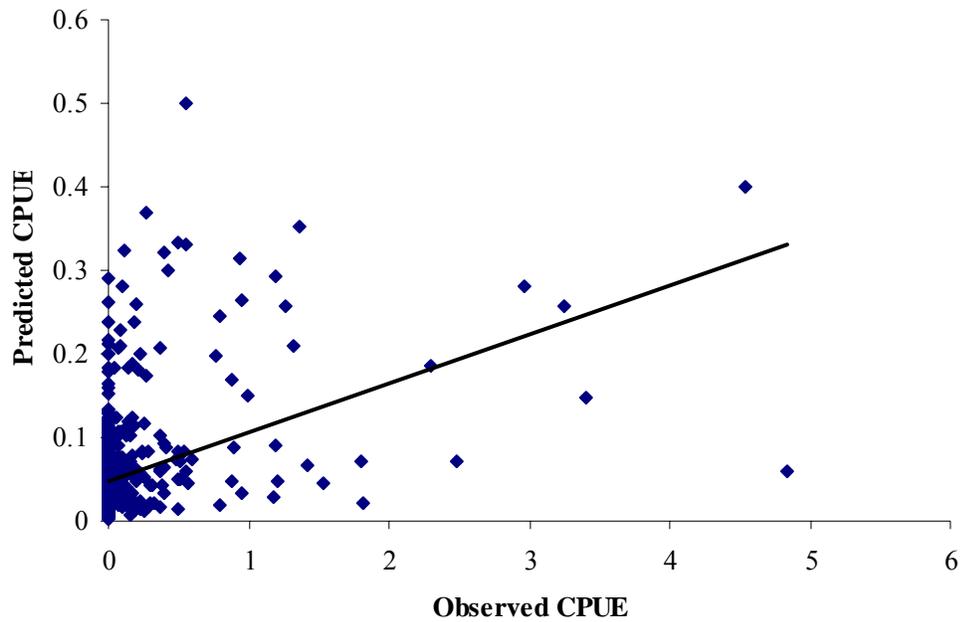
Figure 6. Relationship between predicted hogchoker relative abundance (measured as hogchoker catch per minute of bottom time) from the 2-stage GAM and observed abundance (r = 0.383, r^2 = 0.147). Predicted abundance = 0.059*observed abundance + 0.048.

CHAPTER 3: PATTERNS IN THE DIET AND TROPHIC DEMAND OF THE HOGCHOKER IN THE CHESAPEAKE BAY

INTRODUCTION

Recently, there has been an increased interest in ecosystem approaches to fisheries management (May et al. 1979; NMFS 1999; NRC 1999; Mace 2001; Brodziak and Link 2002; Link 2002; Link et al. 2002). Traditionally, fisheries have been managed through single-species approaches, where the species of interest is considered in isolation of its interactions with the surrounding ecosystem. These single species approaches generally require the assumption that species interactions, such as predation and competition, are minimal (Larkin 1977; May et al. 1979). Yet, in addition to fishing mortality rates, the community dynamics of any marine system are influenced by predator-prey interactions, competition, environmental variability and the interactions between these factors (Rice and Gislason 1996; Collie and DeLong 1999; Hollowed et al. 2000; Tsou and Collie 2001). These interactions are often complex and not necessarily intuitive (Jennings et al. 2001). Thus, the omission of consideration of these interactions in single species approaches has lead to concerns over the reliability of traditional approaches (but see Hilborn (2004) for a contrasting view).

Limitations of single-species approaches have arisen partly because fishing can substantially impact the trophic structure of a system by either removing a predator, prey or competitor species. The reduction in abundance of fish at a single trophic level can cause both direct and indirect responses within the food web of the system, which can be difficult to predict (May et al. 1979; Rice and Gislason 1996; Gislason et al. 2000). Therefore, it is important to incorporate trophic interactions into assessments to

investigate fuller the impacts of fishing. It is generally recognized that a multispecies

perspective, which incorporates species interactions, could improve the sustainability of

current fisheries management (Sissenwine and Daan 1991; NRC 1999; Hollowed et al.

2000; NOAA 2004). Consequently, ecosystem-based approaches to fisheries

management have been both recommended and mandated nationally (NMFS 1999; NRC

1999; CBP 2000; NOAA 2004) and regionally, including in the Chesapeake Bay (CBP

2000; NOAA 2004).

The Chesapeake Bay's natural resources are managed by the states of Virginia,

Maryland and the Potomac River Fisheries Commission. Management is coordinated

through the Chesapeake Bay Program (CBP), a multi-level entity spanning both state and

federal levels. The CBP was formed in the mid 1980's to protect the Chesapeake Bay by

the bordering states of Maryland, Virginia and Pennsylvania, the District of Columbia

and the U.S. Environmental Protection Agency. The goals of the CBP, including the

protection and restoration of living resources, habitat and water quality (through

management of runoff, discharges and nutrient loading into the Bay) are at the ecosystem

level. It has become apparent that the current single-species management approach does

not completely incorporate these system goals (CBP 1987; Miller et al. 1996; CBP 2000;

NOAA 2004). In June 2000, the founding entities of the CBP signed the Chesapeake

2000 agreement (CBP 2000), reaffirming their commitment to the protection and

restoration of the bay. Through this agreement, the CBP formally committed to move

towards ecosystem-based fisheries management through the development of multispecies

management plans for targeted species by 2005 and the incorporation of multispecies

fisheries management and ecosystem approaches into existing fisheries management plans by 2007 (CBP 2000).

Regional management agencies in the Chesapeake region recognized that the implementation of these multispecies management plans was dependent on a deeper understanding of the fisheries ecosystem in the Chesapeake Bay (NOAA 2004). Accordingly, in support of the Chesapeake 2000 agreement, two large initiatives were undertaken. The first was the development of multispecies monitoring surveys to support ecosystem based fisheries management through the investigation of multispecies interactions in the bay. As a result, the Chesapeake Bay Fishery-Independent Multispecies Survey (CHESFIMS) was implemented in 2001 to provide a bay-wide, multispecies survey of the bentho-pelagic fish community. The second initiative was the development of the National Oceanographic and Atmospheric Administration (NOAA) Chesapeake Bay fisheries ecosystem plan, which provides a guide for revising existing single species plans to incorporate these ecological, social and economic considerations (NOAA 2004).

Ecosystem-based fishery management plans must address both economically and ecologically important species and their interactions. As a consequence, these management plans require that data are collected on species that are not traditionally the focus of research studies. A key challenge then is to incorporate the population dynamics and ecology of these relatively unstudied, but ecologically important species into ecosystem-based fishery management plans to establish a more holistic management approach. One approach has been to develop an Ecopath with Ecosim model (EwE) in support of multispecies management (NCBO 2003). The structure of the EwE model

requires the inclusion of diet and biomass data for all major species or aggregate species groups in the ecosystem, regardless of whether they are exploited (Latour et al. 2003). Accordingly, any species in the bay that represent a large biomass, or large trophic demand, has the potential to greatly influence the flow of energy through the ecosystem.

The hogchoker, *Trinectes maculatus* (Achiridae) is a small estuarine flatfish that represents an important component of the Chesapeake Bay ecosystem due to its ubiquitous distribution and substantial biomass (Chapter 1). Hogchoker is common throughout the bay from high salinity waters near the mouth to 40 miles upriver from the boundary of fresh and brackish water in many of the bay's tributaries (Massman 1954; Chapter 2). Prior surveys indicate that hogchoker can reach substantial levels of abundance. In a fishery-independent survey conducted in the Patuxent River, a sub-estuary of the Chesapeake Bay, hogchoker comprised over one-quarter of trawl catches by number on average and a maximum of almost 70 percent of the total catch (McErlean et al. 1969). Hogchoker was the most abundant species in beam trawl samples from shallow water and the second most abundant species in otter trawl samples from deep water in the same system (Mihursky 1968). Recent sampling in the Patuxent River indicates that hogchoker still contributes substantially to survey catches (T. J. Miller, pers. comm.). Hogchoker comprised over 50 percent of the total catch in a fishery independent survey conducted from 1967 through 1971 in the Chesapeake-York-Pamunkey estuary (Markle 1976). Similar levels of abundance in catches were reported by Smith et al. (1984) in the York River. The substantial biomass evident in these fishery-independent surveys is supported further by a study examining seasonal trends in energy flow in the mesohaline region of the Chesapeake Bay (Baird and Ulanowicz

1989). Baird and Ulanowicz's results indicated that hogchoker exhibited a standing stock comparable to or exceeding that of many exploited species, including Atlantic croaker (*Micropogonias undulatus*), bluefish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*) and striped bass (*Morone saxatilis*). Together, these studies demonstrate the widespread distribution and substantial abundance of hogchoker in the Chesapeake Bay. As a consequence of its distribution and abundance, the hogchoker must be incorporated into Chesapeake Bay ecosystem-based fisheries management even though it is neither fished nor a dominant prey species for piscivores.

The substantial hogchoker biomass evident in the Chesapeake Bay suggests that this species could have a substantial impact on energy flow in the system (Baird and Ulanowicz 1989). Previous studies have described the diet of the hogchoker in a variety of systems. The majority of these studies, however, have been descriptive in nature. Castagna (1955) described the annual pattern in the diet of southern hogchoker in the Gulf of Mexico and Wakulla River, Florida. Even though this study was conducted over a year and sampled habitats of varying salinities, spatial, temporal or ontogenetic patterns in hogchoker diet were not quantified. In the Hudson River, hogchoker diets were analyzed over the course of a year from both freshwater and saline habitats (Koski 1973). This study provided a description of hogchoker diet in its northern range in relation to composition of the benthos. Occurrence and number of prey items in hogchoker diets were summarized by month and habitat (freshwater or saline), however, the significance of temporal or spatial patterns was not investigated.

In the Chesapeake Bay, an early study described the composition of hogchoker diet as primarily annelids and to lesser extent small crustaceans (Hildebrand and

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Schroeder 1927). Hogchoker diet was examined in the mesohaline region of the

Chesapeake Bay as part of nuclear power plant siting studies (Homer and Boynton 1977).

In the Rhode River, a sub-estuary of the Chesapeake Bay, hogchoker diet was described

through an examination of guild structure and foraging impact of epibenthic fish and blue

crabs (Hines et al. 1990). In the York River, a southern sub-estuary of the Chesapeake

Bay, hogchoker diet was examined as part of a study of the influence of summer hypoxia

on the diet of demersal fish and crustaceans (Pihl et al. 1992). The diet of hogchoker was

also investigated in the York River through a survey of the nekton community (Smith et

al. 1984). All of these studies, however, were spatially limited to particular regions of the

bay and often limited temporally to a particular season.

One broad scale examination of hogchoker diet in the southern portion of the

Chesapeake Bay has been completed (Derrick and Kennedy 1997). This study sampled

habitats along an estuarine salinity gradient in four tributaries and the mainstem of the

bay. Dietary composition by weight and number was examined in relation to food

availability, enabling the investigation of feeding strategies. The study, however, was

only conducted from July through September, limiting the investigation of temporal

dietary patterns. Furthermore, hogchoker exhibit a seasonal migration pattern dependent

on ontogenetic stage (Dovel et al. 1969; Peterson 1996). During the spring, adults

migrate from overwintering grounds located near the interface of fresh and salt water to

more saline spawning habitats. Juveniles also overwinter in low salinity habitats and

move toward the spawning area in the spring, with their travel range increasing each year

until they reach the spawning area at approximately 4 years of age. Due to this migration

pattern, a size-salinity relationship persists during summer months with increasing

hogchoker size with increasing salinity. Consequently, it was unclear whether the observed pattern in diet along the salinity gradient was a function of changes in benthic composition or hogchoker age/size structure (Derrick and Kennedy 1997). Thus, a comprehensive examination of hogchoker diets in the Chesapeake Bay is still lacking.

Analysis of dietary patterns in fish presents many challenges. A review of the methods used in dietary studies recommended the use of multivariate statistical techniques to describe dietary patterns (Cortés 1997). Stomach contents data frequently violate the assumptions of parametric tests and consequently, semi- and nonparametric alternatives have been used to investigate dietary patterns (Adlerstein et al. 2002; West et al. 2003). Ordination techniques have often been used (Cortés 1997). However, many ordination techniques, including principal component analysis and factor analysis, assume each component of the diet are linearly related to calculated ordination axes, thereby restricting their application. Unlike these multivariate techniques, non-metric multidimensional scaling (nMDS) does not make any assumptions regarding linearity or the underlying distribution of the data (McGarigal et al. 2000). nMDS yields a graphical arrangement of samples that maintains the rank order of the similarity or dissimilarity between samples (Clarke 1993). This procedure is often used in ecological studies to describe patterns in community assemblages and investigate the environmental parameters most responsible for the documented patterns (Dower and Mackas 1996; Engle and Summers 1999; Roy et al. 2003). Examples of the use of nMDS in fisheries include the assessment of seasonal and spatial variability in age composition data (Smith 2003), characterization of temporal, spatial and interspecies patterns in fish diets (West et al. 2003), examination of spatial trends in fish composition of a coral reef marine park

between recreationally fished and sanctuary areas (Westera et al. 2003) and investigation of differences in life history traits among taxonomic groupings of elasmobranchs (Frisk et al. in press).

The objectives of this chapter are to describe the diet of the hogchoker across age classes, strata and seasons and to investigate dietary trends in hogchoker diet using nMDS. This chapter represents the first effort to investigate hogchoker diets throughout the mainstem of the Chesapeake Bay and across multiple seasons. Estimated dietary proportions will then be utilized to quantify the trophic demand of the hogchoker on the Chesapeake ecosystem.

METHODS

Sample Collection

Samples for dietary analysis were collected as part of CHESFIMS, a bay-wide fisheries survey of the bentho-pelagic fish community. CHESFIMS began in 2001 and served as an extension to the fisheries component of the Trophic Interactions in Estuarine Systems (TIES) program conducted from 1995 through 2000, which examined the factors that regulate secondary production (Jung and Houde 2003). CHESFIMS was comprised of two components; a broadscale survey that collected fish in habitats greater than 5 meters deep throughout the mainstem of the bay and a shoal survey that sampled shallow water habitats less than 5 meters deep in the Maryland portion of the bay. Three research cruises were conducted annually in April-May, July and September.

During the broadscale surveys, fish collections were made at night with a midwater trawl (MWT). Full details of the survey design are provided in Volstad et al.

(in press) and are only summarized here. Briefly, an 18-m^2 MWT with 3-mm mesh in the cod end was fished in a standardized 20-minute, stepped oblique tow at each station. The MWT fished the entire water column from surface to bottom in two-minute depth intervals. In 2001, each broadscale survey cruise sampled between 31 and 52 stations allocated to fixed transects spanning the mainstem of the bay. In 2002, the sampling design was modified and comprised of 31 fixed stations with 20 additional random stations. The random stations were selected using a stratified random design proportional to strata volume (upper, middle and lower bay). The 20 random stations were reselected for each cruise and no random station was repeatedly occupied. Deployment profiles were determined from a Minilog™ time-depth recorder placed on the float line of the trawl. Fish catches were enumerated, measured, and immediately frozen after the tow. All hogchokers collected during the broadscale survey from April 2001 through September 2003 were processed for stomach content analyses.

The shoal survey sampled shallow water habitats in the Maryland portion of the bay with an otter trawl during the day. Sampling was conducted using a stratified random design proportional to the areas of nine strata, chosen to represent the variety of shoal habitats. At each station, fish collections were made through six-minute tows with a 16' semi-balloon otter trawl. Fish catches were enumerated, measured, and immediately placed in ethanol after the tow. Hogchokers processed for dietary analysis from the shoal survey were collected in 2002 from Tangier and Pocomoke Sounds.

Analysis of dietary trends

In the laboratory, total length and wet weight were recorded for each fish. Stomachs, defined here as extending from the posterior of the esophagus to the pylorus, were removed and placed in ethanol. Prior to removal of the stomach contents, full stomachs were blotted dry and weighed to obtain a full stomach weight. Stomach contents were then removed and the stomach was subsequently re-weighed to obtain an empty stomach weight. The difference between these two weights represents an estimate of the total weight of prey in the stomach. Stomachs were scored for the presence/ absence of food. A feeding incidence of 1.0 indicated the presence of food in the stomach a feeding incidence of 0 indicated an empty stomach. Stomach contents were sorted and identified to the lowest practical taxonomic level under a dissecting microscope. Individual items comprising each prey group were blotted dry and weighed to obtain an estimate of the total weight of that prey type in the stomach.

The relationship between total stomach content weight and both hogchoker length and weight was investigated using linear regressions with appropriate transformations. When normality or homogeneity of variance assumptions were not met, data were log transformed. Feeding incidence data were highly non-normal and accordingly, contingency analysis was utilized to investigate differences in the incidence of feeding across seasons, years and strata. Exact probabilities for the chi-square goodness of fit statistic could not be ascertained because frequencies were non-integer values, consequently, asymptotic probabilities were utilized to assess significance.

Two indices of the importance of prey in hogchoker diets were calculated. Percent frequency of occurrence (%O), calculated as the percentage of stomachs in which

a particular prey item was present (Hyslop 1980), was calculated for each prey item. Percent composition by weight (%W) was also calculated for each prey item and represents the proportion of the weight of a prey item to the total weight of the stomach contents (Tirasin and Jørgensen 1999). Initial exploration of the seasonal, regional and ontogenetic trends in both the %O and %W of prey items that comprised hogchoker diets was conducted graphically. Seasonal trends were investigated over spring, summer and fall, and regional patterns were examined between the upper, middle and lower portions of the mainstem of the Chesapeake Bay, common delineations of the bay that represent a salinity gradient from oligohaline to polyhaline habitats. To investigate ontogenetic changes in diet, hogchokers were separated into three size classes, determined from visual analysis of size-frequency distributions.

nMDS, based on a matrix of Bray-Curtis similarity coefficients for every pair of stations, was utilized to quantify spatial, seasonal and ontogenetic patterns in diet. The five principal prey items (polychaetes, amphipods, isopods (*Cyathura*), cumaceans and bivalve siphons) identified from the analyses above were included in the nMDS. Fourth root transformations of the average %W of each prey item in hogchoker diet at each station were used in nMDS analyses to weight both common and rare species appropriately (Clarke and Gorley 2001b). A stress value was calculated for each two dimensional ordination to indicate how well the multidimensional relationships between samples were represented (Clarke and Gorley 2001b). Stress values less than 0.1 correspond to a good ordination with minimal chance of misleading interpretations and values less than 0.01 indicate a perfect representation (Clarke and Gorley 2001b).

Configuration plots were constructed to show the relationships between hogchoker diet and several factors, including season, stratum, hogchoker size and year. Samples of hogchoker with more similar diet compositions will be closer to each other on the configuration plot than more dissimilar pairs of samples. Bubble plots were created to portray the importance of individual prey species in relation to the overall hogchoker dietary pattern and indicate which prey species potentially contribute to the observed differences in hogchoker diet across particular factor levels.

Analysis of similarities (ANOSIM), a permutation test analogous to multivariate analysis of variance, was used to quantify patterns in hogchoker diet apparent in the configuration plots. . The ANOSIM test statistic, global R, relates the similarity of samples within a particular factor to the similarity between pairs of samples from different factors. The distribution of the R statistic was constructed through resampling methods (Clarke 1993). When the global R test statistic was significant at the five percent level, individual pairwise comparisons between factor levels were made using the Bonferroni method to control the experiment-wise error rate at 0.05.

A second nMDS ordination was performed to investigate differences in the diets of hogchokers collected in the broadscale compared to the shoal survey. This analysis used data from only those regions in which both the shoal and broadscale cruises were conducted at similar times. Accordingly, only dietary data for hogchokers collected in Tangier and Pocomoke Sounds in 2002 were analyzed. This analysis compares the influence of both survey gear and collection time on diet contents. All similarity, nMDS and ANOSIM analyses were performed using Primer, Version 5 (Clarke and Gorley 2001a).

Trophic Demand

The trophic demand of hogchoker was estimated using data from the CHESFIMS survey. Prey-specific estimates of relative hogchoker trophic demand at each station (P_{ij}) were quantified as

$$P_{ij} = N_j * I_j * C_j * W_{ij}$$

where N_j is the hogchoker CPUE (grams per minute bottom time) at station j, I_j is the average feeding incidence at station j, C_j is the ration at station j predicted from hogchoker weight, and W_{ij} is the proportion of category i in the diet at station j.

To compute relative abundance (CPUE), the effective effort of each tow was adjusted for the time the MWT was within five meters of the bottom, a zone in which demersal hogchoker would have been vulnerable to the gear. Five meters was chosen based on the estimated height of the net when it was fully open. For each station, the time that the net was within five meters of bottom, subsequently referred to as bottom time, was determined from the Minilog. The station depth utilized to calculate bottom time was assumed to be the deeper of the station depth recorded during the beginning of the MWT tow and the deepest depth measurement from the minilog file. All stations where bottom time equaled zero were eliminated from relative abundance calculations.

Hogchoker CPUE was converted to catch/m^2 swept by the MWT. Previous work estimated the average volume swept by a 20-minute MWT tow as 4961 cubic meters (Jung and Houde 2004). The conversion from volume to area swept by the MWT was conducted using the average height of the MWT during a tow, 1.895 meters, determined from two logging devices attached to the head rope and foot rope of the net that were deployed in 2003 tows.

Direct estimates of daily ration were unavailable. Accordingly, I estimated daily ration based on allometric relationships for hogchoker and a meta-analysis of ration estimates from other flatfish. The relationship between stomach content weight and hogchoker weight was considered to be an estimate of weight-specific ration size (gram of prey weight per gram of hogchoker). Average ration size by station was calculated from the relationship between hogchoker weight and stomach content weight using station-specific estimates of average hogchoker weight. Consumption at each station was mapped using ArcGIS and interpolated through an inverse distance weighting procedure to obtain a measure of trophic demand of hogchoker throughout the Bay.

Station-specific relative trophic demand estimates were aggregated to the stratum level using estimates of stratum area obtained from Jung (2002). Estimates of trophic demand must be converted from relative to absolute values if they are to be compared to observed standing stocks of prey. However, the catchability of hogchoker in the survey gear is unknown. We used three values for q (0.2, 0.5 and 1) to develop a range of absolute trawlable biomass estimates. Calculations in which q=1 represent a minimum trawlable biomass estimate. Estimates of absolute trophic demand were then compared to stratum-specific estimates of macrobenthic standing stock (Hagy 2002). Estimates of hogchoker consumption were quantified as grams of prey wet weight, however, stratum-specific estimates of macrobenthic biomass were measured as grams of ash free dry weight. Consequently, a conversion factor of 20 grams wet weight to 1 gram ash free dry weight was utilized to facilitate comparisons between hogchoker trophic demand and macrobenthic standing stock (Lin and Shao 2002).

RESULTS

313 hogchoker stomachs were examined in dietary analyses (Table 1). Of this total, 281 were from the broadscale survey, providing estimates of diets in all three cruise seasons throughout the mainstem of the Chesapeake Bay. A further 32 stomachs were examined from the shoal survey. These stomachs provide estimates of diets of fish in shallow (<5 meter depth) habitats not sampled in the broadscale survey.

The distribution of hogchoker collected during the broadscale survey and used in dietary analyses was a function of station catch. With the exception of the spring 2001 cruise, all collected hogchoker were utilized in dietary analyses. During the spring 2001 cruise, only a subsample of collected hogchoker was brought back to the lab. Sample distributions varied over year, season and strata (Table 1). Almost twice as many hogchoker stomachs were analyzed in 2001 than in the remaining two years. Sample distribution across seasons was approximately even. Over twice as many stomachs were analyzed from the upper bay than the middle or lower bays. All analyzed hogchokers from the shoal survey were collected during 2002 from Tangier and Pocomoke Sounds, therefore, the distribution of hogchokers samples from the shoal survey could only be investigated across seasons. Across all seasons, the greatest number of samples was analyzed from the summer in comparison to spring and fall.

Inspection of the spatial distribution of feeding incidence showed a high degree of variability among cruises (Figure 1). Approximately one-third of all stomachs examined were empty. Estimates of feeding incidence per strata, season and year varied from a high of 100% empty (n=1 stomach) in the upper bay in fall 2003 to 0% empty in the middle bay spring 2001 (n=2), upper bay summer 2001 (n=13) and upper bay spring

2003 samples (n=11). Even when analysis is limited to estimates based on 5 or more stomachs, feeding incidence estimates still ranged form 0 – 81.3%. Accordingly, feeding incidence varied across years, seasons and strata (Table 2). A two-factor contingency analysis between season and strata, controlling for year, indicated significant differences in the proportion of hogchokers with empty stomachs across season, strata combinations for each year using the chi-square goodness of fit statistic (2001: $X^2_{(4)}$ = 321.12, p<0.001; 2002: $X^2_{(4)}$ = 297.74, p<0.001; 2003: $X^2_{(4)}$ = 677.97, p<0.001).

Based on data from nonempty stomachs only, there was a significant relationship between log transformed stomach content weight and log fish length (adjusted r^2 = 0.4028, p<0.001). Removal of one apparent outlier from this data set whose estimated stomach contents were within the measurement limit strengthened the relationship (adjusted r^2 = 0.454, p < 0.001, Figure 2). The outlier was not included in subsequent analyses with stomach content weight. Significant linear relationships were apparent between hogchoker weight and both stomach content weight and weight specific ration (Figures 3 and 4).

Identification of hogchoker stomach contents was difficult because of the highly digested nature of much of the stomach content. Indeed, unidentifiable organic remains were the second most frequently encountered prey item (50.5%). Quantitative comparisons were made at the level of Class or Order. Polychaetes were the most frequently encountered prey type in hogchoker stomachs across all seasons and years, with an average of 52.0% of all examined hogchoker nonempty stomachs containing at least one polychaete (Figure 5). It is likely that a substantial proportion of the unidentified prey contents comprised severely digested polychaetes. The frequency of

occurrence of other prey items, including amphipods, isopods and bivalve siphons,

revealed strong seasonal trends (Figure 5). In spring and summer surveys, amphipods

were the third most abundant prey category, occurring in 16.0 % and 15.4%, respectively,

of the stomachs examined. In fall surveys, isopods and bivalve siphons were common.

In the fall surveys, isopods occurred in 21.4% and bivalve siphons in 17.5% of stomachs,

with an overall occurrence across all seasons of 8.5% and 6.8%, respectively.

Hogchoker diet was also examined in terms of percentage composition by weight

of each prey item. These data likely reflect the importance of the prey item to the overall

energetics of hogchoker. Across all seasons, polychaetes represented the greatest

contribution to hogchoker diet (Figure 5). Percentage by weight measures, however, can

be highly influenced by the occurrence of a small number of large prey and are therefore

considered to overestimate the contribution of these rare but heavy prey items. In July,

for example, sand shrimp was an important prey item in terms of percentage by weight,

however, this weight represented only one sand shrimp found in hogchoker stomachs.

Hogchoker diets also exhibited clear regional trends, both in terms of percent

frequency of occurrence and percentage by weight (Figure 6). In the upper bay, several

prey items, including amphipods, *Cyathura* and bivalve siphons were substantial

constituents of hogchoker diets. The importance of these prey items declined in those

individuals collected from the middle bay. In the lower bay, polychaetes represented the

only dominant prey item.

Inspection of size-frequency distributions of hogchoker indicated the presence of

three size classes in the overall length distribution: less than 70mm, 70-119mm and

greater than or equal to 120mm (Figure 7). These size classes were subsequently used to

summarize ontogenetic trends in hogchoker diets. Inspection of diet by size class

potentially indicated ontogenetic shifts in the diet of hogchokers (Figure 8). Polychaetes

and amphipods were the most important prey items for hogchokers smaller than 70mm in

terms of both percent frequency of occurrence and percentage by weight. As hogchoker

size increased, the importance of amphipods generally decreased while that of

polychaetes, *Cyathura* and bivalve siphons increased.

nMDS analysis identified clear patterns in hogchoker diets. Fifty random MDS

restarts used in the ordination of the broadscale survey resulted in an overall stress value

of 0.05, indicating a good ordination. The configuration plot revealed a clear separation

between hogchoker diet composition in spring and fall (Figure 9a). Summer diet

composition overlapped with both spring and fall compositions. However, results of the

ANOSIM analysis for season, with 10,000 random permutations of dietary classes, did

not detect significant differences in hogchoker diet across seasons (Global R = 0.057, p =

0.134). Accordingly, these ANOSIM results indicated that the overall difference in diet

composition between seasons observed on the configuration plot was not significant.

nMDS ordination exhibited clear differences in the contribution of different prey

(Figure 10). Large amphipod values were associated with left side of the ordination,

corresponding to samples collected during the spring cruises (Figure 10a). In contrast,

high composition of *Cyathura* was strongly associated with fall survey samples,

concentrated on the upper right of the ordination (Figure 10b). Bivalve siphons appeared

to be related to samples collected during the summer and primarily during the fall cruises

(Figure 10c). Polychaetes did not exhibit as clear a seasonal trend as the other prey

items, however, they were more strongly associated with summer and fall than spring

(Figure 10d). Accordingly, the strong association of amphipods, *Cyathura*, and to a lesser extent bivalve siphons, with particular seasons potentially indicate that these prey are likely the taxa that primarily contribute to the difference in spring and fall hogchoker diet composition observed through the configuration plot.

nMDS indicated a size-dependent gradient in diet composition (Figure 9b). The diet composition of the smallest size class of hogchokers was clearly separated in 2-dimensional space from that of the largest hogchoker size class. The samples corresponding to the middle size class did not exhibit a clear pattern, potentially representing an intermediate dietary composition between the smallest and largest size classes. Results of the ANOSIM with 10,000 permutations of dietary classes did not indicate significant differences in hogchoker diet across all size classes (Global R = -0.036, p = 0.565), likely a consequence of the intermediate composition of the middle size class. Furthermore, the observed ontogenetic patterns were not clearly associated with any of the four dominant prey items. NMDS did not reveal spatial (Figure 9c) or annual patterns (Figure 9d) in hogchoker diet.

Analyses of dietary patterns of hogchokers collected during the shoal survey were restricted due to limited sampling resolution and catch distribution (Table 1). Across all seasons, approximately 57% of examined stomachs from hogchokers collected during the shoal survey were empty (Table 2). Contingency analysis indicated a significant difference in the proportion of hogchokers with empty stomachs across seasons ($X^2_{(2)} = 222.0$, p < 0.001).

Graphical analysis of hogchoker stomachs collected from shallow habitats during the shoal survey showed similar seasonal trends to the data from the broadscale survey

(Figure 13). In contrast to the broadscale survey, however, cumaceans were an important component of hogchoker diets. Cumaceans were most important in the spring and their prominence decreased as the year progressed. No cumaceans were found in the stomachs of hogchokers collected in September. Amphipods were an important constituent of hogchoker diets in the spring, however unlike the broadscale survey, their importance increased in July, both in terms of percent weight and occurrence. In September, amphipods were not present in any stomachs collected from the shoal survey. The importance of bivalve siphons increased from May through September.

Length frequency distributions of the overall shoal survey hogchoker catch from all years and regions indicated the presence of three length classes (Figure 12), approximately equal to those of the broadscale survey (Figure 7). A lack of small (<70 mm) hogchoker from Tangier and Pocomoke Sounds in 2002 prevented analysis of trends in diet over all size classes. Across the remaining two size classes, however, ontogenetic trends in the diet of hogchokers collected during the shoal survey were similar to those trends observed in the broadscale survey (Figure 13). As hogchoker size increased, the importance of amphipods decreased while that of polychaetes and bivalve siphons increased. Since all examined hogchokers from the shoal survey were collected from the middle bay in Tangier and Pocomoke Sounds, spatial trends in the diet of hogchokers collected from shallow habitats could not be explored.

Hogchoker diet was compared between the shoal and mainstem surveys to investigate the influence of location/gear and time of day. Contingency analyses indicated a significant difference in feeding incidence between fish from the shoal and broadscale surveys ($X^2_{(1)} = 340.2$, $p < 0.001$). Fifty random nMDS restarts used in the

ordination to compare the two surveys resulted in an overall stress value of zero, indicating a perfect representation. Neither the two-dimensional configuration plot (Figure 14) nor the ANOSIM results (Global R = -.206, p = 0.95) revealed a distinct separation of average dietary composition at each station by survey, indicating that hogchoker diet composition did not significantly differ between surveys.

The consumption of hogchoker was estimated from station-specific estimates of hogchoker relative abundance, feeding incidence and ration. Hogchoker relative abundance varied between $0 - 0.955$ g.m^{-2} across stations. Considering only those stations where hogchoker were collected, wet weight total consumption estimates across all years varied between both seasons and strata in the bay (Figure 15). In the spring, greatest hogchoker consumption occurred at the head of the bay (Figure 15a). Across the remainder of the bay, consumption was patchy and concentrated primarily near Tangier/Pocomoke Sounds. Areas of high consumption generally corresponded with regions of high abundance, indicated by the size of the station symbols on the map. In the summer, the greatest hogchoker consumption occurred in Tangier/Pocomoke Sounds and adjacent waters, with minimal consumption in the remaining portions of the bay (Figure 15b). Areas of greatest consumption overlapped with those of highest abundance levels, however, localized areas with substantial abundance levels but low consumption were observed. Consumption patterns in the fall were similar to those of the spring with greatest consumption at the head of the bay (Figure 15c). In the fall, however, consumption in the remaining portions of the bay was minimal. With the exception of one station at near the mouth of the bay, high levels of consumption coincided with high hogchoker abundance.

Estimates of total consumption were multiplied by station-specific dietary proportions to obtain consumption estimates of individual prey categories. In the fall, patterns in the consumption of individual prey categories followed that of total consumption. In the spring and summer, however, consumption patterns varied across prey categories (Figures 16 and 17). In the summer, bivalve and polychaete consumption was greatest in Tangier/Pocomoke Sounds similar to total consumption and abundance (Figure 16a and 16c). In contrast, the greatest consumption of crustaceans was found at the head of the bay, with intermediate consumption at the mouth of the Rappahannock extending to the southern portion of Pocomoke Sound (Figure 16b). In the spring, crustacean consumption was concentrated at the head of the bay (Figure 17b), bivalve siphons were not found in any hogchoker stomachs (Figure 17a) and polychaete consumption was greatest at the head of the bay but also substantial in Tangier/Pocomoke Sounds (Figure 17c).

To facilitate comparisons with the standing stocks of prey, relative consumption was converted to absolute consumption using a range of values of catchabilities (q), reflecting the uncertainty in this parameter. Assuming q=1, a minimum estimate of hogchoker wet weight consumption by year ranged from 0.029 – 0.057 metric tons of polychaetes, 0.002 – 0.013 metric tons of crustaceans and 0 – 0.011 metric tons of bivalves (Table 4). With a catchability of q=0.2, these consumption estimates increased to 0.14 – 0.28 metric tons of polychaetes, 0.008 – 0.064 metric tons of crustaceans and 0 – 0.054 metric tons of bivalves. Using the minimum estimate of hogchoker abundance, total consumption across all prey types varied from 0 – 0.00097 g/m^2 across stations and when scaled to the entire mainstem, 0.043 – 0.093 metric tons over the three years.

Using a catchability of q=0.2, bay-wide consumption varied from 0.22 – 0.46 metric tons (Table 3).

Comparison of summer wet weight consumption estimates (assuming the minimum hogchoker abundance) to those of macrobenthic standing stock indicated that hogchoker consumed between $0 - 3.9*10^{-4}$ % of the standing stock of particular taxa in different year/strata combinations. With a catchability of q=0.2, hogchoker consumed between $0 - 1.9*10^{-3}$ % of the standing stock of particular taxa.

DISCUSSION

Mandates for multispecies management in the Chesapeake Bay (CBP 2000) and the subsequent development of the Chesapeake Bay EwE ecosystem model (NCBO 2003) require the investigation of the ecology and population dynamics of ecologically important species. This study represented an effort to quantify the diet and feeding patterns of hogchoker, an abundant but unexploited species in the Chesapeake Bay. In support of multispecies management efforts and the need for enhanced knowledge of species interactions, the individual dietary components of the study were combined to ultimately quantify the trophic demand of the hogchoker in the Chesapeake Bay ecosystem.

Station-specific estimates of average feeding incidence (I_j), ration (C_i) and prey-specific diet proportion (W_{ij}) were used to calculate bay-wide estimates of hogchoker trophic demand from hogchoker CPUE. Hogchoker likely consumed between $0 - 1.9*10^{-3}$ % of the standing stock of particular macrobenthic taxa based on a survey catchability of q = 0.2. Even bearing in mind uncertainties associated with these

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calculations, these values indicate that hogchoker do not have a substantial impact on the macrobenthic community. Caging experiments in the York River demonstrated that hogchokers, unlike blue crab (*Callinectes sapidus*) and spot (*Leiostomus xanthurus*), did not significantly reduce benthic infaunal densities, indicating that hogchoker did not exhibit controlling influence on infauna (Virnstein 1977). However, in this and an additional caging study in a South Carolina estuary (Sharrer 1993), caged hogchokers exhibited a negative change in body weight. Accordingly, it is possible that the lack of controlling influence on benthic infauna in these studies was in part a function of the cage and not hogchoker consumption. Regardless of the cage influence, however, these studies, together with the results presented here, indicate that hogchoker likely do not consume a substantial portion of macrobenthic standing stock.

Conclusions regarding hogchoker trophic demand depend on assumptions regarding survey catchability. However, inferences regarding patterns of relative trophic demand among species can be drawn directly from relative CPUEs. This approach does not require an explicit assumption regarding catchability, only that catchability is the same for all species. In summer CHESFIMS cruises, average hogchoker catch in each cruise was only 23.7% of spot catch, 2.5% of croaker (*Micropogonias undulatus)* catch and 5.1% of white perch (*Morone americana*) catch (Curti, unpublished data). The small CPUE of hogchoker compared to other demersal fish species of similar dietary habits (Smith et al. 1984; Baird and Ulanowicz 1989) supports the small trophic demand of hogchoker on Chesapeake Bay macrobenthic biomass.

Estimates of trophic demand are also sensitive to estimates of ration (C_i) used in calculations. I assumed that stomach content weight was a proxy for daily ration.

Hogchoker collected in the mainstem of the bay exhibited significant relationships between stomach content weight and both hogchoker total length and weight. The observed positive relationship between prey weight and fish size is supported by previous work indicating a positive relationship between fish weight and daily ration (Elliott 1975). Stomach content weight, represented as percent hogchoker body weight, indicated an estimated ration between 0.006 and 2.02% body weight per day with an average of 0.30% body weight per day. These proportions were consistent with those reported by Derrick (1994) for hogchoker collected in the upper Chesapeake Bay. A significant negative linear relationship was also apparent between ration, represented as a percent hogchoker body weight, and hogchoker weight. This relationship is supported by multiple studies that indicate a decrease in consumption, measured as percent body weight, with increasing age (Lagardère 1987; Paul et al. 1992).

The use of stomach content weight as a surrogate for ration size required the assumptions that all examined hogchokers were in the same digestive state and the contents of all hogchoker stomachs represented total daily consumption. Previous studies of various demersal fish species, including winter flounder and common, rock, flathead and yellowfin sole, in a variety of systems resulting in varying temperature regimes, including the Bering Sea, French Atlantic coast, Woods Hole Harbor and under laboratory conditions, have indicated a daily ration between 0.35 and 7.3% body weight (Huebner and Langton 1982; Worobec 1984; Lagardère 1987; Oñate 1991; Smith et al. 1991; Paul et al. 1992).

Gastric evacuation rates, however, increase with temperature (Wootton 1990) and it is therefore important to consider temperature when comparing daily ration estimates

across studies. Previous work on the common sole of the French Atlantic coast indicated a daily ration of 7.3% body weight under an average water temperature of 19.8º Celsius (Lagardère 1987). Furthermore, a study of winter flounder in a Rhode Island pond yielded rations between 2.84 and 3.31% dry body weight when temperature was approximately 22.0º Celsius (Worobec 1984). Water temperatures in the Chesapeake Bay can reach as high as 28º - 30º Celsius during summer months (Murdy et al. 1997), therefore, studies from the French Atlantic coast and Rhode Island represent better studies for comparison than those conducted in the Bering Sea and Woods Hole Harbor where water temperatures ranged between 1.0º and 9.3º Celsius. These estimates of daily ration from mid-latitude studies suggest that hogchoker daily ration may have been underestimated in this study.

Accordingly, it is likely that the obtained estimate of ration from stomach content weight does not represent daily ration but instead represents one of several daily meals. Hogchoker exhibit a marked diel feeding pattern with peaked gut fullness at night, decreased fullness during morning hours, lowest fullness levels during the afternoon and increased fullness during the evening (Derrick 1994). Furthermore, a nocturnal activity pattern has been suggested through previous work on hogchoker tidal rhythm (O'Connor 1972) and by distinct differences in day versus night hogchoker collections in the mesohaline region of the bay (Homer and Boynton 1977). Even with consideration of a nocturnal activity pattern and a night sampling protocol, however, it is likely that the analyzed samples do not capture daily ration. Consequently, an investigation of hogchoker gastric evacuation rates is needed to obtain a more accurate estimate of hogchoker daily ration that will improve current estimates of trophic demand.

Estimated ration size may be further underestimated by the consideration of only stomach instead of both stomach and intestinal content weight in the calculation of ration. Soleidae generally exhibit a long intestinal tract with a comparatively small esophagus and stomach (De Groot 1971). The buccal cavity, pharyngeal cavity, esophagus and stomach together comprise approximately 20% of the alimentary tract in Soleidae (De Groot 1971). Accordingly, Oñate (1991) recommended that daily ration should not be determined from examination of only stomach contents due to the small amount of food likely to be in the stomach at the time of capture. Even though hogchoker are a member of the Achiridae family (Murdy et al. 1997), they once were classified as Soleidae and were included under Soleidae in the review of flatfish alimentary tract morphology (De Groot 1971). Therefore, the use of only stomach content weight in this study likely underestimated hogchoker ration.

It is probable that the assumptions regarding the relationship between measured stomach content weight and daily ration are not completely valid, however, stomach content weight still serves as a crude estimate of ration size. The assumptions generally result in an underestimation of daily ration, resulting in a conservative estimate of hogchoker trophic demand. If daily ration was assumed to be 7.5% of body weight, consistent with the previous common sole and winter flounder studies of Lagardère (1987) and Worobec (1984), and catchability was assumed to be 0.2, hogchoker would consume between $0 - 1.5*10^{-3}$ % of the standing stock of bivalves, $0 - 0.014$ % of the standing stock of crustaceans and $0 - 0.10$ % of the standing stock of polychaetes in different year/strata combinations. These values are an order of magnitude greater than those calculated using measured stomach content weight as an estimate of daily ration,

suggesting that the use of stomach content weight contributes significantly to the underestimation of hogchoker trophic demand.

The presence of unidentified organic remains in hogchoker diet may also contribute to the underestimation of hogchoker trophic demand. Unidentified organic remains, likely comprised of severely digested polychaetes, was the second most frequently encountered prey item in hogchoker diet. These remains could not be positively identified as polychaetes, therefore, this component of hogchoker diet was not incorporated into trophic demand estimates, resulting in further underestimation of hogchoker trophic demand of polychaetes. Variability in the percent contribution by weight of each prey item to hogchoker diet, however, does not significantly contribute to the variability in estimates of trophic demand. Assuming that the contribution of polychaetes to hogchoker diet is underestimated by between 25 and 50%, which is unrealistic because the contribution of all other prey taxa would be zero, would not even double the proportion of polychaete standing stock consumed.

An additional source of variation to the calculation of trophic demand is the estimation of macrobenthic standing stock. However, the extent of the variability associated with macrobenthic standing stock estimates is unclear. If it was assumed that the standing stocks of each prey taxa varied by a factor of two, resulting trophic demand estimates would also vary by approximately a factor of two. This variability could result in either an underestimation or overestimation of hogchoker trophic demand.

However, regardless of the absolute magnitude of hogchoker trophic demand, it is important to note that hogchoker, and thus their trophic demand, was not uniformly distributed throughout the Chesapeake Bay or across the years studied. In both the

broadscale and shoal surveys, hogchoker exhibited a moderate feeding incidence. Between 33% (broadscale) and 57% (shoal) of examined stomachs did not contain food material. These estimates of feeding incidence are consistent with those of previous studies describing hogchoker diet (Koski 1973; Homer and Boynton 1977; Derrick 1994). Results from contingency analysis indicated a significant difference in feeding incidence between the broadscale and shoal surveys. Although habitat differences were confounded with differences in sampling protocol (night verses day sampling), it is likely that the observed difference in feeding incidence was primarily a function of the day (shoal) versus night (broadscale) fish collections. Previous studies suggesting a nocturnal activity pattern for hogchoker (O'Connor 1972; Homer and Boynton 1977; Derrick 1994) support the increased level of feeding observed in the broadscale survey.

Within the broadscale survey, contingency analysis indicated significant differences in feeding incidence between particular combinations of season and stratum. It is unclear, however, whether these differences are a consequence of true differences in feeding incidence or an absence of hogchoker catch in particular combinations. Within the shoal survey, feeding incidence differed significantly across seasons. This difference could be a function of prey availability. Benthic biomass and production in temperate estuarine systems often exhibit marked seasonal variation (Day et al. 1989). Accordingly, seasonal changes in benthic biomass could potentially result in differences in feeding incidence.

Furthermore, maps of relative trophic demand, which integrated differences in feeding incidence, ration and abundance, also indicated that hogchoker trophic demand exhibited both seasonal and spatial variation. The concentration of greatest hogchoker

total consumption at the head of the bay in the spring and fall and near

Tangier/Pocomoke Sounds in the summer is likely a consequence of hogchoker seasonal

movements from oligohaline overwintering grounds to saline spawning grounds. This

correlation is supported by the overlap of the highest levels of total consumption with that

of greatest hogchoker relative abundance. The patchy distribution of hogchoker in the

spring in the remaining portion of the bay, and in particular Tangier/Pocomoke Sounds,

may be due to the timing of the spring cruises. The spring CHESIMS cruises were all

conducted in the end of April/beginning of May and hogchoker's spawning season is

typically from May-September (Dovel et al. 1969). Accordingly, it is likely that the

spring cruises were conducted after hogchoker began their seasonal migration to saline

spawning grounds.

In the fall, the relative trophic demand of polychaetes, bivalves and crustaceans

each exhibited approximately the same spatial pattern as total consumption. In the

spring, however, crustacean consumption, total consumption and hogchoker relative

abundance were concentrated at the head of the bay, whereas substantial consumption of

polychaetes occurred both at the head of the bay and in Tangier/Pocomoke Sounds. The

polychaete consumption in Tangier and Pocomoke Sounds is potentially due to high

polychaete abundance in mesohaline and polyhaline waters (Derrick and Kennedy 1997).

In the summer, total, polychaete and bivalve consumption, in addition to hogchoker

relative abundance, were concentrated in Tangier/Pocomoke Sounds, but crustacean

consumption was greatest at the head of the bay. This peak in crustacean consumption at

the head of the bay is consistent with greatest arthropod abundance in oligohaline waters

(Derrick and Kennedy 1997). The large crustacean consumption could also be a

consequence of the substantial amphipod consumption by small (<70mm) hogchokers, which are typically immature (Mansueti and Pauly 1956; Koski 1973) and therefore remain in oligohaline habitats throughout the year.

Although differences in feeding incidence and trophic demand were apparent, the nMDS ordination did not indicate significant variation in the prey composition of hogchoker diet between surveys. In both surveys, hogchoker diet was primarily comprised of polychaetes. Polychaetes were the most dominant prey item in terms of both %W and %O. These two dietary measures indicate different aspects of predator diet (Cailliet 1977). Percent occurrence (%O) gives an indication of prey species variability and population-wide food habits (Cailliet 1977; Macdonald and Green 1983; Tirasin and Jørgensen 1999). Percent contribution by weight (%W) reflects the nutritional value of a prey species (Cailliet 1977; Macdonald and Green 1983) and therefore is a better measure of prey importance in terms of the contribution to hogchoker energetics. Accordingly, the %O and %W estimates for polychaetes indicate their high nutritional value and common consumption by hogchokers (Macdonald and Green 1983; Tirasin and Jørgensen 1999). Previous descriptions of hogchoker diet have also demonstrated that annelids are generally dominant dietary constituents (Hildebrand and Schroeder 1927; Carr and Adams 1973; Smith et al. 1984; Pihl et al. 1992; Derrick 1994).

In particular seasons and strata, bivalve siphons and crustaceans, in particular amphipods, isopods and cumaceans, were also important constituents of hogchoker diet. The importance of crustaceans and bivalve siphons in hogchoker diet are consistent with previous studies (Castagna 1955; Koski 1973; Homer and Boynton 1977; Smith et al. 1984; Hines et al. 1990; Derrick and Kennedy 1997; Schwartz 1997). The nMDS

ordination of the broadscale survey indicated that amphipods were predominant in the upper bay in the spring and to a lesser extent in the summer. In contrast, *Cyathura* were important in the fall in the upper bay and bivalve siphons were important in the fall in the upper bay and to a lesser extent in the summer and in the middle bay. These dietary trends are likely due to differences in prey selection, prey availability and hogchoker seasonal movements. nMDS configuration plots supported the strong seasonal trends observed through graphical analysis of %O and %W, but they did not indicate clear regional patterns. The seasonal configuration plot indicated a clear separation of spring and fall samples. Results of the ANOSIM procedure, however, did not depict significant seasonal or regional differences in hogchoker diet. The insignificance of an overall seasonal effect was likely due to the variability in the diet of those hogchokers collected during the summer.

In oligohaline and freshwater habitats of Virginia waters, oligochaetes are the most dominant annelid, whereas polychaetes are the most abundant annelid in polyhaline waters (Derrick and Kennedy 1997). In addition, amphipod abundance and biomass decreases with increasing salinity (Derrick and Kennedy 1997). It is likely that these trends in benthic composition observed in Virginia waters are also apparent in the mainstem of the Chesapeake Bay. Furthermore, hogchoker exhibit a negative selection for oligochaetes in freshwater, oligohaline and mesohaline regions and a positive selection for polychaetes in polyhaline regions (Derrick and Kennedy 1997). Selection for amphipods, isopods and siphons is more variable across regions (Derrick and Kennedy 1997). Accordingly, the spatial trends observed in this study are potentially a function of variability in benthic composition.

Graphical analysis of changes in prey composition with hogchoker size indicated a potential ontogenetic shift in hogchoker diet. ANOSIM results did not indicate a significant relationship between size and prey composition in the broadscale survey, however, the corresponding ordination plot exhibited a distinct separation in diet composition between the smallest and largest size class. Similar to the ANOSIM results for season, the absence of a significant overall effect of size could be a function of the variability in the diet of the intermediate size class. Samples from the smallest and largest size classes were not clearly associated with any of the four dominant prey items, therefore, it was difficult to determine the nature of the shift in prey composition.

Overall, results indicated a general trend of declining amphipod importance with a concurrent increase in polychaete and bivalve siphon predominance as hogchoker size increased. Similar trends in prey composition with regard to amphipods, polychaetes and bivalves were observed in the York River (Smith et al. 1984). In contrast, an ontogenetic shift in hogchoker diet was not evident in stomachs collected from the mesohaline portion of the bay (Homer and Boynton 1977). However, examined fish ranged from 70 to 124mm in standard length (Homer and Boynton 1977), corresponding only to the two largest size classes of current efforts. In samples collected during the broadscale survey, the most distinct shift in prey composition appeared to occur between hogchokers less than 70mm and those between 70 and 119mm. This shift would not have been detected in Homer and Boynton (1977) due to limited sample resolution.

The observed ontogenetic, spatial and seasonal trends in hogchoker diet were incorporated into the calculation of trophic demand. Estimates of trophic demand, however, indicated that hogchoker did not substantially influence the macrobenthic

community of the Chesapeake Bay. A consideration of likely errors in these calculations suggested the potential of up to an order of magnitude error. Even in this worse case, trophic demand was still less than 1% of the standing stock of hogchoker benthic prey. This lack of a controlling influence potentially indicates that the incorporation of hogchoker into multispecies management in the Chesapeake Bay is not critical. Regardless of hogchoker trophic demand, bay-wide hogchoker dietary proportions can still be incorporated into Chesapeake Bay ecosystem models to more accurately model energy flow. In support of multispecies management, similar studies should be conducted for other unexploited, but abundant species in the Chesapeake Bay, such as spotted hake and striped anchovy.

Table 1. Distribution of examined hogchokers utilized in dietary analyses from the CHESFIMS broadscale and shoal surveys.

Survey	Year	Season	Strata	Samples
Broadscale	2001	Spring	Lower	8
			Middle	2
			Upper	49
		Summer	Lower	9
			Middle	7
			Upper	13
		Fall	Lower	0
			Middle	0
			Upper	57
	2002	Spring	Lower	9
			Middle	3
			Upper	10
		Summer	Lower	7
			Middle	5
			Upper	2
		Fall	Lower	9
			Middle	0
			Upper	31
	2003	Spring	Lower	8
			Middle	0
			Upper	11
		Summer	Lower	7
			Middle	28
			Upper	0
		Fall	Lower	5
			Middle	0
			Upper	1
	2001			145
	2002			76
	2003			60
		Spring		100
		Summer		78
		Fall		103
			Lower	62
			Middle	45
			Upper	174
Broadscale Total				281
Shoal	2002	Spring	Middle	8
		Summer		14
		Fall		10
Shoal Total				32
TOTAL				313

Table 2. Distribution of the proportion of examined hogchokers from the broadscale and shoal surveys with empty stomachs.

Survey	Year	Season	Strata	Percent Empty
Broadscale	2001	Spring	Lower	28.6
			Middle	0.0
			Upper	18.6
		Summer	Lower	81.3
			Middle	10.0
			Upper	0.0
		Fall	Lower	n/a
			Middle	n/a
			Upper	32.3
	2002	Spring	Lower	33.3
			Middle	0.0
			Upper	5.6
		Summer	Lower	6.7
			Middle	12.5
			Upper	50.0
		Fall	Lower	50.0
			Middle	n/a
			Upper	32.5
	2003	Spring	Lower	70.8
			Middle	n/a
			Upper	0.0
		Summer	Lower	73.3
			Middle	31.8
			Upper	n/a
		Fall	Lower	40.0
			Middle	n/a
			Upper	100.0
	2001			27.1
	2002			26.6
	2003			48.2
		Spring		24.9
		Summer		34.7
		Fall		43.3
			Lower	46.9
			Middle	13.3
			Upper	25.4
	Broadscale Total			32.7
Shoal	2002	Spring	Middle	55.6
		Summer		59.4
		Fall		54.8
	Shoal Total			57.4

Table 3. Hogchoker relative abundance and total consumption in each year and strata. Strata average catch represents the average catch of hogchoker (grams) per square meter swept by the MWT. Strata abundance represents total hogchoker abundance (metric tons) in each stratum. Strata consumption represents total hogchoker consumption (metric tons) in each stratum. Strata abundance and consumption were calculated for three catchability estimates: q=1, 0.5 and 0.2.
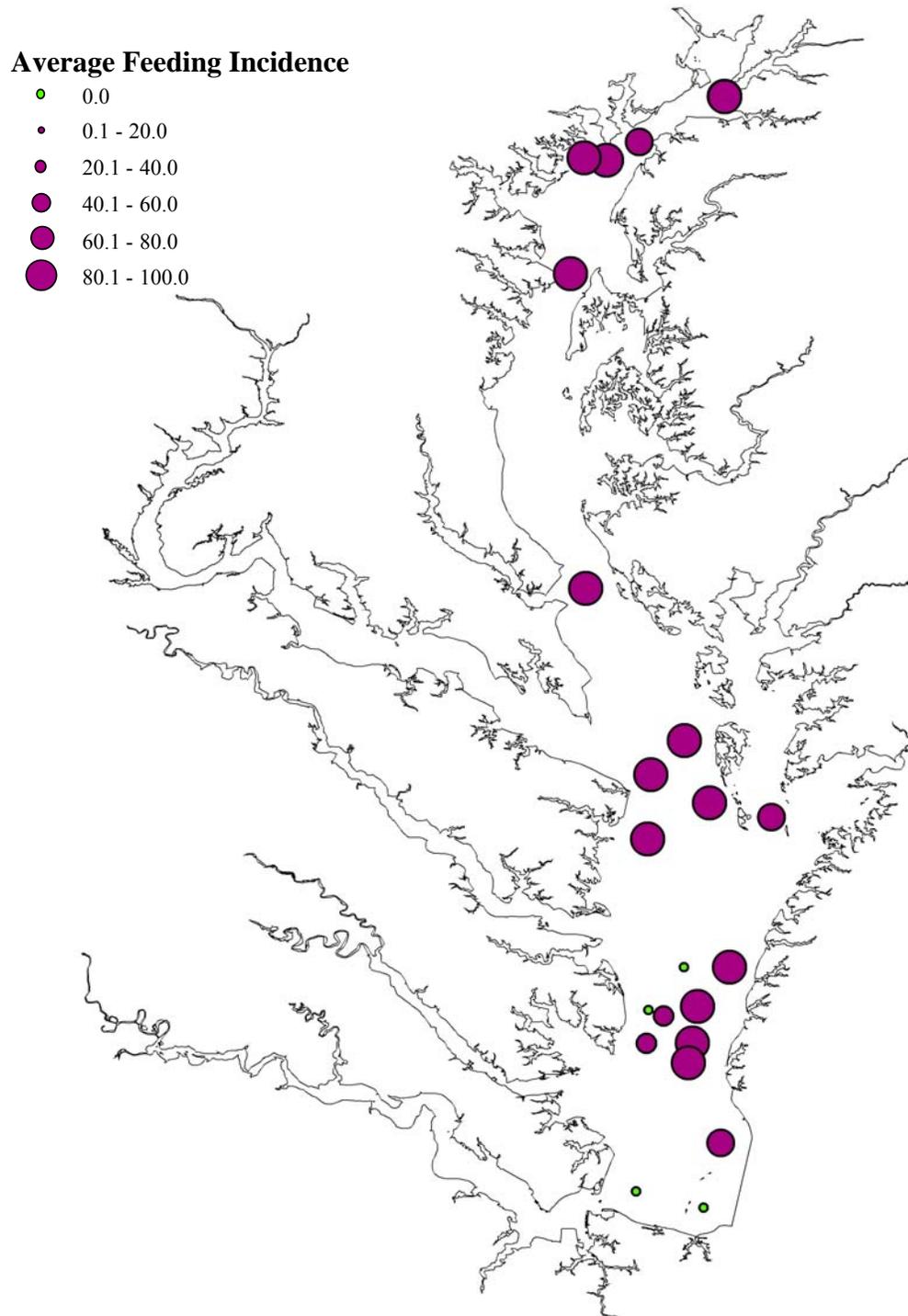
Year	Strata	Strata area (m^2)	Strata average catch (g per m^2)	Minimum strata abundance (q=1) (metric tons)	Minimum strata consumption (q=1) (metric tons)	Intermediate strata abundance (q=0.5) (metric tons)	Intermediate strata consumption (q=0.5) (metric tons)	Maximum strata abundance (q=0.2) (metric tons)	Maximum strata consumption (q=0.2) (metric tons)
2001	Lower	2.956E+09	0.019	56.658	0.025	113.316	0.049	283.291	0.123
	Middle	1.952E+09	0.007	14.093	0.018	28.185	0.036	70.463	0.089
	Upper	6.060E+08	0.077	46.368	0.051	92.736	0.101	231.839	0.253
	Total	5.514E+09	0.103	117.119	0.093	234.237	0.186	585.593	0.465
2002	Lower	2.956E+09	0.011	31.845	0.021	63.691	0.043	159.227	0.107
	Middle	1.952E+09	0.002	3.605	0.005	7.209	0.011	18.023	0.027
	Upper	6.060E+08	0.035	21.196	0.018	42.392	0.036	105.981	0.090
	Total	5.514E+09	0.048	56.646	0.045	113.293	0.090	283.232	0.224
2003	Lower	2.956E+09	0.013	39.294	0.020	78.587	0.039	196.469	0.098
	Middle	1.952E+09	0.011	20.532	0.020	41.064	0.040	102.659	0.101
	Upper	6.060E+08	0.005	2.897	0.003	5.794	0.006	14.485	0.016
	Total	5.514E+09	0.029	62.723	0.043	125.445	0.086	313.613	0.215

Table 4. Hogchoker consumption of macrobenthic taxa (crustaceans, bivalves and polychaetes) in each year and strata assuming three different levels of hogchoker catchability (q=1, 0.5 and 0.2).

Year	Strata	Strata area	Minimum Consumption (q=1.0) metric tons			Intermediate Consumption (q=0.5) metric tons			Maximum Consumption (q=0.2) metric tons		
		(m2)	Bivalve	Crustacean	Polychaete	Bivalve	Crustacean	Polychaete	Bivalve	Crustacean	Polychaete
2001	Lower	2.956E+09	0	0	0.024	0	0	0.047	0	0	0.118
	Middle	1.952E+09	0	1.587E-03	0.013	0	3.173E-03	0.026	0	7.933E-03	0.065
	Upper	6.060E+08	0.011	0.011	0.020	0.022	0.022	0.040	0.054	0.056	0.099
	Total	5.514E+09	0.011	0.013	0.057	0.022	0.026	0.113	0.054	0.064	0.283
2002	Lower	2.956E+09	0	1.671E-03	0.012	0	3.342E-03	0.024	0	8.355E-03	0.059
	Middle	1.952E+09	0	0	5.427E-03	0	0	0.011	0	0	0.027
	Upper	6.060E+08	0	3.851E-03	0.013	0	7.701E-03	0.026	0	0.019	0.064
	Total	5.514E+09	0	5.522E-03	0.030	0	1.104E-02	0.060	0	0.028	0.150
2003	Lower	2.956E+09	0	9.485E-04	0.011	0	1.897E-03	0.021	0	4.742E-03	0.053
	Middle	1.952E+09	0.001	7.366E-05	0.016	2.212E-03	1.473E-04	0.032	5.531E-03	3.683E-04	0.079
	Upper	6.060E+08	0	5.858E-04	2.353E-03	0	1.172E-03	4.706E-03	0	2.929E-03	0.012
	Total	5.514E+09	1.11E-03	1.608E-03	0.029	2.212E-03	3.216E-03	0.057	8.040E-03	8.040E-03	0.143

Table 5. Summer hogchoker trophic demand, measured as percent of standing stock biomass, of macrobenthic taxa (crustaceans, bivalves and polychaetes) in each year and strata assuming three different levels of hogchoker catchability (q=1, 0.5 and 0.2). Macrobenthic standing stock estimates obtained from Hagy (2002).

Year	Strata	Standing Stock (MT)			Minimum Consumption (q=1.0) % standing stock			Intermediate Consumption (q=0.5) % standing stock			Maximum Consumption (q=0.2) % standing stock		
		Bivalve	Crustacean	Polychaete	Bivalve	Crustacean	Polychaete	Bivalve	Crustacean	Polychaete	Bivalve	Crustacean	Polychaete
2001	Lower	7787.737	719.534	29718.702	0	0	6.056E-06	0	0	1.211E-05	0	0	3.028E-05
	Middle	2556.237	48.514	547.049	0	0	1.441E-04	0	0	2.883E-04	0	0	7.207E-04
	Upper	12295.437	159.958	233.203	0	9.118E-05	4.239E-05	0	1.824E-04	8.478E-05	0	4.559E-04	2.119E-04
2002	Lower	7787.737	719.534	29718.702	0	1.638E-05	2.043E-06	0	3.275E-05	4.086E-06	0	8.188E-05	1.022E-05
	Middle	2556.237	48.514	547.049	0	0	9.569E-05	0	0	1.914E-04	0	0	4.784E-04
	Upper	12295.437	159.958	233.203	0	0	4.981E-05	0	0	9.962E-05	0	0	2.490E-04
2003	Lower	7787.737	719.534	29718.702	0	1.620E-05	1.177E-06	0	3.240E-05	2.354E-06	0	8.101E-05	5.884E-06
	Middle	2556.237	48.514	547.049	5.815E-06	2.040E-05	3.880E-04	1.163E-05	4.080E-05	7.759E-04	2.908E-05	1.020E-04	1.940E-03
	Upper	12295.437	159.958	233.203	0	0	0	0	0	0	0	0	0

1a)

Figure 1. Spatial distribution of average feeding incidence in the mainstem of the bay across seasons: spring (a) summer (b) and fall (c).

1b)

Average Feeding Incidence

- 0.0
- 0.1 - 20.0
- 20.1 - 40.0
- 40.1 - 60.0
- 60.1 - 80.0
- 80.1 - 100.0

1c)

**Average Feeding Incidence**
- 0.0
- 0.1 - 20.0
- 20.1 - 40.0
- 40.1 - 60.0
- 60.1 - 80.0
- 80.1 - 100.0
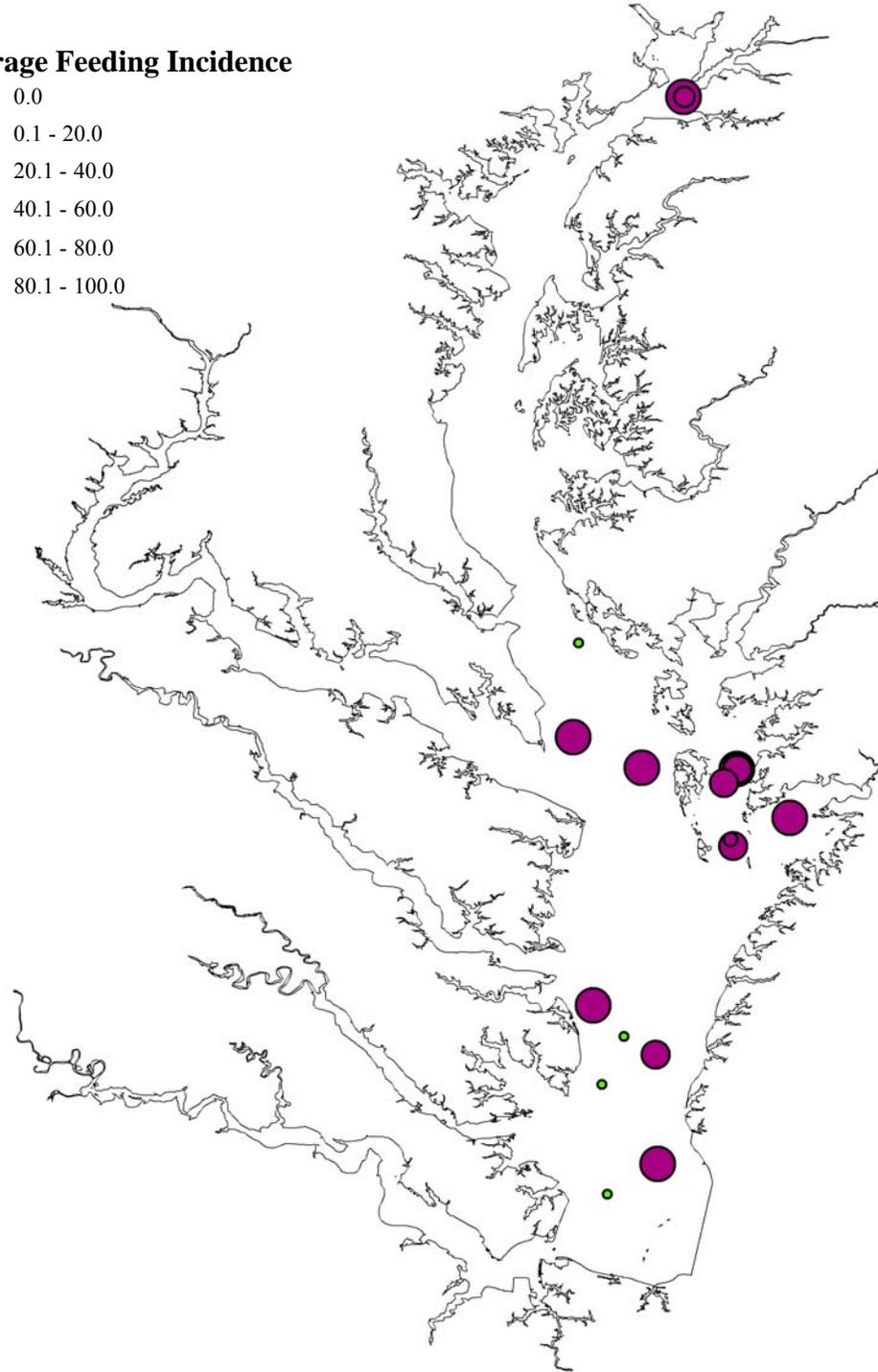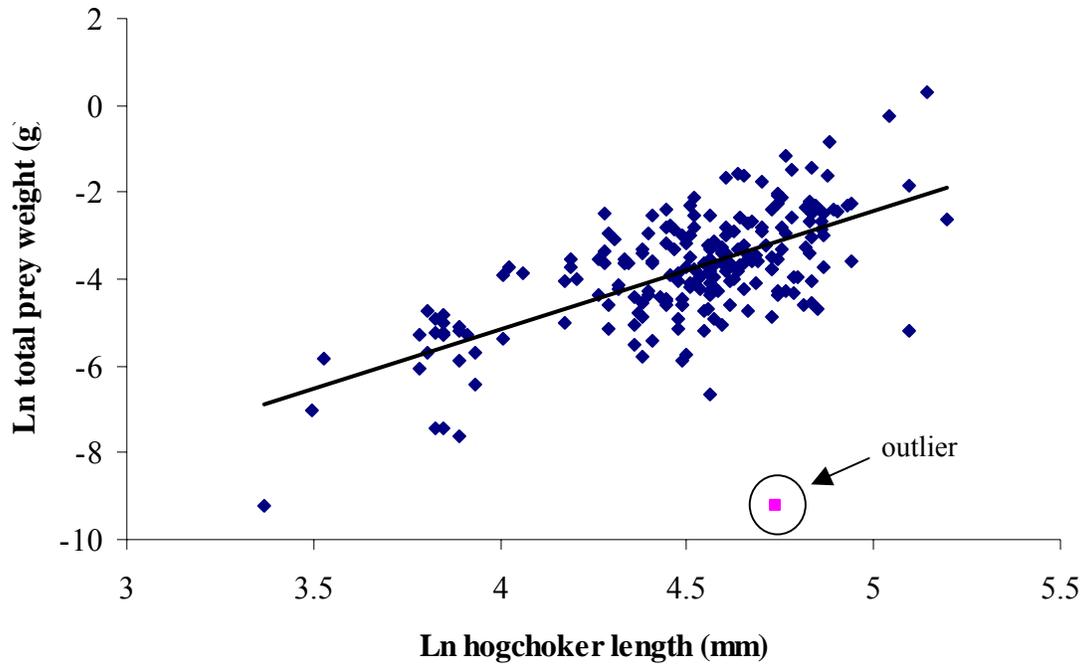
Figure 2. Linear regression between the natural log of total prey weight and the natural log of hogchoker length from broadscale survey data. The marked outlier was not included in the final regression model (adjusted $r^2 = 0.454$, p<0.001).
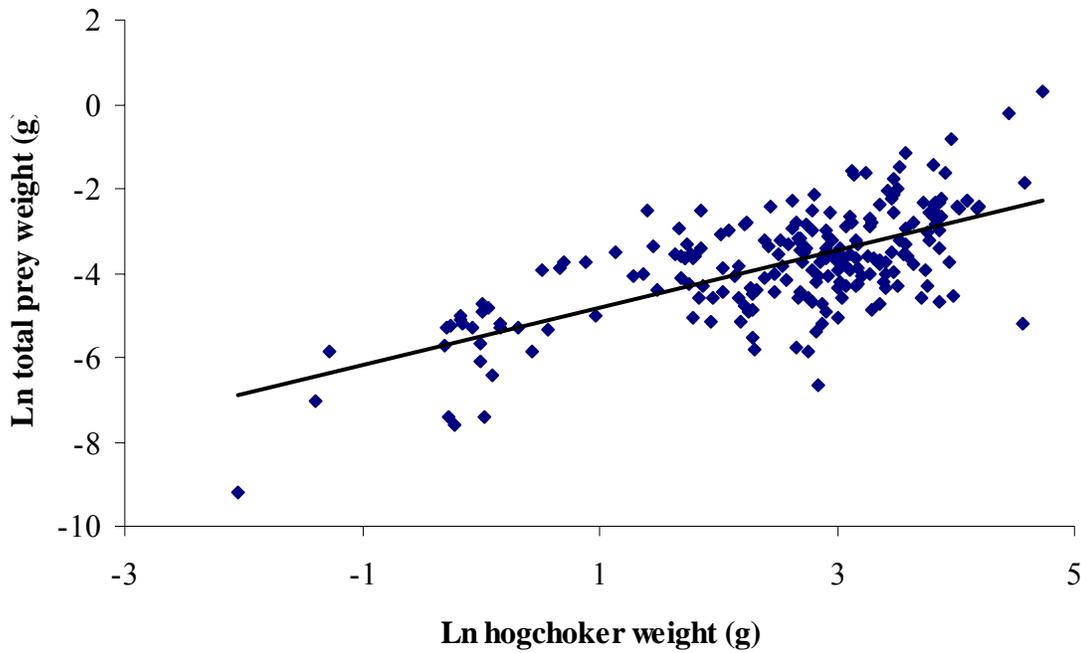
Figure 3. Linear regression between the natural logs of total prey weight and hogchoker weight from broadscale survey data (adjusted $r^2 = 0.434$, $p < 0.001$).
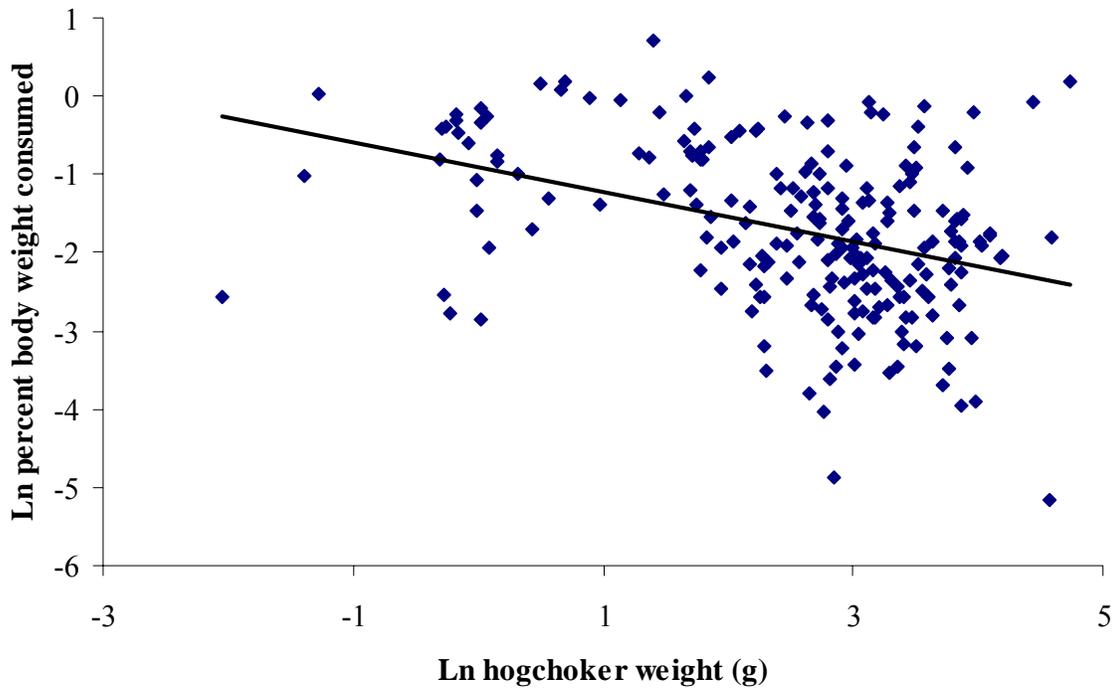
Figure 4. Linear regression between the natural log of stomach content weight, represented as percent of hogchoker body weight, and the natural log of hogchoker weight (adjusted $r^2 = 0.146$, $p<0.001$).
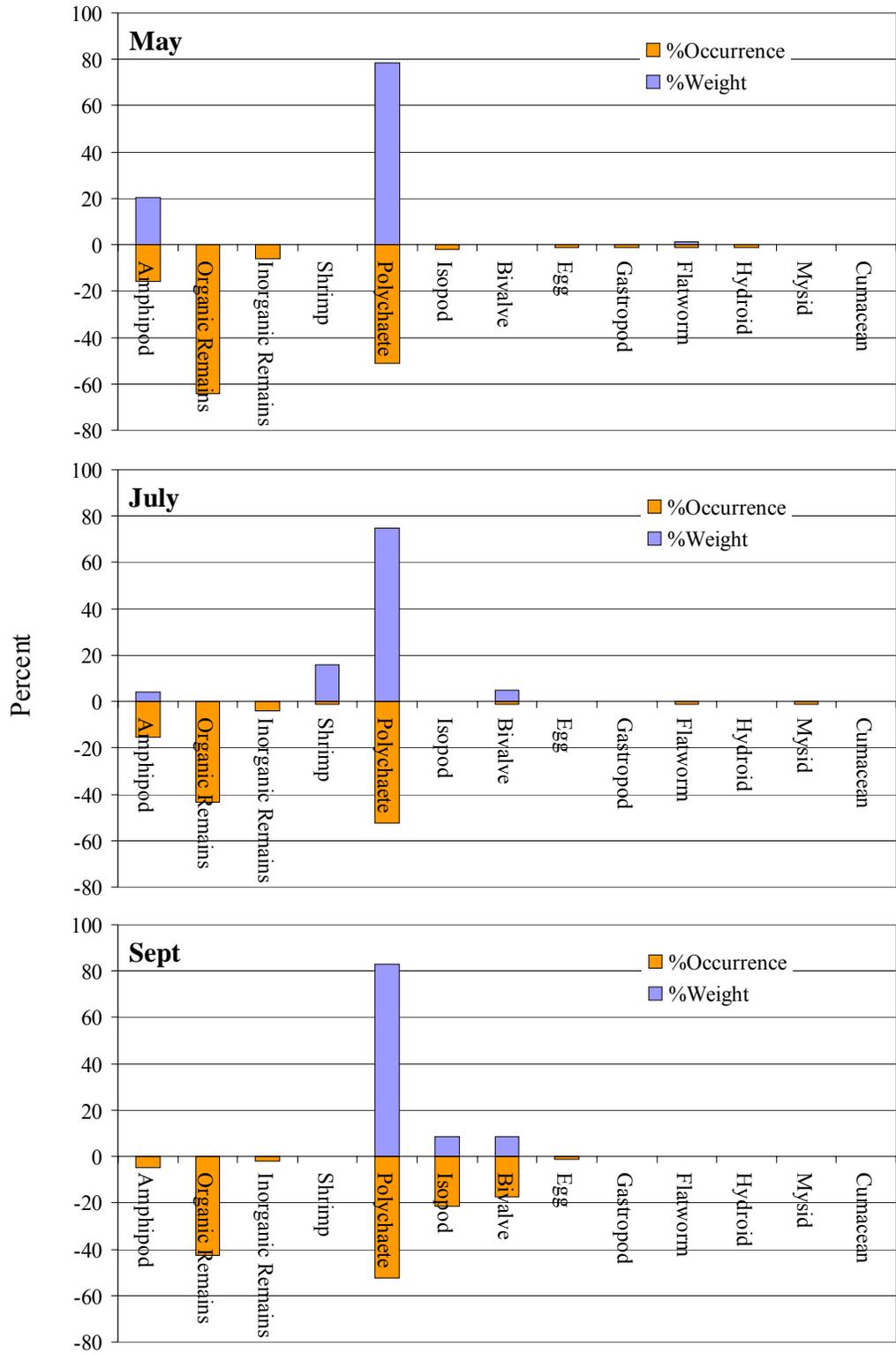
Figure 5. Hogchoker diet by season in the mainstem of the bay quantified as percent frequency of occurrence on the negative y-axis (% occurrence) and percentage composition by weight (% weight) on the positive y-axis (n=281).
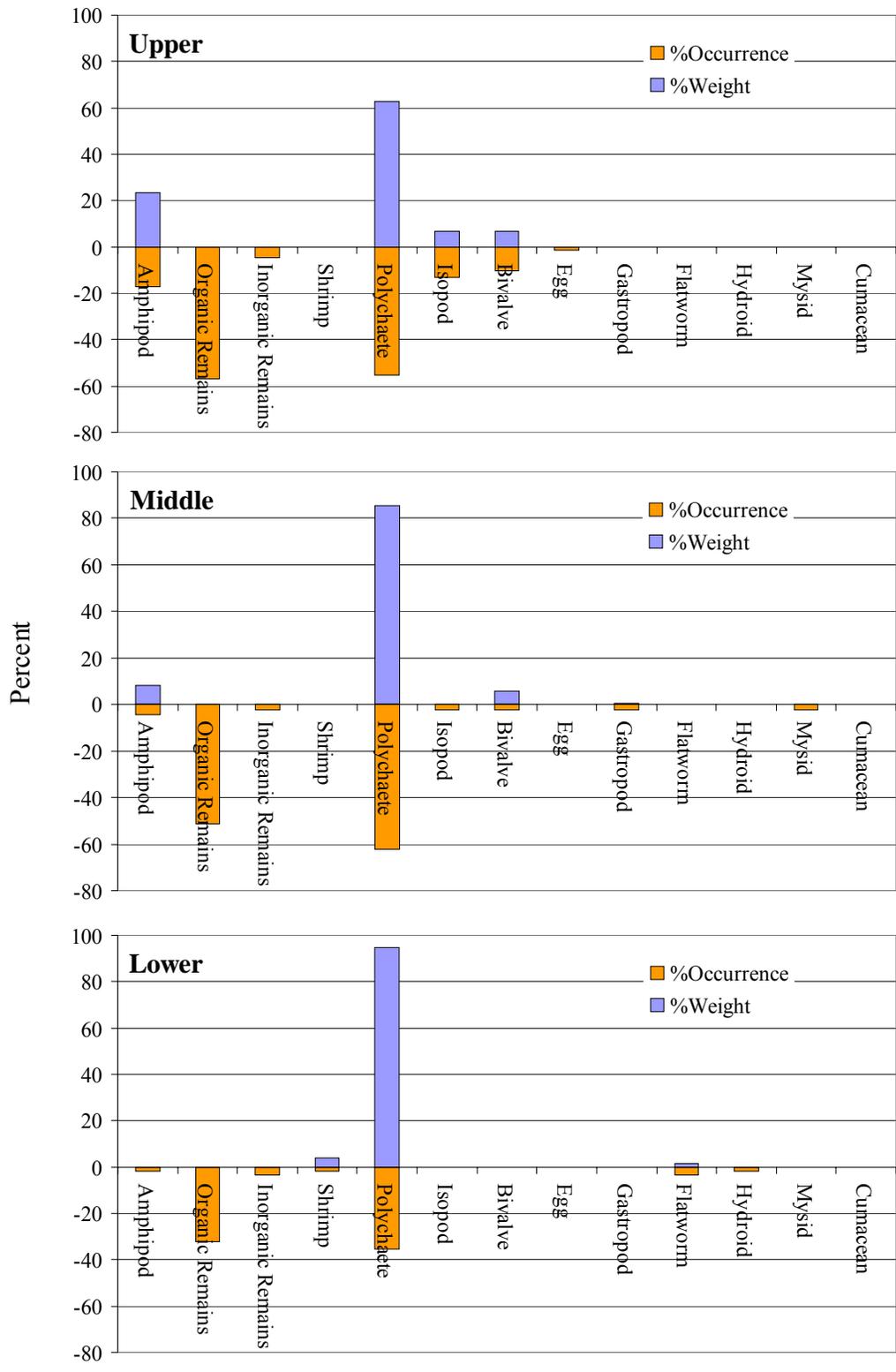
Figure 6. Hogchoker diet by stratum in the mainstem of the bay quantified as percent frequency of occurrence (% occurrence) on the negative y-axis and percentage composition by weight (% weight) on the positive y-axis (n=281).
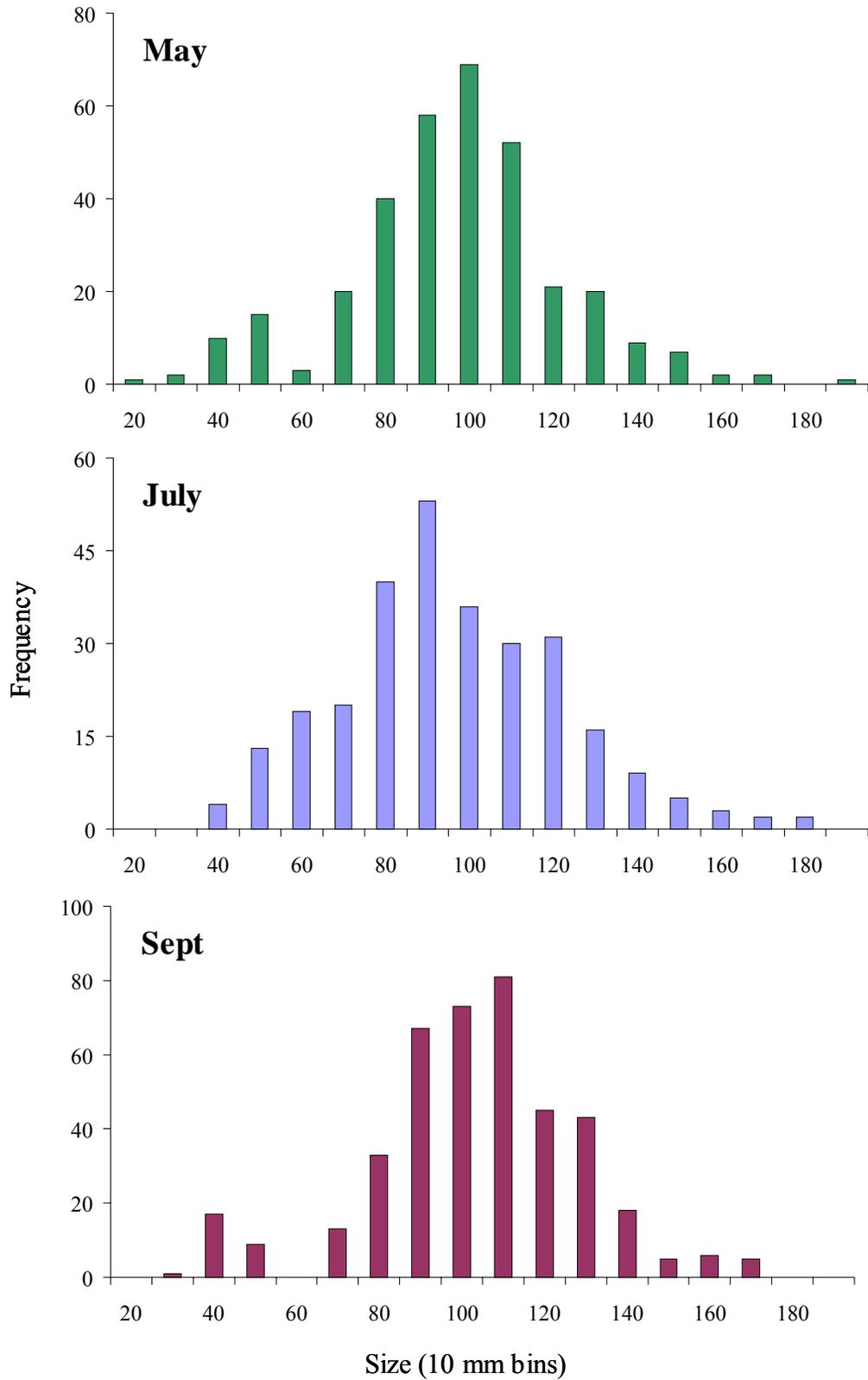
Figure 7. Hogchoker length frequency distribution by season of individuals collected in the mainstem of the bay from 1995-2003.
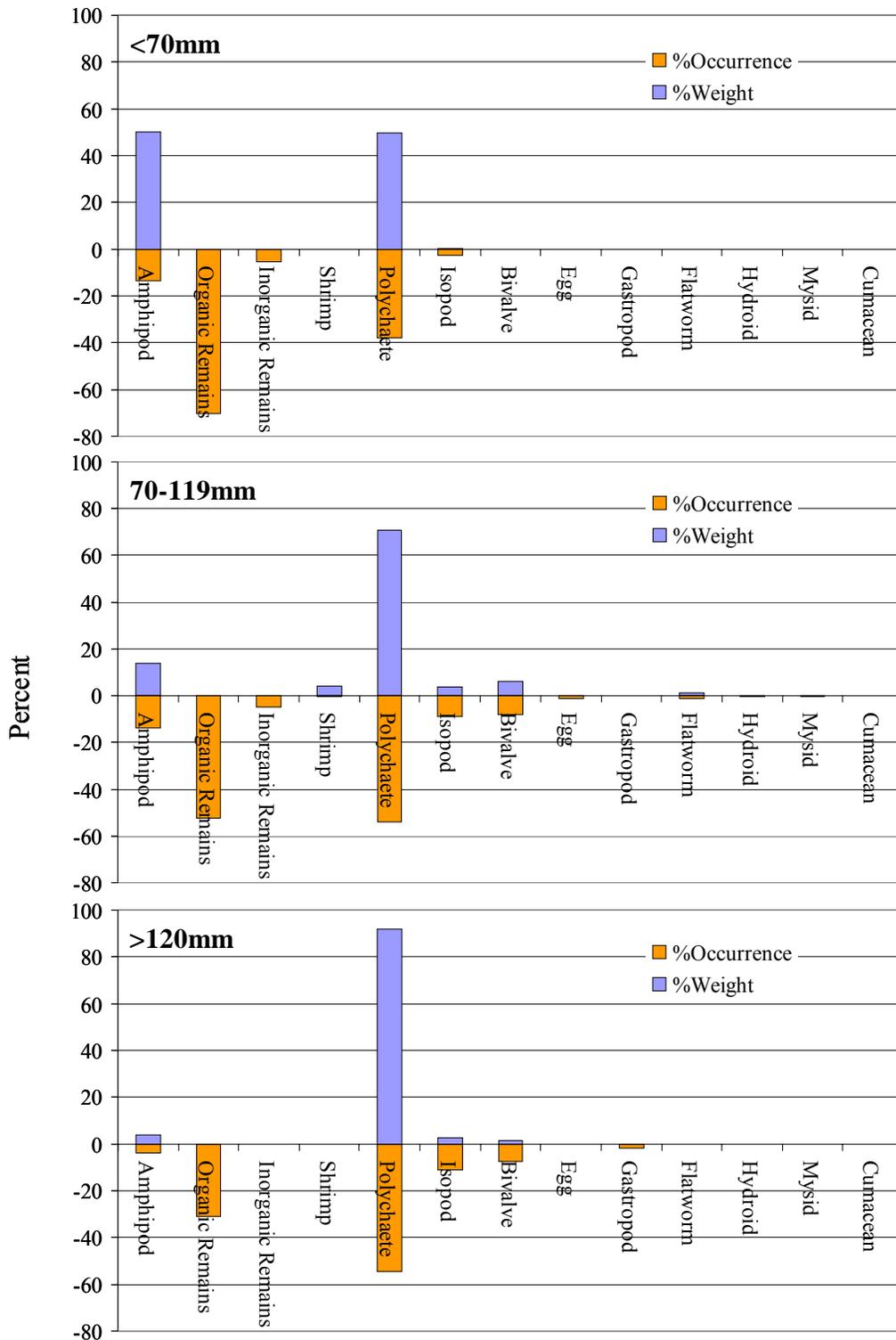
Figure 8. Hogchoker diet by size class in the mainstem of the bay quantified as percent frequency of occurrence on the negative y-axis (% occurrence) and percentage composition by weight (% weight) on the positive y-axis (n=281). Size classes were constructed from inspection of length frequency distributions.

9a)

9b)
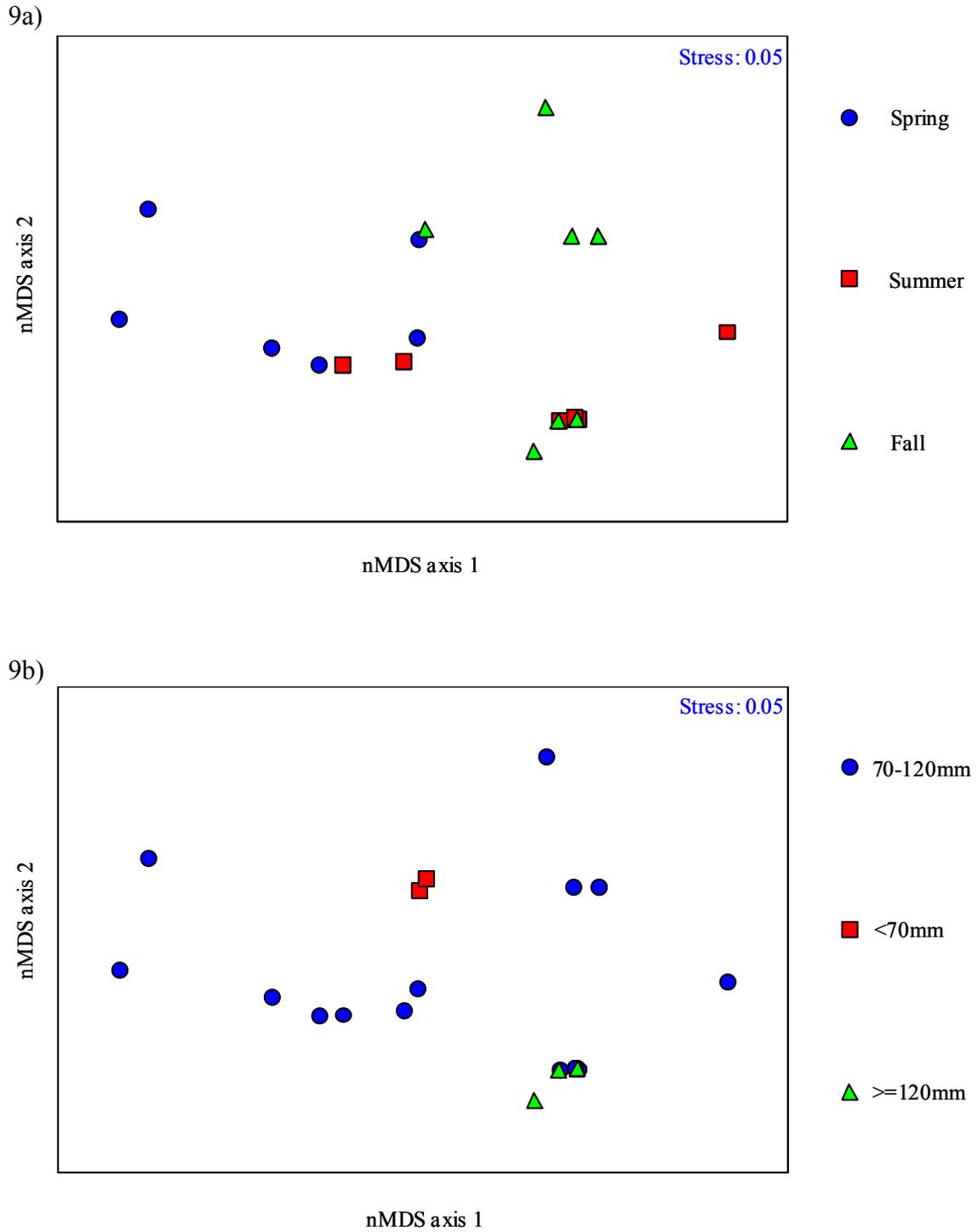
Figure 9. nMDS ordination of hogchoker diet composition in the mainstem of the bay across seasons (a) size classes (b) strata (c) and years (d). This analysis was based on the five principal prey items found in hogchoker diet: amphipods, polychaetes, *Cyathura*, bivalve siphons and cumaceans.

9c)
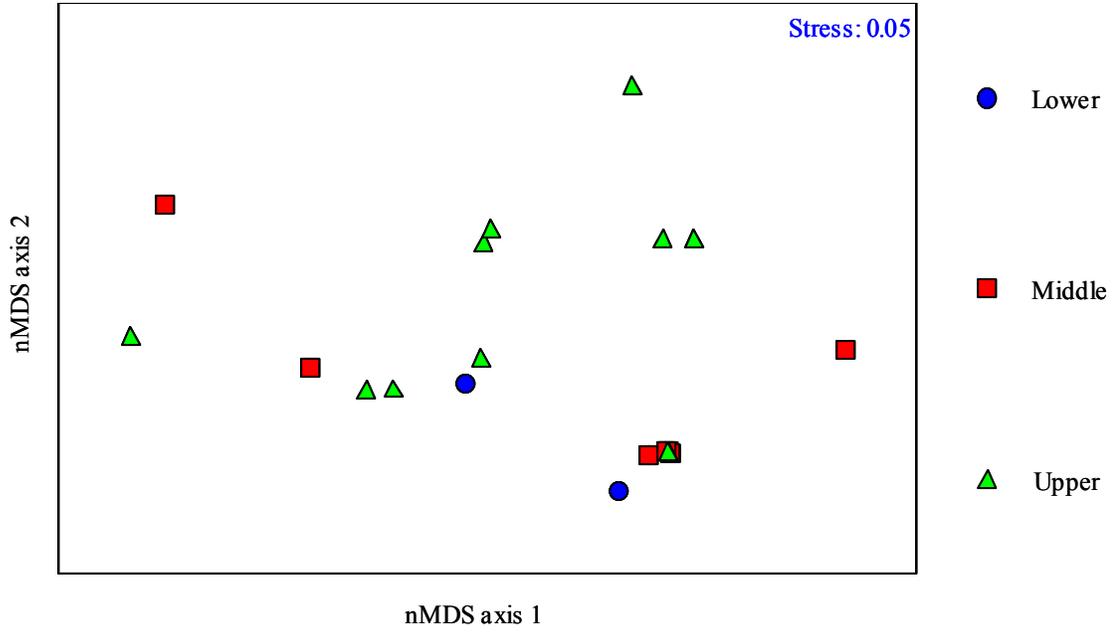
9d)
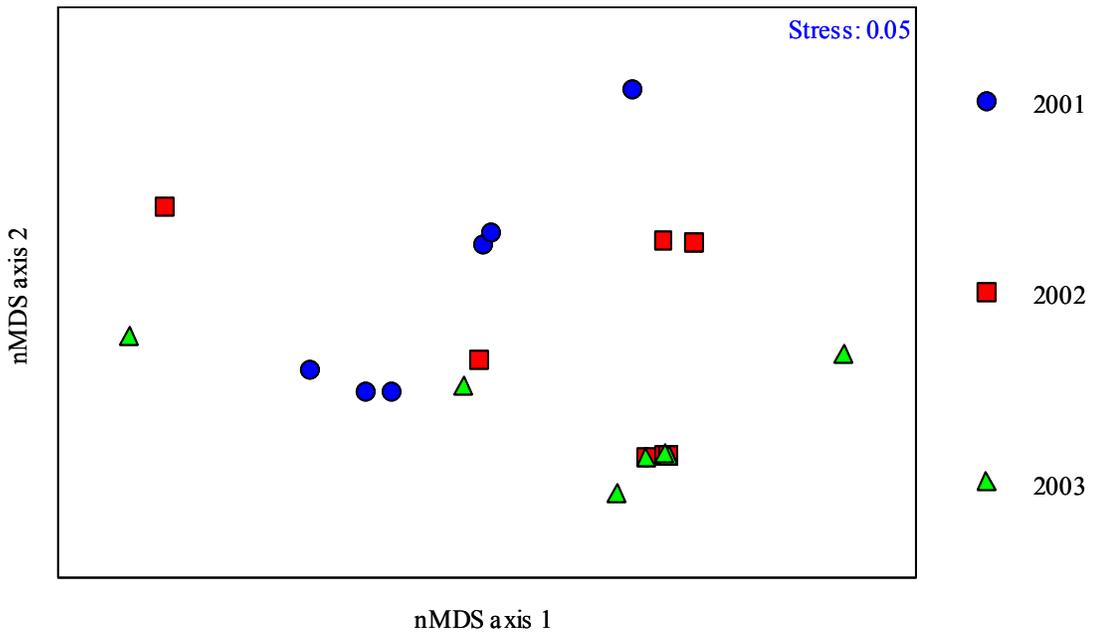
10a)
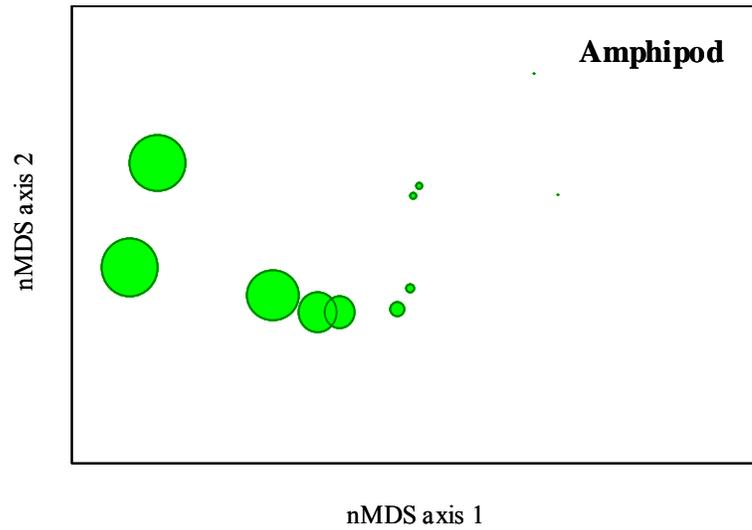
10b)
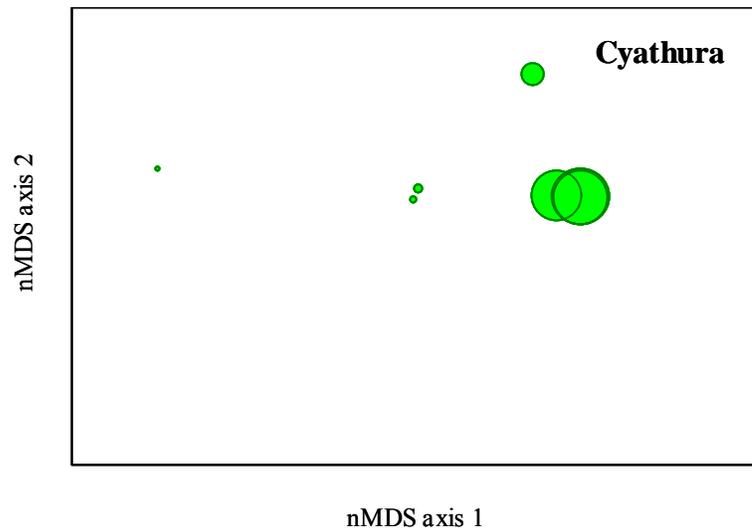
Figure 10. Bubble plots from the nMDS ordination of hogchoker diet composition in the mainstem of the bay demonstrating the relative magnitude of each prey item: amphipods (a) *Cyathura* (b) bivalve siphons (c) and polychaetes (d). Cumaceans were not found in stomachs of those hogchokers collected during the broadscale, therefore, a cumacean bubble plot was not constructed.
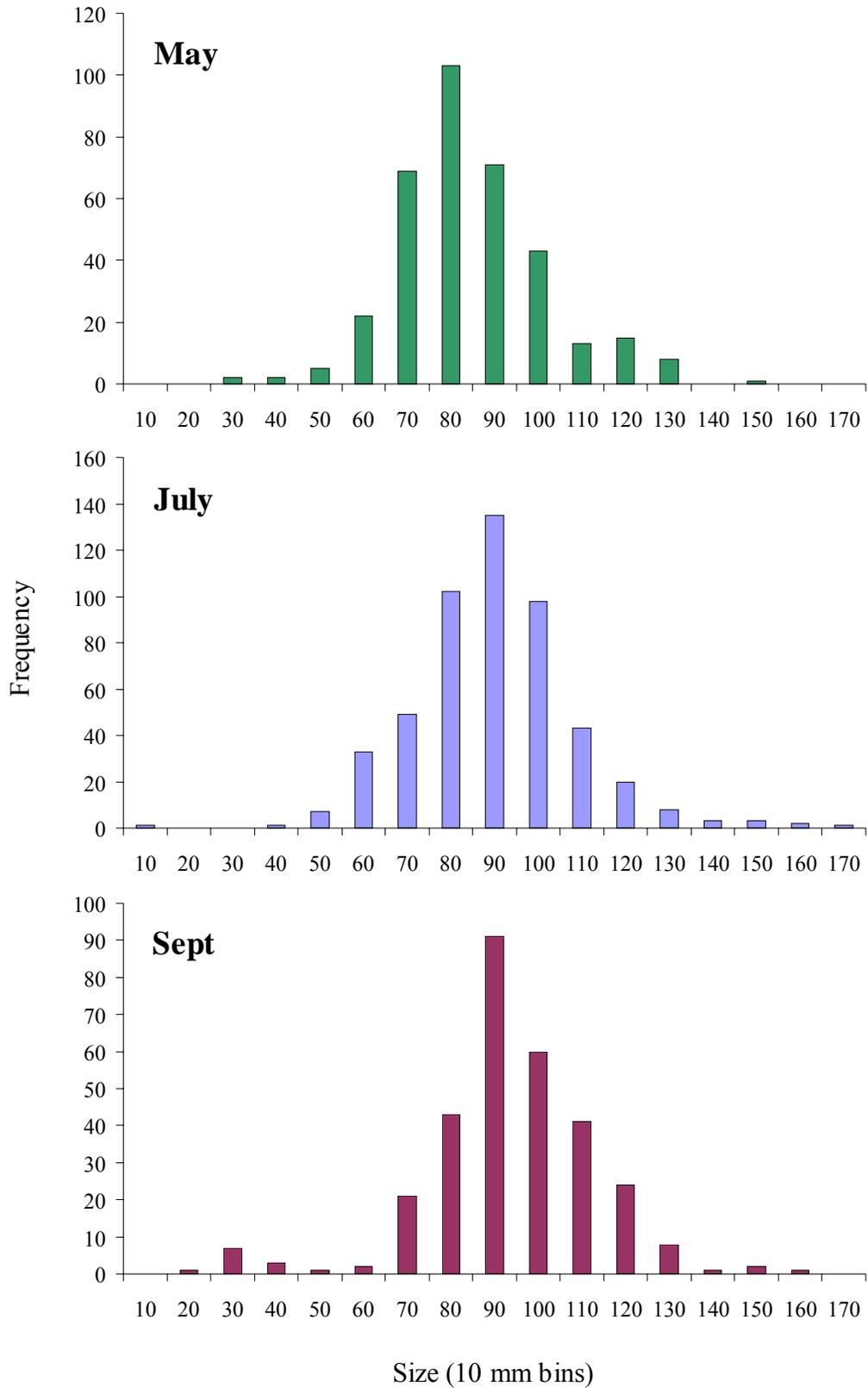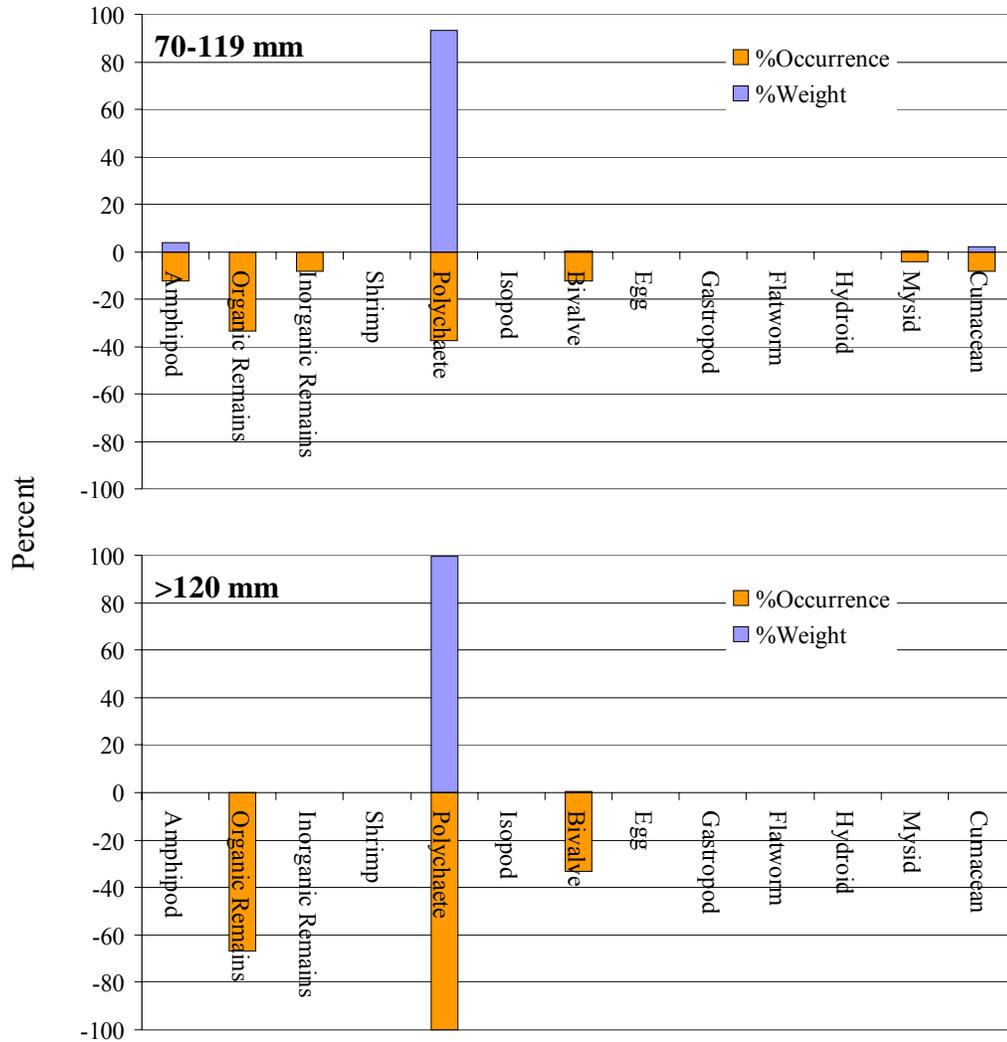
10c)
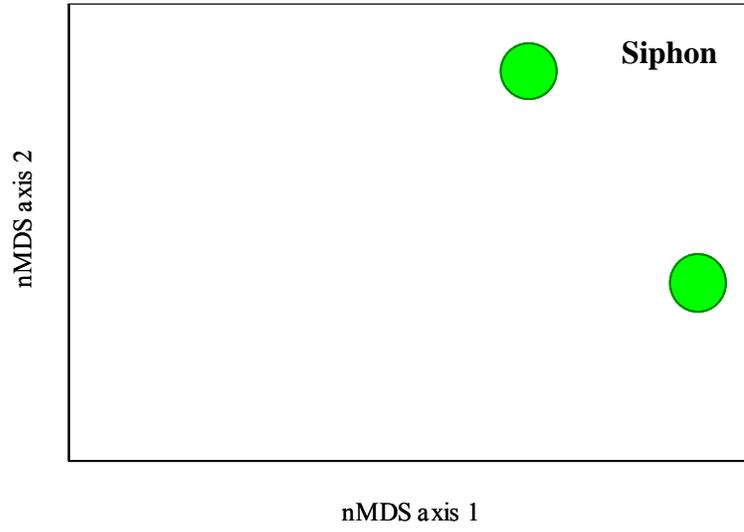
10d)
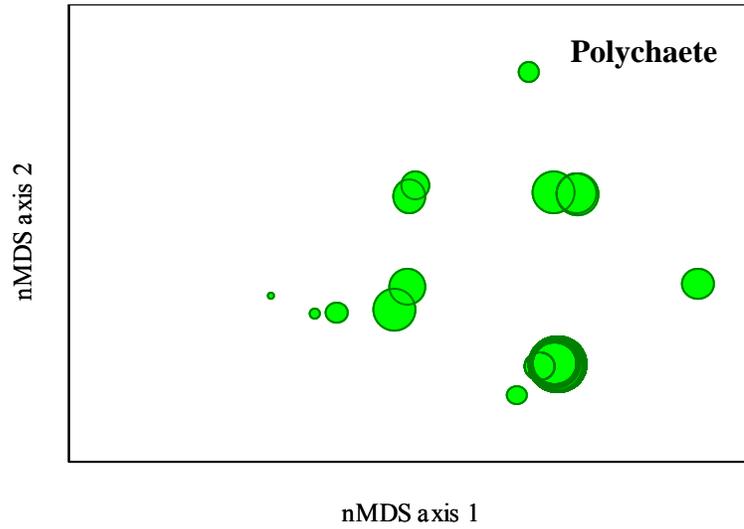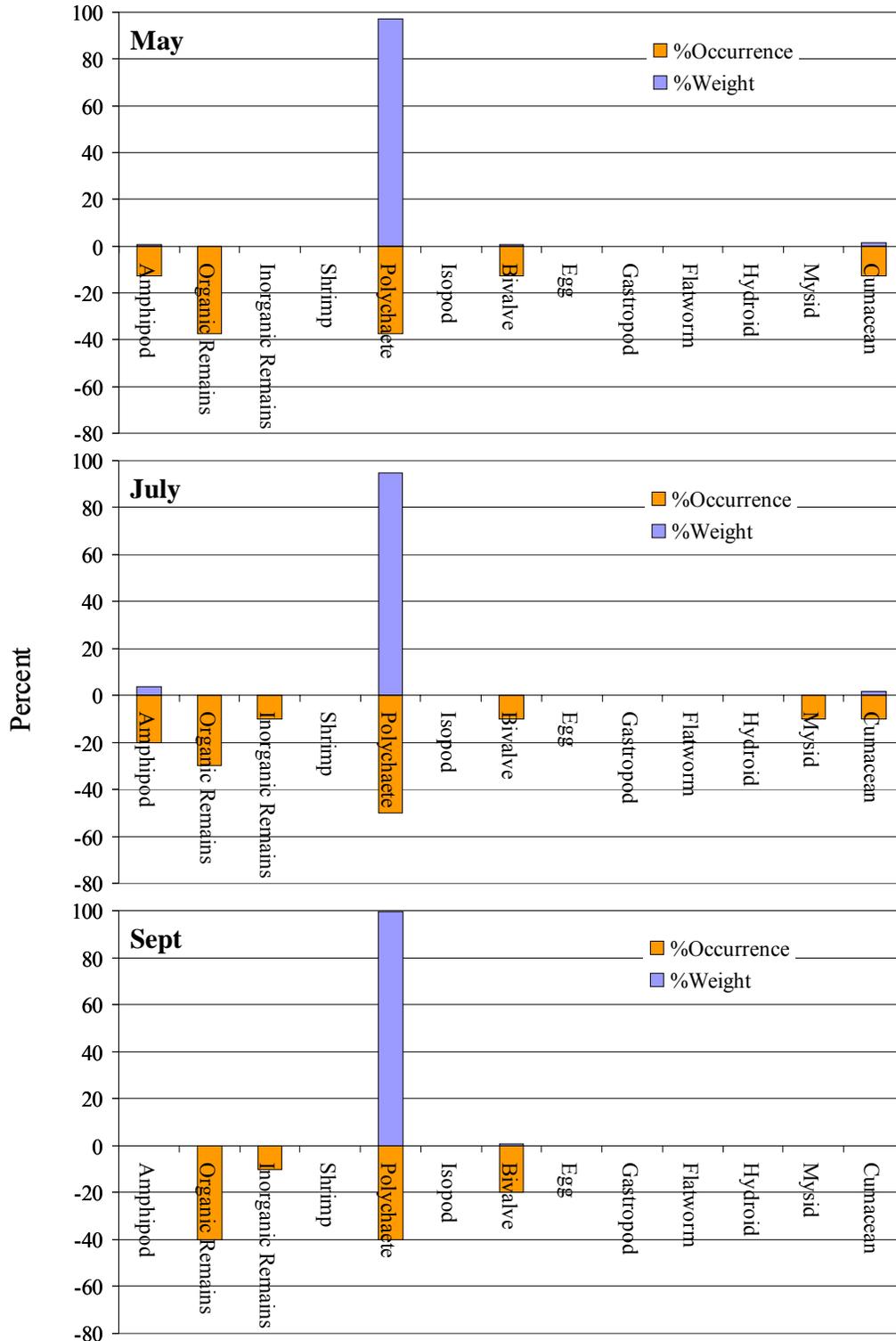
Figure 11. Hogchoker diet by season in the shoal habitats of Tangier and Pocomoke Sounds quantified as percent frequency of occurrence on the negative y-axis (% occurrence) and percentage composition by weight (% weight) on the positive y-axis (n=32).

Figure 12. Length frequency distribution by season of hogchokers collected in Maryland shoal habitats from 2001-2003.

Figure 13. Hogchoker diet by size class in the shoal habitats of Tangier and Pocomoke Sounds quantified as percent frequency of occurrence on the negative y-axis (% occurrence) and percentage composition by weight (% weight) on the positive y-axis (n=32). Size classes were constructed from inspection of length frequency distributions.
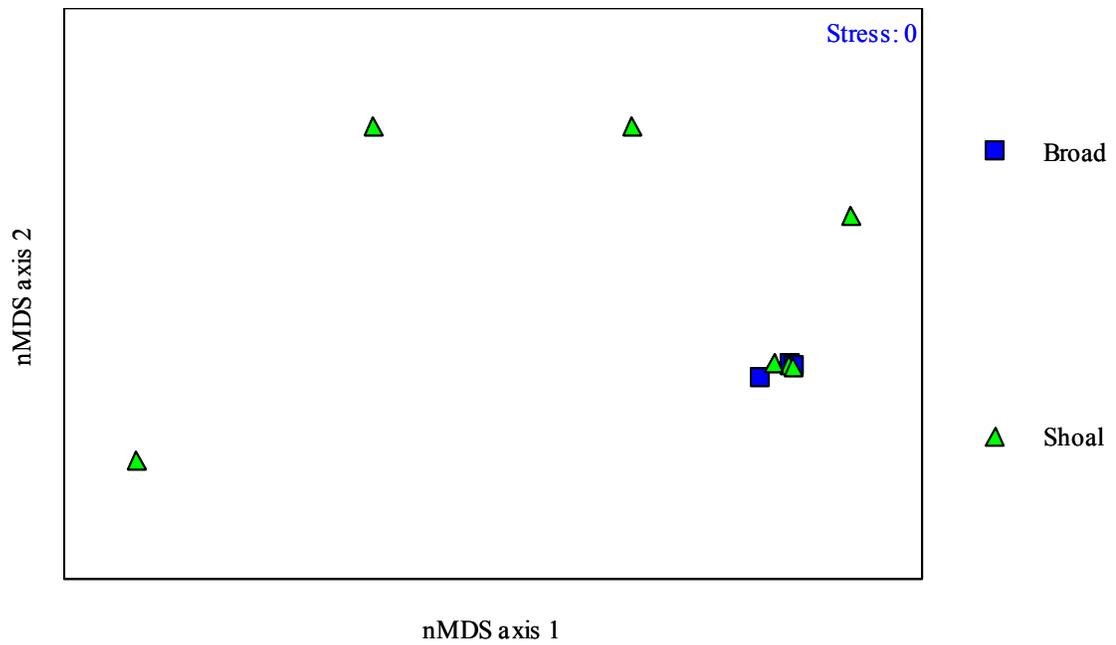
Figure 14. nMDS ordination of hogchoker diet composition across surveys. This analysis was based on the five principal prey items found in hogchoker diet: amphipods, polychaetes, *Cyathura*, bivalve siphons and cumaceans.
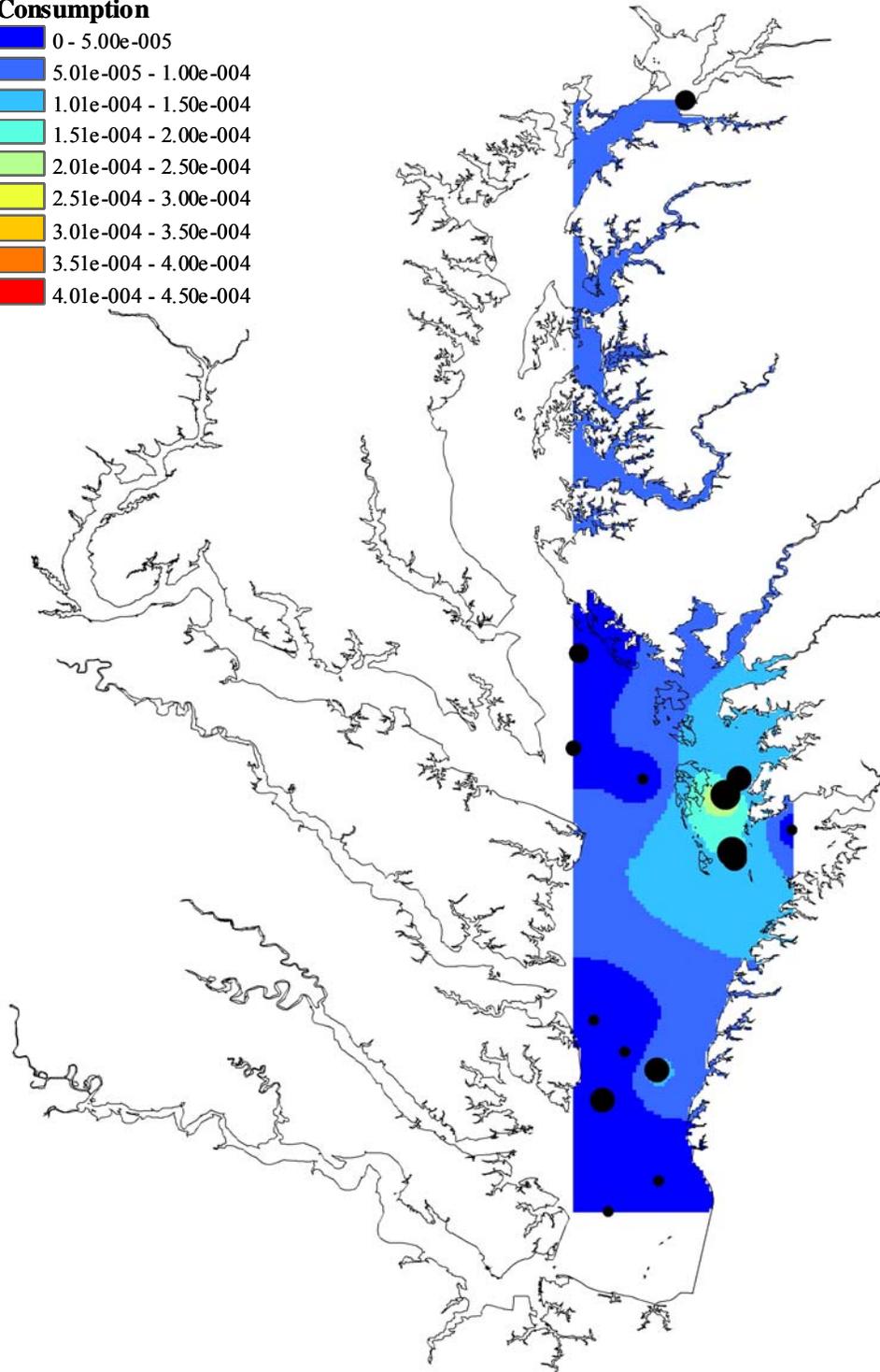
15a)
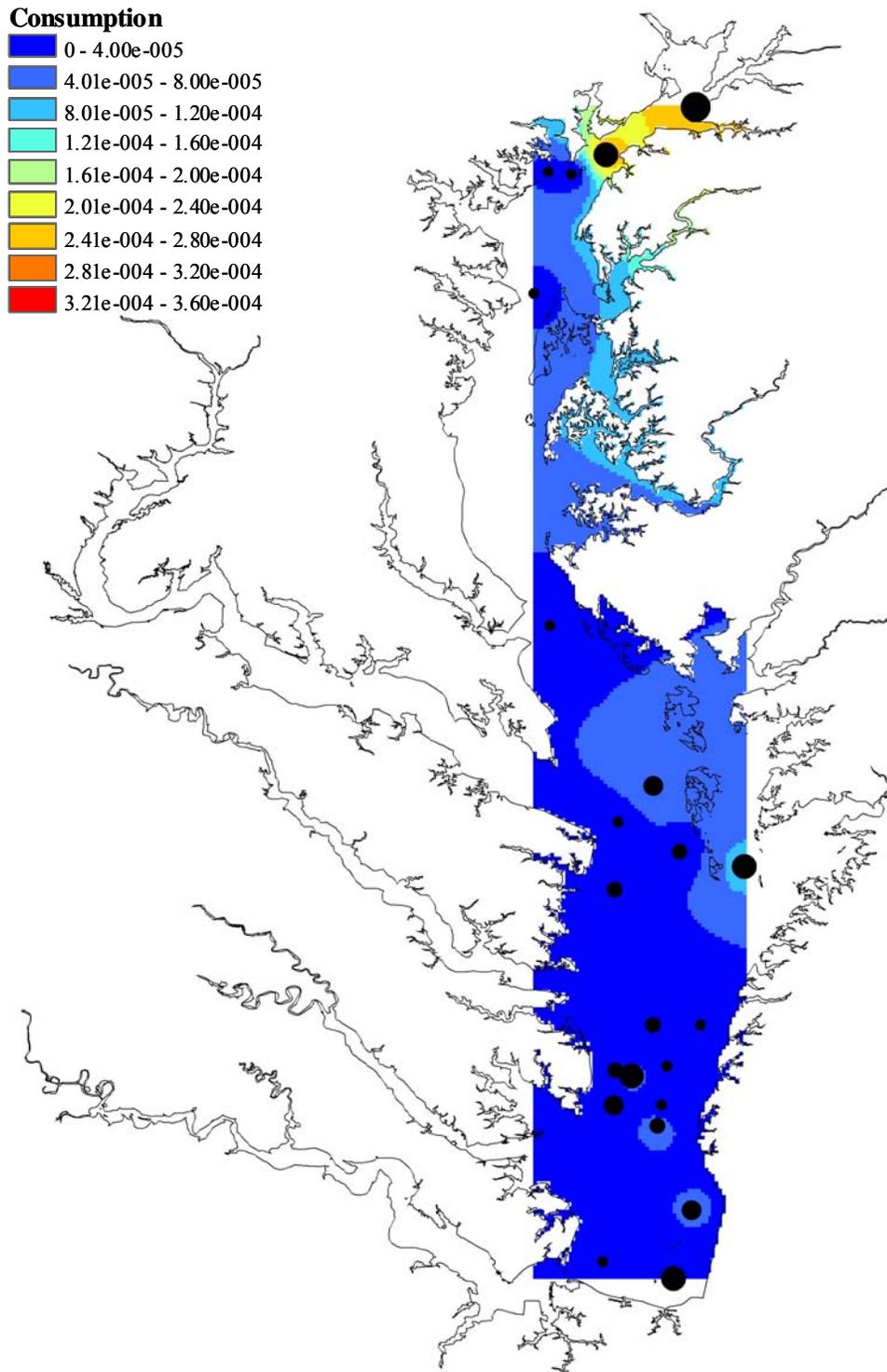
Figure 15. Total consumption (g/m^2) of hogchoker across all years in the spring (a), summer (b) and fall (c). The size of the station symbols corresponds to the average hogchoker relative abundance at each station.

15b)

Consumption
- 0 - 5.00e-005
- 5.01e-005 - 1.00e-004
- 1.01e-004 - 1.50e-004
- 1.51e-004 - 2.00e-004
- 2.01e-004 - 2.50e-004
- 2.51e-004 - 3.00e-004
- 3.01e-004 - 3.50e-004
- 3.51e-004 - 4.00e-004
- 4.01e-004 - 4.50e-004

15c)

Consumption
- 0 - 1.10e-004
- 1.11e-004 - 2.20e-004
- 2.21e-004 - 3.30e-004
- 3.31e-004 - 4.40e-004
- 4.41e-004 - 5.50e-004
- 5.51e-004 - 6.60e-004
- 6.61e-004 - 7.70e-004
- 7.71e-004 - 8.80e-004
- 8.81e-004 - 9.90e-004
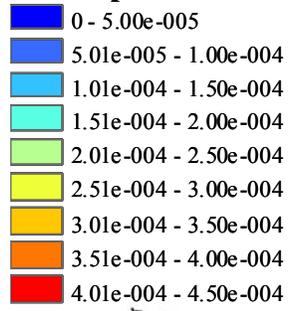
16a)

Bivalve Consumption

- 0
- 0
- 0
- 0
- 0
- 0
- 0
- 0
- 0

Figure 16. Prey-specific consumption (g/m^2) of bivalves (a), crustaceans (b) and polychaetes (c) in the spring. The size of the station symbols corresponds to the average hogchoker relative abundance at each station.

16b)

Crustacean Consumption
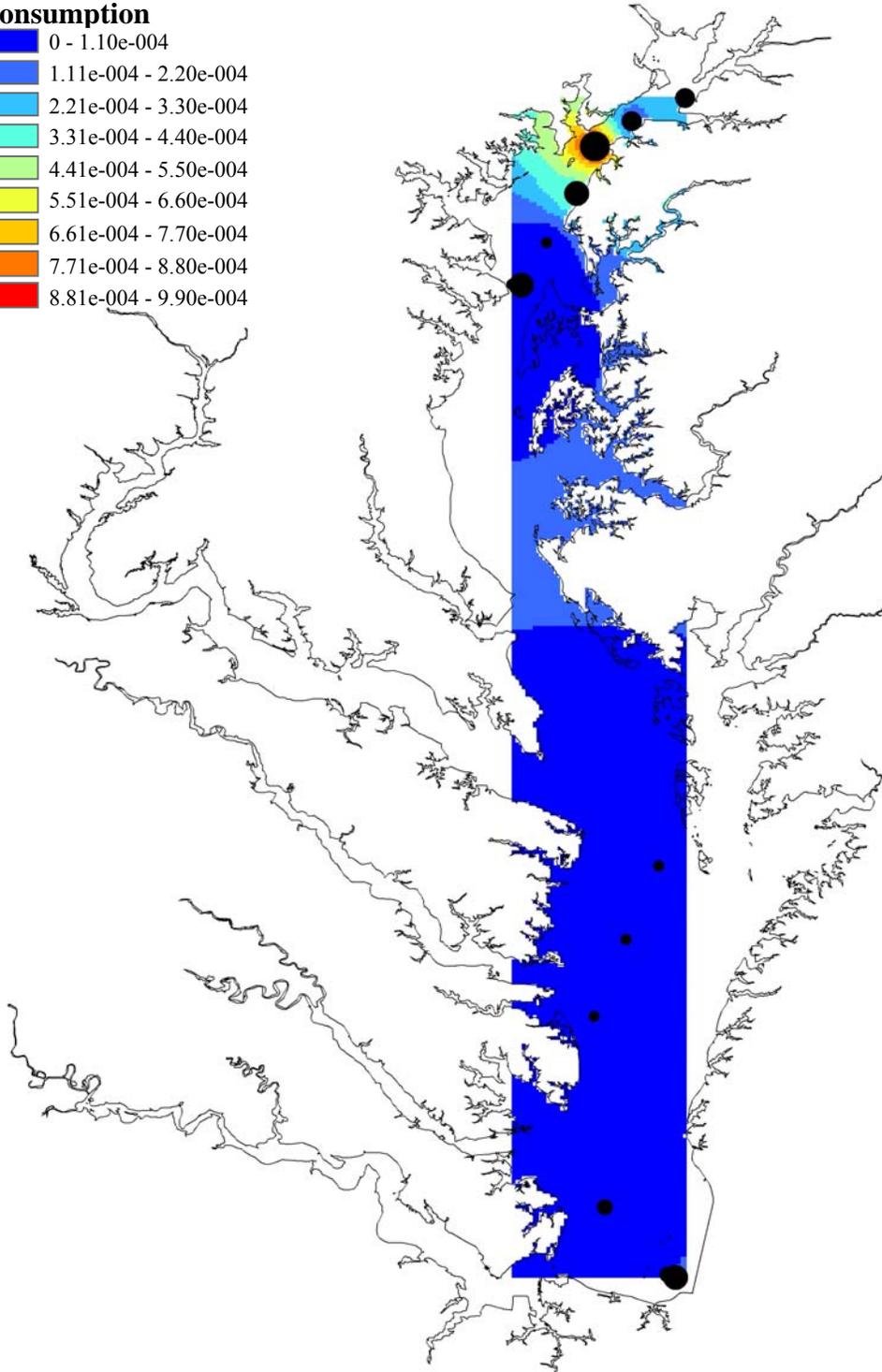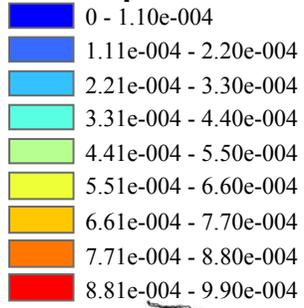
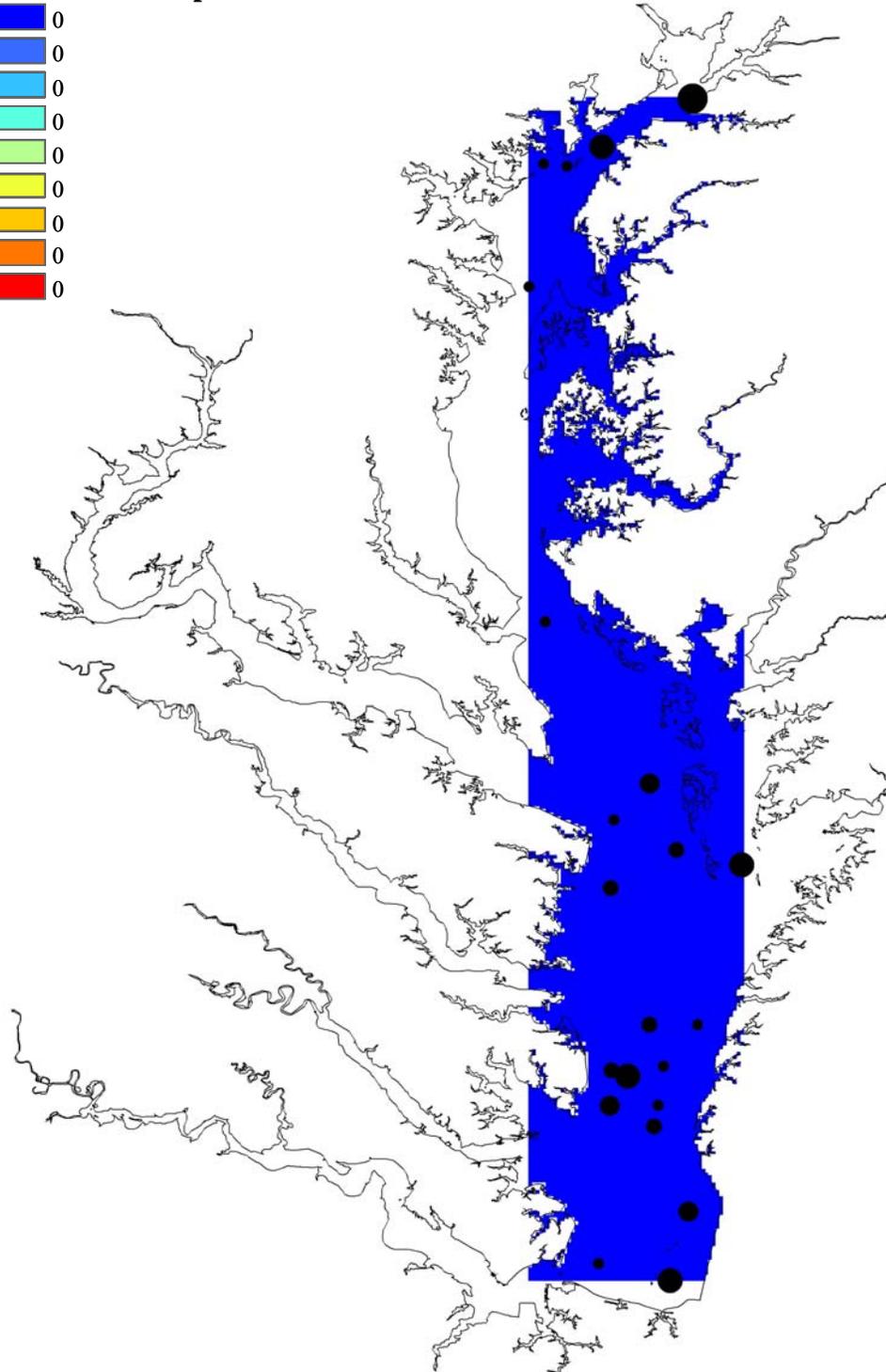- 0 - 2.50e-005
- 2.51e-005 - 5.00e-005
- 5.01e-005 - 7.50e-005
- 7.51e-005 - 1.00e-004
- 1.01e-004 - 1.25e-004
- 1.26e-004 - 1.50e-004
- 1.51e-004 - 1.75e-004
- 1.76e-004 - 2.00e-004
- 2.01e-004 - 2.25e-004

16c)

Polychaete Consumption

- 0 - 2.00e-005
- 2.01e-005 - 4.00e-005
- 4.01e-005 - 6.00e-005
- 6.01e-005 - 8.00e-005
- 8.01e-005 - 1.00e-004
- 1.01e-004 - 1.20e-004
- 1.21e-004 - 1.40e-004
- 1.41e-004 - 1.60e-004
- 1.61e-004 - 1.80e-004

17a)

Bivalve Consumption

- 0 - 1.50e-006
- 1.51e-006 - 3.00e-006
- 3.01e-006 - 4.50e-006
- 4.51e-006 - 6.00e-006
- 6.01e-006 - 7.50e-006
- 7.51e-006 - 9.00e-006
- 9.01e-006 - 1.05e-005
- 1.06e-005 - 1.20e-005
- 1.21e-005 - 1.35e-005

Figure 17. Prey-specific consumption (g/m^2) of bivalves (a), crustaceans (b) and polychaetes (c) in the summer. The size of the station symbols corresponds to the average hogchoker relative abundance at each station.
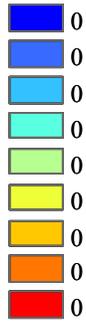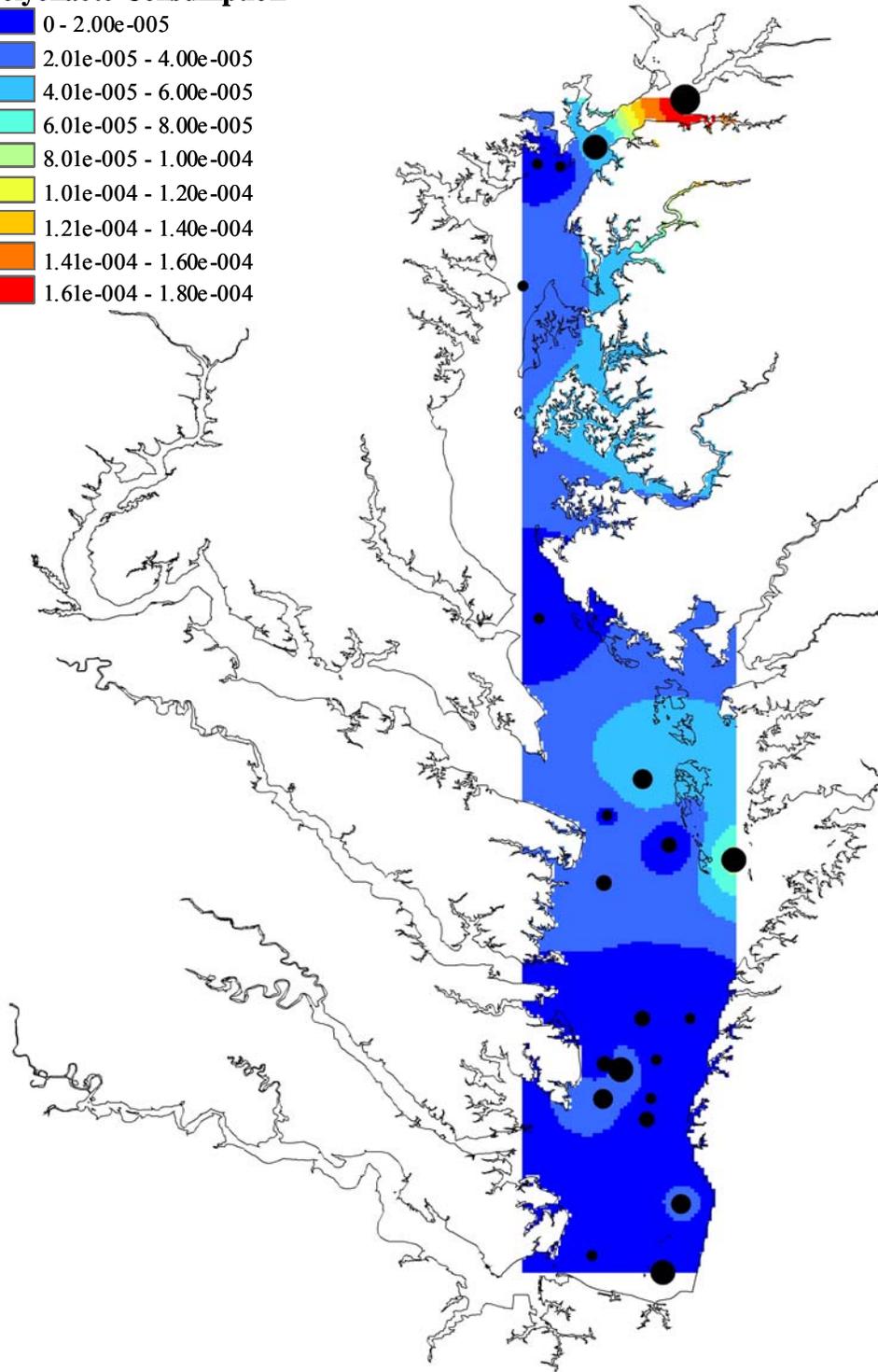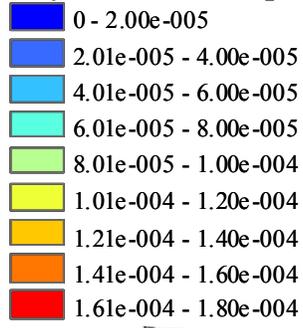
17b)

Crustacean Consumption

- 0 - 5.00e-006
- 5.01e-006 - 1.00e-005
- 1.01e-005 - 1.50e-005
- 1.51e-005 - 2.00e-005
- 2.01e-005 - 2.50e-005
- 2.51e-005 - 3.00e-005
- 3.01e-005 - 3.50e-005
- 3.51e-005 - 4.00e-005
- 4.01e-005 - 4.50e-005

17c)

Polychaete Consumption

■	0 - 4.00e-005
■	4.01e-005 - 8.00e-005
■	8.01e-005 - 1.20e-004
■	1.21e-004 - 1.60e-004
■	1.61e-004 - 2.00e-004
■	2.01e-004 - 2.40e-004
■	2.41e-004 - 2.80e-004
■	2.81e-004 - 3.20e-004
■	3.21e-004 - 3.60e-004
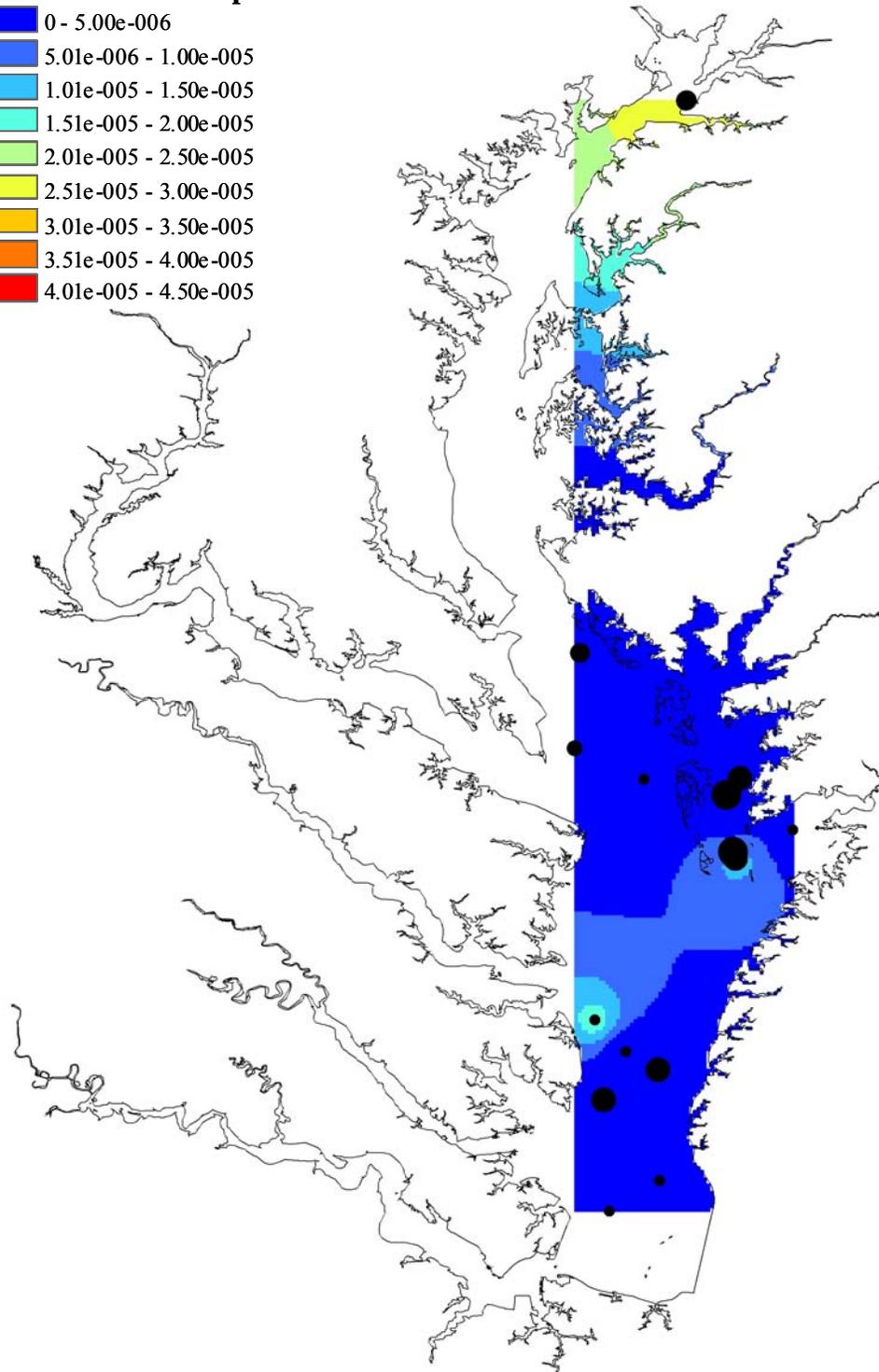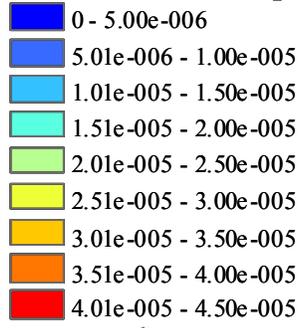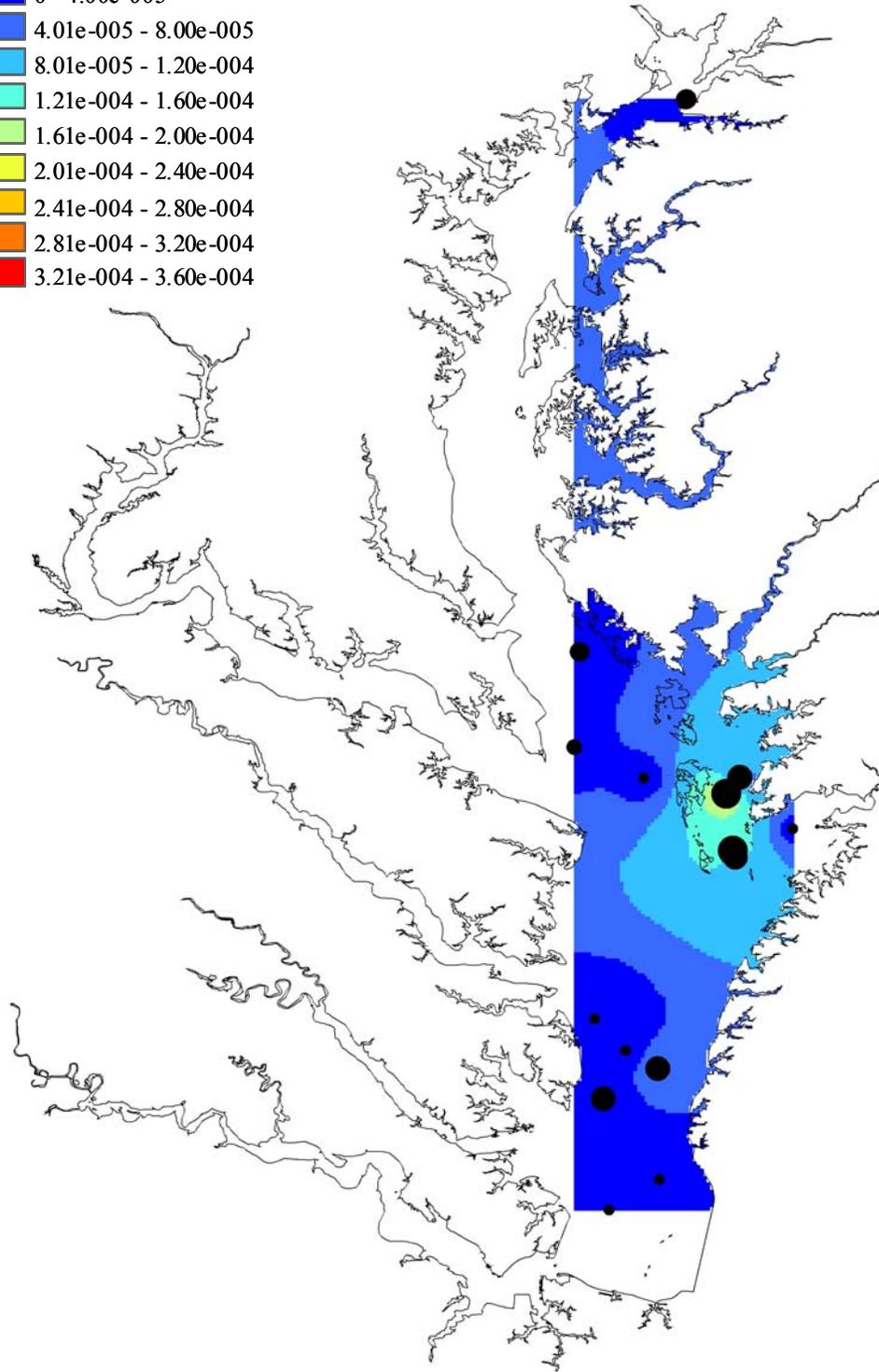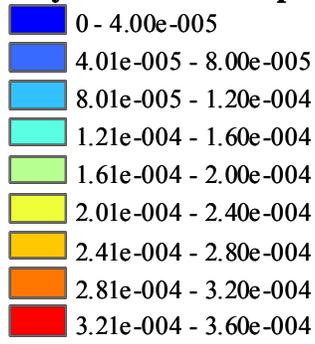
CHAPTER 4: SUMMARY

In support of the development of ecosystem-based fisheries management in the Chesapeake Bay (CBP 2000; NOAA 2004), I examined the ecology of the hogchoker, *Trinectes maculatus*, an unexploited yet abundant and widely distributed flatfish in the bay ecosystem. The specific goals of my thesis aimed at improving the community's knowledge of hogchoker ecology to ultimately aid in the incorporation of this species into ecosystem based fishery management plans that must address both commercially and ecologically important species. One multispecies management initiative in the Chesapeake Bay has been the development of an Ecopath with Ecosystem model (NCBO 2003) that requires the inclusion of both diet and biomass data for all major species in the ecosystem (Latour et al. 2003). As a consequence of this requirement, any particular species, regardless of exploitation state, that represents a large biomass or predatory demand in the bay can potentially have a substantial impact on the flow of energy through the ecosystem. Accordingly, the development of both this ecosystem model and ecosystem based fishery management plans in the Chesapeake Bay require the investigation of potentially ecologically important species, such as the hogchoker, that are not traditionally the focus of research studies.

In chapter 2, I constructed a generalized additive model (GAM) to investigate patterns in hogchoker distribution and abundance in the mainstem of the Chesapeake Bay. This model indicated the importance of several abiotic factors, including temperature, salinity, depth and fishing effort in controlling hogchoker occurrence. Temperature and salinity were also important in controlling hogchoker relative abundance. Furthermore, the GAM demonstrated that the relationship between species

abundance and particular abiotic factors varied across years. The constructed GAM, however, only explained approximately 15% of the variation in hogchoker abundance. Consequently, additional abiotic or biotic factors, such as benthic substrate, prey availability, competition and predation, not included in the full model may be important in controlling hogchoker abundance.

In chapter 3, I analyzed trends in hogchoker diet, both in the mainstem and shoal habitats of the Chesapeake Bay. This chapter represented the first effort to investigate hogchoker diet throughout the mainstem of the bay and across multiple seasons. Results from both graphical analyses and nonmetric multidimensional scaling indicated that hogchoker diet varied substantially across season, region and hogchoker size in the Chesapeake. These dietary trends are likely a consequence of prey availability and hogchoker seasonal movements. These findings, however, were not supported by an Analysis of Similarities, which did not demonstrate significantly different diet compositions across any factors. For season and hogchoker size, the absence of significant differences could be a consequence of the variability in the diet of individuals collected in the summer or comprising the intermediate size class.

Throughout my thesis, a key challenge was the analysis of ecological data, which typically exhibit complex, nonlinear relationships between factors. Furthermore, observational studies, such as CHESIMS and TIES, are often characterized by a large number of zero observations. As a consequence, these ecological data often do not meet the assumptions of parametric statistical tests and both semi- and nonparametric methods have been used as alternatives to traditional parametric models. Generalized additive modeling and nonmetric multidimensional scaling are two nonparametric methods that

make few assumptions about the distribution and nature of the data (Hastie and

Tibshirani 1990; McGarigal et al. 2000; Barry and Welsh 2002; Guisan et al. 2002). This

enhanced flexibility ultimately permits the data to demonstrate the relationship between

response and explanatory variables (Barry and Welsh 2002). Furthermore, generalized

additive modeling and nMDS enabled the investigation of the distribution and diet of the

hogchoker without the constraints of meeting the assumptions of parametric tests.

The final objective of my thesis was to quantify the trophic demand of hogchoker

in the Chesapeake Bay to gain insight of its role as a benthic predator in the ecosystem.

Estimates of hogchoker relative abundance, feeding incidence, ration and diet

composition were utilized to determine the percentage of macrobenthic production

consumed by hogchoker. Although hogchoker are year-round residents of the

Chesapeake Bay, relatively abundant and widely distributed, they appear to only

consume between zero and 0.1% of the standing stock biomass of particular

macrobenthic taxa. This small trophic demand likely indicates that hogchoker do not

have a substantial impact on the macrobenthic community of the bay. This insignificant

demand may be due to a small abundance of hogchoker compared to other benthic

feeders collected in the CHESFIMS survey. In summer CHESFIMS cruises, for

example, average hogchoker catch in each cruise comprised only 23.7% of spot

(*Leiostomus xanthurus*) catch, 2.5% of croaker (*Micropogonias undulatus)* catch and

5.1% of white perch (*Morone Americana*) catch (Curti, unpublished data).

The small trophic demand of hogchoker could also be a consequence of

underestimations of hogchoker daily ration or absolute abundance. The estimates of

absolute abundance utilized to quantify trophic demand only incorporated hogchoker

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present in the mainstem of the bay. Juvenile hogchoker, however, do not migrate into

saline waters during the summer and as a consequence, their biomass would be

underestimated in summer CHESFIMS cruises. Accordingly, additional work on the

quantification of hogchoker abundance both in the mainstem and associated tributaries of

the bay should be conducted to more precisely quantify the trophic demand of the

hogchoker on the Chesapeake Bay ecosystem.

APPENDIX: JUSTIFICATION OF THE USE OF A GENERALIZED ADDITIVE MODEL TO MODEL HOGCHOKER DISTRIBUTION IN THE CHESAPEAKE BAY

With the development of computer-intensive methods, new techniques have emerged that permit the modeling of complex, nonlinear relationships that are typical of ecological data. These techniques can also model data from observational studies, which are often characterized by a large number of zero value observations (Maravelias 1999; Barry and Welsh 2002). Abundance data are typically zero inflated and exhibit a greater proportion of zeros than expected from pure count data of a Poisson distribution (Welsh et al. 1996; Borchers et al. 1997; Barry and Welsh 2002). Fisheries surveys also typically exhibit zero inflated data, due to both the nature of count data and the patchy distributions of aquatic organisms (Maravelias 1999; Jensen et al. in press). This zero inflation is a form of overdispersion, where the empirical sampling variance of the response variable exceeds the variance predicted under the chosen statistical distribution of the data (Guisan et al. 2002). Multiple linear regression techniques, with appropriate data transformations to account for the underlying Poisson distribution of count data, can be utilized to investigate the relationship between species abundance and habitat variables. If the data are zero-inflated, however, assuming a true Poisson distribution will result in inference problems due to the violation of distributional assumptions including homogeneous variance and normal distribution of error terms (Welsh et al. 1996; Barry and Welsh 2002).

Generalized additive modeling is a semi-parametric regression technique that relaxes the assumptions of linear regression (Guisan et al. 2002). By utilizing a two-stage

approach, generalized additive models (GAMs) can be used to model zero inflated abundance data. The first stage of the analysis reduces abundance data to a binomial variable (presence/absence) and models probability of occurrence as a function of multiple covariates. The second stage incorporates only those stations where the species is present and models abundance as a function of environmental covariates. The covariates included in the second stage of the model do not have to be the same as those in the first stage. The predicted species abundance at a particular location is subsequently determined by multiplying together the results from both stages of the GAM.

In GAMs, the relationship between the response variable and predictors can be described with nonparametric smooth functions (Hastie and Tibshirani 1990; Maravelias 1999; Guisan et al. 2002; Wood and Augustin 2002). Each explanatory variable can be modeled with a unique smooth function, requiring only that the response variable be modeled as the sum of the smooth functions (Maravelias 1999; Stoner et al. 2001; Guisan et al. 2002). The use of nonparametric smooth functions enhances the flexibility of the GAM and ultimately allows the data to determine the relationship between response and explanatory variables by not confining relationships to a single probability distribution (Maravelias et al. 2000a; Stoner et al. 2001; Barry and Welsh 2002). The flexibility in the model, directly related to the amount of smoothing for each explanatory variable, can be selected by specifying the effective degrees of freedom. There must be a balance between the number of degrees of freedom and observations in the model. This balance can be achieved through the use of penalized regression splines, which allow a relatively large number of degrees of freedom but penalize the fit based on the degrees of freedom utilized, thereby preventing over-fitting of the model (Wood and Augustin 2002).

As a consequence of the incorporation of these smooth functions, GAMs are capable of modeling the complex relationships typically exhibited in ecological data, including the relationship between organism abundance and distribution with habitat variables (Stoner et al. 2001; Barry and Welsh 2002). Several studies have used GAMs to model this relationship (Swartzman et al. 1992; Swartzman et al. 1994; Swartzman et al. 1995; Maravelias et al. 2000a; Maravelias et al. 2000b; Stoner et al. 2001; Zheng et al. 2002) and to model the relationship between recruitment and both biotic and abiotic factors (Daskalov 1999; Cardinale and Arrhenius 2000). Through the expansion of the GAM into a two-stage modeling process, GAMs have been utilized to model the relationship between zero-inflated abundance data and environmental parameters (Borchers et al. 1997; Maravelias 1999; Barry and Welsh 2002; Piet 2002; Jensen et al. in press). A two-stage GAM has also been applied to stomach contents data to investigate patterns in salmon feeding and growth (Rand 2002).

The objective of the second chapter of my thesis was to quantify the relationship between hogchoker distribution and multiple habitat variables within the mainstem of the Chesapeake Bay. Across all years, however, hogchoker were not collected at over 79% of the sampled stations. Accordingly, a two-stage GAM was used to eliminate inference problems associated with the analysis of zero inflated data with traditional regression techniques.

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