# ABSTRACT

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| Title of Document: | **BIOENERGETIC AND ECOLOGICAL CONSEQUENCES OF DIET VARIABILITY IN ATLANTIC CROAKER *MICROPOGONIAS UNDULATUS* IN CHESAPEAKE BAY** |
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Atlantic croaker *Micropogonias undulatus* is a commercially and ecologically important bottom-associated fish that occurs in marine and estuarine systems from Cape Cod, MA to Mexico. I documented the temporal and spatial variability in the diet of Atlantic croaker in Chesapeake Bay and found that in the summer fish, particularly bay anchovies *Anchoa mitchilli,* make up at least 20% of the diet of croaker by weight. The use of a pelagic food source seems unusual for a bottom-associated fish such as croaker, but appears to be a crepuscular feeding habit that has not been previously detected. Thus, I investigated the bioenergetic consequences of secondary piscivory to the distribution of croaker, to the condition of individuals within the population and to the ecosystem. Generalized additive models revealed that the biomass of anchovy explained some of the variability in croaker occurrence

and abundance in Chesapeake Bay. However, physical factors, specifically temperature, salinity, and seasonal dynamics were stronger determinants of croaker distribution than potential prey availability. To better understand the bioenergetic consequences of diet variability at the individual level, I tested the hypothesis that croaker feeding on anchovies would be in better condition than those feeding on polychaetes using a variety of condition measures that operate on multiple time scales, including RNA:DNA, Fulton's condition factor (K), relative weight (Wr), energy density, hepatosomatic index (HSI), and gonadosomatic index (GSI). Of these condition measures, several morphometric measures were significantly positively correlated with each other and with the percentage (by weight) of anchovy in croaker diets, suggesting that the type of prey eaten is important in improving the overall condition of individual croaker. To estimate the bioenergetic consequences of diet variability on growth and consumption in croaker, I developed and validated a bioenergetic model for Atlantic croaker in the laboratory. The application of this model suggested that croaker could be an important competitor with weakfish and striped bass for food resources during the spring and summer when population abundances of these three fishes are high in Chesapeake Bay. Even though anchovies made up a relatively small portion of croaker diet and only at certain times of the year, croaker consumed more anchovy at the population level than striped bass in all simulated years and nearly as much anchovy as weakfish. This indicates that weak trophic interactions between species are important in understanding ecosystem processes and should be considered in ecosystem-based management.

# BIOENERGETIC AND ECOLOGICAL CONSEQUENCES OF DIET VARIABILITY IN ATLANTIC CROAKER *MICROPOGONIAS UNDULATUS* IN CHESAPEAKE BAY

By

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# Dedication

For my family

# Acknowledgements

# Table of Contents

# List of Tables

# List of Figures

# CHAPTER 1: RATIONALE

Estuaries are some of the most productive ecosystems in the world relative to their size in comparison to other aquatic ecosystems (Kennish 1986, Nixon 1988). The fates of this production are diverse, and include internal cycling within the estuarine foodweb (Baird and Ulanowicz 1989), exports to the coastal ocean (Boynton et al. 1995, Dame and Allen 1996), and removals of biomass by commercial and recreational fisheries (Blaber et al. 2000). Estuaries are important habitat for many fishes, particularly those that are of economic interest to humans. Some fishes may live their entire life within the estuary, while others use estuarine habitat during different life history stages or migrate into estuaries seasonally. Many fish spawn within or at the mouths of estuaries so that their young spend the first year of life or more within the estuary. For this reason, estuaries are thought of as "nursery grounds" because they promote high growth rates, provide refuge from predators, effectively reduce competition, and thus, increase survivorship and fitness of young fish (Able and Fahay 1998, Miller et al. 1985). Some of the most ecologically and economically important fishes of the southeast Atlantic Ocean use estuaries as juveniles (Miller et al. 1985).

The study of estuaries has increased dramatically since the 1950s, in part because of an increase in development within the watersheds of estuaries and the growing anthropogenic impacts upon these coastal waters (Kennish 1986). The structure and function of many estuaries has changed substantially in response to human population growth in many ways. The increase in eutrophication is probably the most widely documented change to estuarine and coastal waters worldwide (Diaz

and Rosenberg 1995, Karlson et al. 2002, Kemp et al. 2005). While some eutrophication can actually increase production in estuaries (Grimes 2001, Iverson 1990, Nixon and Buckley 2002), hypoxia or anoxic events caused by intense eutrophication can negatively affect estuarine organisms in many ways. The most obvious effect of hypoxia or anoxia is direct mortality if the animal cannot move to find oxygenated water. As a result, chronic hypoxia or anoxia causes shifts in benthic community composition to one consisting of primarily small, opportunistic species. Fish can also suffer direct mortality in anoxic or hypoxic events, but many can move to avoid anoxia or hypoxia (Tyler and Targett 2007). Eby et al. (2005) identified additional ways that hypoxia negatively impact demersal fish. First, hypoxic events restrict the area suitable to fish which effectively limits the amount of food available for foraging. This contraction of habitat not only limits food resources, but causes density dependent reduction in growth rates. These combined effects effectively decrease fish production, particularly of bottom-associated fish.

Some have hypothesized that eutrophication changes estuarine ecosystems so that the ratio of pelagic to demersal fish is higher in systems with eutrophication-induced degradation (Caddy 2000, de Leiva Moreno et al. 2000). It follows that with fewer benthic food items there would be fewer groundfish that rely on these prey items. However, the enriched pelagic waters above may still flourish with primary productivity, zooplankton and the pelagic fish which feed on the pelagic food web. Although landings data support this hypothesis, this hypothesis is difficult to test because fish in coastal ecosystems are also subject to high levels of fishing mortality. Furthermore, the ubiquitous nature of seasonal migration makes drawing firm

2

conclusions regarding overall energy budgets difficult.  A change in the ratio of

pelagic to demersal fish may be the result of "fishing down" or "fishing through" the

food web (Essington et al. 2006, Pauly et al. 1998).  A shift in community structure

induced by eutrophication from a more benthic to more pelagic food web may be

manifested in changes in diet and trophic linkages within the ecosystem.

Additionally, reductions in food sources may force fish to shift their distribution

and/or feeding habits (Pihl 1994, Pihl et al. 1991, Pihl et al. 1992, Powers et al. 2005).

For example, Powers et al. (2005) found that Atlantic croaker consumed less-

energetically rich food following hypoxic events in a North Carolina estuary.

Frequently coincident with eutrophication are high levels of fishing which

may act synergistically effect with eutrophication to alter ecosystems (Deegan et al.

2007).  Fishing and its impact on the ecosystem have been shown to alter trophic

interactions (Jackson et al. 2001, Pandolfi et al. 2003).  The act of fishing itself, by

commercial trawlers can alter benthic community structure (de Juan et al. 2007b,

Kaiser et al. 2006, Simpson and Watling 2006, Tillin et al. 2006), biogeochemical

cycles in the benthic and pelagic food web (Allen and Clarke 2007), and the diets of

demersal fish (de Juan et al. 2007a).  Fishing may affect trophic processes in many

ways.  Some have suggested that the failure of some stocks to recover may be a result

of competitive release (Garrison and Link 2000, Persson and Hansson 1998).

Similarly, cascading effects have been detected in aquatic ecosystems following the

removal of top predators (Campbell and Pardede 2006, Parsons 1992)

It is clear from these studies that aquatic ecosystems and especially estuaries

are being impacted and altered at multiple trophic levels.  The changes in estuarine

and coastal ecosystems have been an important motivator for change from single species to ecosystem-based approaches to fisheries management. Traditional single species management has often used maximum sustainable yield (MSY) to set biological reference points for each fish species. This practice assumes that there is some surplus production of the stock that is available for harvest and by extension, is not needed by the ecosystem. However, studies have shown that piscivory can exceed MSY (Link and Garrison 2002). MSY estimated for several species simultaneously to include technical or predatory interactions is often lower than the values estimated with single species models. Achieving MSY for all interacting species is likely not possible (Jennings et al. 2001, Link 2002). In addition to the use of MSY, single species management often ignores competitive interactions between species and how the removal of one species causes unexpected changes in ecosystem structure (May et al. 1979, Yodzis 1994).

Ecosystem-based management also attempts to account for climate-induced changes in the ecosystem. Although managers cannot control environmental variability, understanding these processes will help incorporate precautionary measures into the aspects of fisheries that can be controlled. There is a large body of research on regime shifts in aquatic systems (Alheit and Niquen 2004, Bailey 2000, Steele 2004) and the role of fisheries in observed regime shifts (Collie et al. 2004, Cury and Shannon 2004, Reid et al. 2001, Rothschild and Shannon 2004). Accordingly, the basic science informing management must shift its focus from one of population dynamics to community ecology in order to avoid unexpected ecosystem changes (Mangel and Levin 2005). A fundamental difference between

single species and ecosystem-based approaches to fisheries management is the requirement of the latter to describe and quantify trophic relationships between elements in fishery ecosystems (Chesapeake Bay Fisheries Ecosystem Advisory Panel 2006).

Traditional single species management models often assume constant natural mortality (M). However, in an ecosystem-based fisheries management approach, M is permitted to vary, especially in response to predation. Ecosystem-based approaches also take into account the effects of variability in prey resources for commercially important fishes. For example, the liver condition of cod has been shown to vary with capelin abundance, a preferred prey of cod (Yaragina and Marshall 2000). Consequently, liver condition can be used as a bioenergetic index of reproductive potential, thereby improving the stock-recruitment relationship which is often used to delineate biological reference points (Marshall et al. 1998, Marshall et al. 2006). This is one example of how ecosystem-based approaches and an emphasis on community ecology can improve single species assessment models as the transition is made from single species to multispecies to ecosystem-based management.

Ecosystem-based management is of particular interest in Chesapeake Bay, an ecosystem that yields more than $100 million in landings of fish and shellfish (Miller et al. 1996). The states of Virginia, Maryland, Pennsylvania, District of Columbia, the Chesapeake Bay Commission, and the US Environmental Protection Agency established an aggressive plan to restore and protect the Chesapeake Bay ecosystem codified with the Chesapeake Bay 2000 Agreement. The goal was to implement

5

ecosystem-based multispecies management for economically important species by 2007. Many goals to improve the health of Chesapeake Bay were set for 2010, including restoration of oysters, seagrasses, wetlands, and a reduction in nutrient and sediment loads. Much of the emphasis for fisheries management included developing ecosystem-based multispecies stock assessments in Chesapeake Bay. However, these models are data intensive requiring basic data on food habits, consumption, biomass, and ecotrophic efficiency that do not exist for all fish species within the bay. Basic research on the ecology of many fishes is needed for inputs into these models. This requires that we understand the ecology of not only commercially important fish, but ecologically important fish.

Atlantic croaker *Micropogonias undulatus* (hereafter croaker) is a commercially and ecologically important bottom-associated fish that occurs in marine and estuarine systems. Croaker ranges from Cape Cod, MA to Mexico, although it is not common north of New Jersey, as its northern distribution is restricted by low water temperature. It is one of thirteen species of sciaenids known to occur in the Chesapeake Bay. Croaker is ranked as one of the top ten commercial and top ten recreational fisheries on the East and Gulf coast and is the most important recreational fishery in Chesapeake Bay in terms of number and biomass harvested (www.st.nmfs.gov). Croaker is managed by the Atlantic States Marine Fisheries Commission (ASMFC). Croaker landings and abundance have fluctuated over the last 50 years, but have risen in the past ten years (Figure 1.1). Landings and recruitment are thought to vary due to climatic effects and tend to be higher when

6

temperatures are warm (Hare and Able 2007, Lankford and Targett 2001, Wood 2001, Joseph 1972, Dovel 1968).

Throughout its range, Atlantic croaker spawns at the mouth of bays and estuaries and in the coastal ocean from August to November. In the Chesapeake Bay region, there is an extended spawning season in coastal waters, although limited spawning may occur within the estuary (Barbieri et al. 1994). Spawning occurs from July to December, peaking in late August or September (Barbieri et al. 1994). Larval croaker may enter Chesapeake Bay as early as July or August in some years, but typically attain peak abundance in September in the lower bay (Nixon and Jones 1997, Norcross 1991). Immigrating larvae are typically 20 - 26 days old (post hatch) and are 5-7 mm standard length, SL (Nixon and Jones 1997). As they move into the bay and grow, croaker transition from a pelagic to a demersal habit. Young of the year (YOY) croaker spend their first year of life in bays and estuaries, moving to deep water in the winter. Larvae likely move into the estuary as a result of a combination of behavioral and physical processes (Hare et al. 2005, Norcross 1991). Hurricanes have been shown to increase the ingress of larval croaker into Chesapeake Bay in the fall (Montane and Austin 2005). However, overwintering temperatures are better predictors of recruitment success in croaker (Hare and Able 2007). Lankford and Targett (2001) found that juvenile croakers were intolerant of temperatures below $3^{\circ}C$, but cold tolerance increased slightly with increasing salinity. Thus, year class strength is generally low when winter water temperatures are below $3^{\circ}C$. Age-1 croakers leave the bay with adults in the following fall. Barbieri et al. (1994) found

that 85% of croaker are mature at age 1 and all are mature by age 2. However, others report that croaker mature at age 2 or 3 (Murdy et al. 1997).

Numerous diet studies have been conducted on croaker. Several studies describe the diet of larval (Govoni et al. 1983) and juvenile croaker (Nemerson 2002, Sheridan 1979, Homer and Boynton 1978). Sheridan (1979) characterized the diet of YOY croaker and found that croaker of all stages rely heavily on polychaetes. Small croaker (10-69mm) also consumed detritus, nematodes, insect larvae and amphipods. In the same study, croaker between 40-89 mm TL changed food habits and relied more heavily on large organisms such as mysids and fish (Sheridan 1979). Large YOY croaker specialized on food items that were abundant locally and diet was highly dependent on the area of sampling. For example, croaker from shallow stations ate insect larvae, detritus, amphipods and small crustaceans, whereas croaker from deep-water stations ate polychaetes, shrimp, and fish. Nemerson and Able (2004) reported the diet of juvenile croaker in Delaware Bay. These authors indicate a diet dominated by polychaetes and crustaceans (80%) with fish comprising < 4%. In Chesapeake Bay, Homer and Boynton (1978) reported that the diet of croaker (<165mm) consisted of mostly polychaetes (>80% by weight) and observed no fish consumption. Adult croaker has been described as opportunistic bottom-feeders that occasionally eat small fishes (Murdy et al. 1997, Hildebrand and Schroeder 1928). Hildebrand and Schroeder (1928) noted that of 392 fish whose stomach contents were examined only three contained fish. However, several studies have found that the amount of piscivory increases as croakers obtain larger sizes (Darnell 1961, Overstreet and Heard 1978, Sheridan 1979). Recent studies in Chesapeake Bay also

8

suggest a primarily benthic diet, but with some piscivory (Bonzek et al. 2007). From these studies it is clear that the trophic ecology of croaker, with respect to ontogenetic, seasonal and spatial patterns is variable and remains poorly understood. More significantly, the consequences of this variability in diet to individual fish, the croaker population, and the ecosystem have been completely ignored.

Since 2001, the diets of croaker have been characterized in the Chesapeake Bay as a part of a multispecies fisheries-independent survey of the Bay's fish community (http://hjort.cbl.umces.edu/chesfims.html). In our diet analysis, 20-40% of croaker diet by weight during summer months consists of bay anchovy *Anchoa mitchilli* and other small fish. Yet, fish caught in the spring and fall have relatively few fish in their stomachs. This prey switching, particularly the use of fish as prey in summer months, has been underemphasized in previous studies of croaker. Although croaker is not traditionally considered a piscivore, fish prey may serve as an important energy source for croaker particularly before migrating and spawning in the fall. Because many other fish such as weakfish, striped bass, bluefish, summer flounder and white perch also consume large amounts of anchovy, croaker may compete with other piscivores for these prey items. Thus, the degree of piscivory in croaker may have implications for the ecosystem and ecosystem-based approaches to fishery management.

A full understanding of croaker ecology and exploitation is relevant to the change from single species to multispecies and ecosystem-based management given the important role of croaker in many estuarine systems. In addition, croaker is a very abundant species in the Bay, but because its diet is variable and the species is not

as well studied as other finfish species, its role in the Chesapeake Bay food web is poorly understood.  Understanding how diet affects the growth, condition, and ultimately population dynamics of a species is fundamentally a bioenergetic question. Bioenergetic models link basic fish physiology and behavior with environmental conditions and when combined with population dynamics lead to system-level estimates of fish production and population consumption (Ney 1990).  Moreover, understanding trophic interactions among species helps quantify potential competitive and predatory interactions among components of the ecosystem.  Thus, the application of bioenergetic models to ecosystem-level questions is a holistic way of understanding how energy is used by an organism in the system, and how that energy propagates from food source to predator to multiple predators and finally ecosystem.

The overall objective of this study was to test the hypothesis that seasonal and annual variation in croaker diet has bioenergetic consequences to individual croaker and to the Chesapeake Bay ecosystem.  First, I documented the seasonal and annual variation in croaker diet and distribution using multivariate analysis and geostatistical techniques.  Subsequently, I tested the hypothesis that variation in croaker diet influences the distribution of this species in Chesapeake Bay using generalized additive models.  To better understand the bioenergetic consequences of diet variability at the individual level, I tested the hypothesis that croaker feeding on anchovies would be in better condition than those feeding on other food resources using a variety of condition measures that operate on multiple time scales.  Then, I developed and validated a laboratory-based bioenergetic model for Atlantic croaker. The application of this model allowed me to estimate population consumption of

Atlantic croaker in 2002-2005 and compare population level consumption of croaker

with weakfish and striped bass while all three fish species are residents of

Chesapeake Bay.

Figure 1.1: Coastwide Atlantic croaker landings (1950-2002) and biomass (1973-2002).
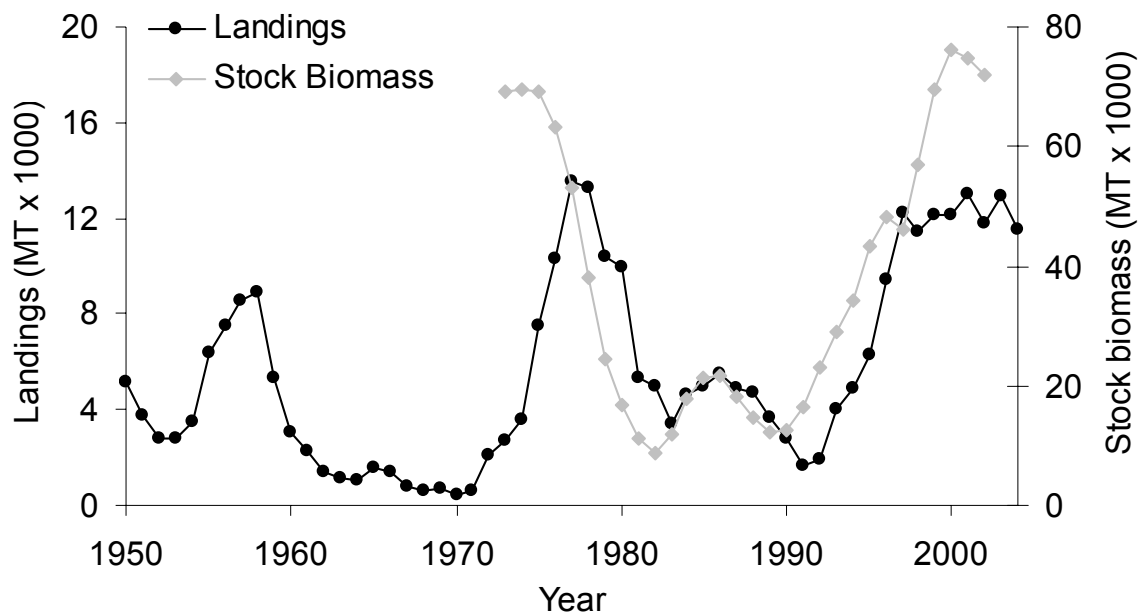
# CHAPTER 2: DISTRIBUTION AND DIET OF ATLANTIC CROAKER *MICROPOGONIAS UNDULATUS* IN CHESAPEAKE BAY

## INTRODUCTION

The relative effect of biotic and abiotic factors in determining the distribution and diets of organisms is a fundamental question in ecology. The distribution and abundance of an organism is ultimately determined by its ecological niche. Hutchinson (1957) was the first to describe and stress the importance of the multifaceted niche as the ecological space in which an organisms lives, building on the works of Grinell (1917) and Elton (1927). While Grinell (1917) was the first to use the term "niche" to describe the geographic location of an organism in its environment, Elton (1927) emphasized food availability and predators in determining the ecological niche of a species. Hutchinson in a sense combined the ideas of these and other works and conceived the ecological niche as defined by many biotic and abiotic variables. As such he defined a niche as a multifaceted "hypervolume" or a multidimensional space occupied by an organism.

Estuaries are good places to study to understand the complexities of niche theory. These highly dynamic physio-chemical environments are influenced by energetic tidal flows and wind-induced turbulence with strong seasonal effects and variability in freshwater input (Kennish 1986, Mann and Lazier 1996). Because of their characteristic circulation patterns, there are strong gradients that provide the full spectrum of physical and chemical properties that might define an organisms' niche.

For example, the full range of salinities are found in estuaries as freshwater rivers and tributaries flowing out of the estuary meet and mix with marine waters flowing into the estuary. Thus, physiological tolerances in defining the niche can be determined. However, estuaries introduce challenges in understanding an organism's niche because these systems are not closed systems and have strong annual and seasonal changes in temperature, salinity, and even dissolved oxygen.

In estuarine environments three abiotic factors: temperature, salinity and dissolved oxygen, are likely the dominant regulators of fish distributions (Jung 2002, Lankford and Targett 1994, Rueda 2001) and their prey (Bottom and Jones 1990, Seitz and Schaffner 1995). These studies exemplify the rich body of research on abiotic factors that affect species distribution. Although temperature and salinity may influence population abundance and distribution based on the physiology of each species, substrate and habitat structure are also important for fish feeding and may influence distribution (Gibson and Robb 1992, Methratta and Link 2006, Stoner et al. 2001). Such studies are important because they are informative at the scale on which a fishery operates and can be used in management decisions such as delineating essential fish habitat and marine reserves (Methratta and Link 2006). However, few studies exist that attempt to quantitatively delineate the biotic and abiotic factors that influence species abundance and distribution.

Atlantic croaker *Micropogonias undulatus*, hereafter croaker, is a common, abundant bottom-associated fish species that is distributed in marine and estuarine systems from the Gulf of Mexico to Delaware Bay (ASMFC 1987). Numerous diet studies have been conducted on croaker. Adult croaker has been described as

14

opportunistic bottom-feeders that occasionally eat small fishes (Murdy et al. 1997, Hildebrand and Schroeder 1928). Young of year (YOY) croaker rely heavily on polychaetes in their diets, but also consume other benthic food such as detritus, nematodes, insect larvae and amphipods (Homer and Boynton 1978, Nemerson 2002, Overstreet and Heard 1978, Sheridan 1979). Croaker appear to change feeding habits as they get larger, relying more heavily on large organisms such as mysids and fish (Nemerson 2002, Overstreet and Heard 1978, Sheridan 1979). Hildebrand and Schroeder (1928) noted that of 392 fish whose stomach contents were examined only three contained fish. Studies also indicate strong ontogenetic patterns in diets. These data studies suggest less reliance on benthic prey than is typically expected of this demersal sciaenid (Chao and Musick 1977). Despite many diet studies the trophic ecology of croaker and the associated ontogenetic, seasonal and spatial patterns in diet remain poorly understood. More significantly, the consequences of this variability have been completely ignored particularly with regard to the spatial distribution and abundance of croaker in the Chesapeake Bay estuary.

The objectives of this study were first, to describe the distribution and diet of croaker in the Chesapeake Bay and secondly, to understand how distribution and diet are related. In quantifying these patterns, I seek specifically to determine the role of abiotic and biotic factors in determining both aspects of croaker ecology. Quantification of the patterns and trends in diet is challenging from both a sampling and statistical view points (Cortes 1997, Tirasin and Jorgensen 1999). No single approach or technique fully captures the spatial and temporal diversity in dietary patterns. Accordingly, I used multivariate analyses to quantify seasonal, regional and

inter-annual patterns in diet. Subsequently, I used a two-stage generalized additive model (GAM) to determine biotic and abiotic factors that influence spatial distribution. The first stage of the GAM predicts the probability of occurrence based on environmental variables using presence/absence data as the response variable. The second stage of the GAM predicts the abundance of croaker but only using stations where croaker were present. I have used GAMs to relate distribution and diet because they allow for linear and nonlinear relationships between explanatory and response variables. GAMs have been widely used to quantify distributions of estuarine organisms (Jensen et al. 2005, Jowett and Davey 2007, Stoner et al. 2001). However, few have attempted to connect diet and distribution using GAMs to elucidate the relative importance of environmental factors and the prey field to understand how each influences distribution. Using GAMs I hypothesize that 1) croaker presence/absence is determined by physiological tolerances to abiotic factors and, 2) that croaker abundance is influenced by availability of suitable prey. Accordingly, abiotic factors should be the most important factors describing croaker occurrence in the 1st stage of the GAM and biotic factors the most important in predicting croaker abundance in the 2$^{nd}$ stage of the GAM.

**METHODS**

*Data collection*

Croaker and environmental data were collected from 1995-2005 as part of two fishery-independent sampling programs in the Chesapeake Bay. The Trophic Interactions in Estuarine Systems (TIES) program surveyed the fish community in Chesapeake Bay from 1995- 2000 (Jung and Houde 2003). Subsequently, the

16

Chesapeake Fishery-Independent Multispecies trawl survey (CHESFIMS) extended the TIES sampling protocols for the fish community from 2001-2005. In both programs, research cruises occurred over 5-7 day periods three times annually, the only difference being that cruises occurred in May, July, and October from 1995 to 2000 and in May, July, and September from 2001 to 2005. During both programs additional cruises supplemented the three annual cruises opportunistically. The survey design changed very little during the eleven year time series. Trawl stations in the TIES program were located along 15 fixed transects spaced approximately 18.5 km (10 nm) apart from the head of the Bay to the Bay mouth to ensure bay wide coverage (Jung and Houde 2003). Within each season, 11 of the 15 transects were occupied. Transects were identified as falling within one of three strata: upper, middle, and lower Bay (Figure 2.1). During CHESFIMS surveys, sampling at fixed stations was supplemented by additional stations allocated proportional to the area of each stratum.

The individual strata have distinctive characteristics, and their boundaries broadly correspond to ecologically relevant salinity regimes. The upper Bay is generally shallow, with substantial areas less than 5 m in depth, and well mixed waters with high nutrient concentrations. The bottom topography in the mid Bay includes a narrow channel in the middle of the Bay with a stratified water column and broad flanking shoals. This region has relatively clear waters and experiences seasonally high nutrient concentrations and periods of hypoxia. The lower Bay has the clearest waters, greatest depths and lowest nutrient concentrations (Kemp et al.,

1999). The strata volumes are 26,608 km$^3$ (Lower), 16,840 km$^3$ (Mid) and 8,664 km$^3$ (Upper).

Survey deployments throughout the 11-year time series followed the TIES trawling procedures (Jung and Houde 2003) with standardized 20-minute oblique, stepped tows conducted at each station using midwater trawls of the same design.   A midwater trawl with an 18-m$^2$ mouth-opening with 6-mm cod end was deployed to collect primarily pelagic and benthopelagic fishes.  Oblique tows of the net were fished from top to bottom, and were 20 minutes in duration.  The trawl was towed for two minutes in each of ten depth zones evenly distributed throughout the water column from the surface to the bottom, with minimum trawlable depth being 5 m. The section of the tow conducted in the deepest zone sampled epibenthic fishes close to or on the bottom. The remaining portion of the tow sampled pelagic and neustonic fishes.  A minilog was attached to the float line of the net and measured depth, temperature, and time during each tow.  The depth profile from the minilog was inspected after each tow to ensure that the trawl was deployed in the manner described above and that the net fished the bottom portion of the water column, important in the case of the demersal croaker.  All tows were conducted between 18:00 and 7:00 Eastern Standard Time to minimize gear avoidance and to take advantage of the reduced patchiness of multiple target species at night.   At each station, a CTD was deployed to measure dissolved oxygen, salinity, and temperature in the water column.

Catches at every station were identified, enumerated, measured and weighed onboard.  For each species, all fish or for large catches a subsample of 50-100 fish

were measured (total length in mm). Total weight of the catch of each species was measured. Croaker was one of the most frequently caught species caught in this time series. Croaker from the 2002-2005 cruises were collected from each tow when present and were frozen for subsequent processing in the laboratory. At each station, a CTD was deployed to measure dissolved oxygen, salinity, and temperature throughout the water column. Data from the CHESFIMS collections were used to map spatial distributions and describe diets. Data from the combined TIES and CHESFIMS collections were used to develop two-stage GAM models to predict croaker distributions.

*Spatial distribution*

To visualize the spatial distribution of croaker, spatial maps of croaker were developed. I modeled adult croaker, defined as croaker greater than 100mm because of the sporadic catches of YOY croaker. There were many stations where no croaker were caught, causing the data to be zero-inflated. Thus, to adequately model the spatial distribution of croaker I used indicator kriging to map the probability of croaker occurrence in the mainstem of the bay. Indicator kriging in this application modeled presence/absence data rather than abundance data and does not require the data to meet the assumptions of normality or stationarity (Chica-Olmo and Luque-Espinar 2002). The abundance variables are transformed to categorical presence/absence variables before the kriging process by picking a threshold level, in this case an abundance equal to one fish. Points above this threshold are given a value of one and points below are given a value of zero. Thus, indicator kriging is

19

robust to outliers (Journel 1983). This analysis provides maps of probability of occurrence, rather than spatial abundance estimates of Atlantic croaker.

Maps were developed for each of the three annual CHESFIMS cruises from 2002-2005 using the indicator kriging option in ArcMap using a spherical semivariogram in all cases. The semivariogram was adjusted by changing the number of nearest neighbors and geometry of the search sectors in ArcMap (v8.1 ESRI Corp. Redlands, CA). By changing these parameters, the model with the lowest Root Mean Square (RMS) and lowest average standard error was chosen to represent croaker distribution. In most cases, the search geometry had four sectors with a $45^o$ offset.

*Diet analysis*

Frozen croaker collected during the CHESFIMS cruises (2002-2005) were thawed and individual fish were weighed (wet weight, g), measured for total length (TL, nearest mm), and their otoliths and stomachs removed. To quantify diets, the preserved stomach was blotted dry and weighed with contents intact. The stomach contents were removed and the remaining stomach tissue reweighed. The dissected stomach contents were examined and quantified under a dissecting microscope at 10-40x magnification. Prey items were identified to the lowest taxon feasible. Each prey type was weighed and the number of individuals determined. Diet was quantified using percent composition by weight (%W). Mean proportional contribution of a prey type by weight was calculated for each experimental unit or station with a two-stage clustering scheme (Buckel et al. 1999, Cochran 1977). For each group, i, the total weight $w_{ik}$, of prey item k was divided by the total weight of

all identifiable prey items at the station, $w_i$. Thus, the mean proportional contribution of a prey type ($W_k$) was calculated as:

$$W_k = \Sigma M_i(w_{ik}/w_i)/ \Sigma M_i$$

where $M_i$ is the number of fish >100mm caught at the station. This method was used to calculate %W for two clustering schemes, 1) where group (i) were equal to the year and strata and 2) where the group (i) was simply the cruise (or year and season).

I used simple graphic analyses and summary statistics to describe croaker diet composition by age, season, region and year. To quantify patterns in croaker diets more fully, I applied Canonical Correspondence Analysis (CCA) to analyze patterns in %W (ter Braak 1986). CCA is an ordination technique, but unlike ordination approaches such as principal components analysis, CCA does not seek to explain all the variation in the data, rather it seeks to explain only that variation directly associated with specified factors. For my analyses I examined contributions of year, season, and strata of the bay. Analyses were conducted using the Vegan package (Version 1.8.8) in R (Oksanen et al. 2007).

To understand trends in croaker diet composition by size, two-stage clustering was not used and data was pooled from 2002-2005. Instead total weight of each prey item was divided by the total weight of all prey items to arrive upon %W for each individual fish. Subsequently, %W for each individual was averaged by 10mm length class and displayed graphically. To determine if the incidence of anchovy in croaker stomachs exhibited diel trends the average total weight (not %W) of anchovy in stomach was plotted against the time of capture for each season. The average weight of anchovy in stomachs was also compared between males and females using

21

a non-parametric Mann-Whitney U test. For stomachs collected in 2004 and 2005, fish were assigned one of three levels of digestion; high, medium, or low to determine if anchovies in stomachs were the result of net-feeding. Percent occurrence (% O) is also reported for each prey category for individual fish pooled from 2002-2005 and is calculated by dividing the number of stomach in which a prey item occurred by the total number of stomachs.

*Effect of environmental variables and diet on croaker presence and abundance*

To understand the biotic and abiotic factors that influence spatial distribution of adult croaker as illustrated in maps produced by indicator kriging, I developed two-stage Generalized Additive Models (GAMs). I chose four environmental parameters and two biotic parameters to include in the GAM. The parameters selected were chosen to reflect parameters believed to influence the distribution of croaker. Salinity, temperature, and dissolved oxygen were averaged over the entire water column for each CTD cast at each station. Maximum depth was determined as the maximum depth from the CTD cast. Average grain size was estimated using data from the Chesapeake Bay Program data collected from 1975-1981. Grain size was reported on $\log_2$ (phi) scale where a value of 1 is the grain size for gravel and a grain size of 8 and above corresponds to clay. Most of the area of the Chesapeake Bay floor consists of sand (Phi ~0 to 4). The locations of stations at which sediment analyses were conducted differed from TIES and CHESFIMS stations. Therefore, a map of interpolated phi values for the entire Chesapeake Bay mainstem was created. Subsequently, I overlaid the TIES and CHESFIMS station locations on the interpolated grain size map and the appropriate interpolated values of phi were

22

obtained using Hawth Tools (http://www.spatialecology.com/htools/) in ArcGIS
software.

Maximum depth and grain size are physical properties that may represent a
habitat quality that croaker prefer. However, I have interpreted these variables as
proxies for benthic food resources available to croaker. Anchovy biomass was also
used as a biotic variable because it is a frequent food item in adult croaker stomachs.
Anchovy biomass was log transformed so that the data would be normally distributed
and values would be within an order of magnitude of the other variables in the model.
The Pearson correlation coefficients among these variables were quantified to
understand the relationships among biotic and abiotic parameters used in the model.

I first conducted a two stage GAM for data pooled over all years (1995-2005)
and seasons to explore broad trends in distribution. The predictions from the two
stage GAM using pooled data allowed evaluation of the method to predict croaker
abundance. However, the purpose of the two-stage GAM was to determine factors
that influence distribution other than seasonal migrations as timing of seasonal
migrations can be easily discerned from distribution maps. Therefore, I conducted
three separate two stage GAMS for spring, summer, and fall to understand factors
that influence croaker distribution on a shorter temporal scale.

To evaluate how important each factor was in predicting croaker presence and
secondarily abundance I took 100 random samples of 79% of the data (n=1000), fit
the GAM, and then tallied the number of times a parameter was significant. Those
factors that were consistently significant in the GAMs were considered more
important factors in determined croaker distribution. All statistical analysis was done

in R (Version 2.4.1) using the mgcv package (Wood 2007). It should be noted that in the mgcv library the degree of smoothing is part of model fitting so rather than set the degrees of freedom a priori, the best model is chosen in part by changing the degrees of freedom. Model fits with more degrees of freedom indicate more "curviness" and the overall model fit is penalized by high degrees of freedom.

**RESULTS**

*Spatial distribution*

The incidence of croaker occurrence exhibits seasonal and annual variation (Figure 2.2). However, Atlantic croaker were consistently located in the lower to middle part of the Chesapeake Bay. As indicated by the overall low probabilities of occurrence in spring cruises, there are relatively few croaker in the Bay in the spring as adult croaker are just beginning to migrate into the Bay. In the summer months, there are higher incidences of occurrence with large aggregations of croaker in the low to mid section of the bay. However, in some years - notably 2002 and 2003, there is another aggregation of croaker in the Upper Bay.

*Diet Analysis*

Eleven categories of prey were recognized in croaker diets collected between 2002 and 2005 (Table 2.1). Overall, polychaetes were the dominant component of croaker by weight (61.5%) and by occurrence (83.6%). Anchovy (8.9%) and mysids (8.2%) followed polychaetes in importance by weight. However, in combination

mysids, amphipods, and other benthic organisms were more common in croaker

stomachs than anchovy.  Detritus and miscellaneous pelagic prey were the least

common food items and in many years were not recorded in stomachs at all.  The diet

of Atlantic croaker varied annually and seasonally (Figure 2.3).  Croaker consumed

more anchovies, fish, and mysids in the summer and fall of several years.  In the

summer, at least 20% of the diet of croaker consistently consisted of anchovies and

fish.  In particular, in the summer of 2002, about 50% of the diet of croaker by weight

consisted of anchovy in the middle strata of the bay.

The CCA of croaker diet explained approximately 4.1% of the data, but

reinforced annual and seasonal trends (Figure 2.4).  Polychaetes and other organisms

which were consistently present in croaker stomachs were located centrally in the

ordination.  Anchovy, fish, and detritus occurrence in diet was attributable to most of

the explained variation on an interannual basis, as reflected by the strong coherence

of these three prey categories and the year variable in the ordination.  The presence of

crabs in croaker diet was more strongly associated with season than with region, but

the coherence was not strong.  In general, it appears that bivalves were more

frequently eaten in the upper part of the Bay and shrimp in the lower part of the Bay

(Figure 2.3).

Correlations of environmental variables (temperature, salinity, dissolved

oxygen, and grain size) with prey categories were tested, but all correlation

coefficients were very low and only one comparison was significant at the $P=0.001$

level (Bonferroni adjustment, $P=0.05/44=0.001$).  Proportion of amphipods in diets

was positively correlated with salinity ($r=0.246$, $P=0.001$), indicating that amphipods

are consumed in waters of higher salinity, perhaps in the lower Bay. Grain size and other benthic prey category were positively correlated (r=0.17, P=0.0248). Dissolved oxygen and %W of anchovy was weakly negatively correlated (r=-0.15, P=0.0468).

There was an ontogenetic change in croaker diets with small croaker eating small crustaceans, particularly amphipods (Figure 2.5). As croaker got larger their diet seemed to become more diverse, but this may in part be a result of a greater number of individual stomachs examined in moderate size classes. Size classes were pooled for fish <100m and >390 because of small sample size. Larger croaker tended to have higher proportion of anchovies and fish in their diet. Polychaetes were the staple diet item in all size classes.

The weight of anchovy in the stomachs of croaker was highest following sunset in spring and summer (Figure 2.6). In the spring, the weight of anchovy in croaker stomachs was also high near sunrise. However, this trend was not seen in other seasons. In contrast, there did not appear to be any diel trend in polychaetes consumption. The high incidence of anchovies in the diets did not appear to be the result of net-feeding. If anchovy feeding were primarily a result of net-feeding, a high percentage of anchovies found in the stomachs of croaker should be in a very low state of degradation. However, there was no difference in the percentage of anchovies in high (33.3%), medium (33.3%), or low (33.3%) degradation states.

*Effect of environmental variables and diet on croaker presence and abundance*

Croaker occupied waters of the Bay exhibiting a wide range of temperatures, salinities, and dissolved oxygen (Figure 2.7). The log of croaker abundance was weakly, but significantly positively correlated with salinity and negatively correlated

with grain size (Table 2.2). Croaker biomass was not significantly correlated with any other factors examined and appeared to be present and abundant at a wide range of values for all physical parameters examined (Figure 2.3). There were several correlations between variables used in the GAMs (Table 2.2). Salinity was negatively correlated with dissolved oxygen and grain size, but positively correlated with depth, croaker biomass, and anchovy biomass. The significant negative correlation with grain size can be explained by the estuarine gradients in both salinity and grain size from the freshwater input at the head of the estuary to the mouth of the bay. Grain size decreases from large to small grain sizes in general from the head to the mouth of the bay (Figure 2.8). Other correlations with salinity were relatively low. The correlation between dissolved oxygen and temperature was relatively high which can be explained by the decrease in oxygen solubility as temperature increases. Interestingly, salinity was correlated with both anchovy and croaker biomass, reflecting the high abundance of croaker in the lower to middle parts of the Bay (Figure 2.2).

Bootstrapping each stage of the GAM with data pooled over all seasons indicated that of all the included main effects, croaker presence was most influenced by temperature and salinity when year and the interaction of temperature and salinity were not included in the model (Table 2.3). In 100 iterations, temperature was significant at the $p=0.01$ level 100% of the time and salinity 93% of the time. However, when year and the interaction of temperature and salinity were included, the main effects of both temperature and salinity were significant only 16 and 12% of the time in predicting croaker presence respectively. This suggests that the main

effects of temperature and salinity are reflective of the seasonal migrations of croaker. Interestingly, anchovy biomass was a predictor of croaker presence in every run with or without year effects included in the model.

In the second stage of the model in which croaker abundance was modeled, temperature and salinity were again important factors in the model when the effect of year or the interaction of temperature and salinity was not included (Table 2.3). In contrast to the first stage bootstrapping results, when year and the interaction of temperature and salinity were included in the model, the main effects of temperature and salinity remained the most important factors in predicting abundance. While anchovy biomass and grain size were frequently incorporated in the 1st stage GAM, these factors were rarely significant in predicting croaker abundance in the 2nd stage of the GAM. Dissolved oxygen was never a significant factor for either the 1st or 2nd stage GAM. Depth was occasionally a significant factor in the 1st stage, but never in the 2nd stage.

After this bootstrapping exercise on 100 subsets of the data, a two stage GAM was run with all data (n=1258) to evaluate the predictive ability of the model. In the first stage, significant factors in predicting croaker presence were temperature, depth, grain size, anchovy biomass, year and the interaction of temperature and salinity (Table 2.4, 2.9). The relationships of croaker occurrence with temperature, depth and year were curvilinear (Figure 2.9). The relationship appears dome shaped with depth and anchovy weight. In the second stage, temperature, salinity, grain size, year, and the temperature and salinity interaction were incorporated to predict croaker abundance (Figure 2.10). The relationship of croaker abundance predicted by the

second stage of the GAM was curvilinear with temperature, dome shaped with grain size and year, and linear with salinity.  Deviance explained in the second stage of the model was 43.2%, much higher than the deviance explained in the first stage of the model, 18.7%.

Predicted croaker abundance was calculated in two ways: 1) by the $2^{nd}$ stage GAM itself using only stations where croaker were present and 2) by the product of the presence and abundance predicted by the $1^{st}$ and $2^{nd}$ stage models respectively.  The explanatory variables from the original data were used in both cases and observed croaker biomass was compared to these predictions.  The second stage GAM alone predicted croaker abundance much better than the full two-stage GAM (Figure 2.11).  However, neither captured the range of values of croaker biomass and the GAM seemed to dampen much of the variability in abundance that was observed.

To eliminate the effects of seasonal migrations, two stage GAMs were run for the spring, summer, and fall.  Year and the interaction between temperature and salinity and Year were important factors in almost all of the seasonal models even though the data was separated by season (Table 2.4).  The relationship of both croaker occurrence and abundance with year was highly curvilinear especially in the spring and fall (Figures 2.12-2.17).  In general, croaker occurrence and abundance increased linearly or approached linearity with salinity.  In the second stage of the seasonal GAMs, croaker abundance increases linearly with dissolved oxygen and depth in the spring (Figure 2.13).  Most other relationships of explanatory variables with croaker occurrence and abundance were curvilinear reflecting the patchiness in croaker distribution.  The deviance explained and $R^2$ values were higher for the

seasonal models than for the pooled model (Table 2.4). The seasonal two stage GAMs also predicted observed croaker abundance better than the pooled model, but again, the modeling approach dampened the range of croaker abundance estimates (Figure 2.18). The maximum observed croaker biomass was much higher than the maximum predicted value in both the pooled and seasonal models.

**DISCUSSION**

Croaker feeds on a wide variety of organisms, but in contrast to previous studies croaker were found to eat a substantial amount of anchovy during the summer months in Chesapeake Bay. Fish have been reported as small components of the diet of adult croaker in previous studies (Darnell 1961, Nemerson 2002, Overstreet and Heard 1978, Sheridan 1979). The work herein suggests that about 20% of the diet of croaker by weight consists of anchovy. While croaker still consistently feed on benthic portions of the food web, these results suggest that a substantial portion of their bioenergetic needs (as indicated by %W) are met by anchovy in the summer months and that croaker predation could influence both the benthic and pelagic portions of the foodweb.

The earliest of croaker diet studies by Hildebrand and Schroeder (1928) reported less than 1% of the stomachs that were examined had fish in them. In contrast, this study and other studies since the 1970s report fish as a relatively small, but common part of croaker diet (Chao and Musick 1977, Nemerson 2002, Overstreet and Heard 1978, Sheridan 1979). There are several potential explanations for this change. Estuarine ecosystems worldwide are increasingly subject to anthropogenic

stresses that have lead to eutrophication, which induces widespread alterations in the ecosystem (e.g. Kemp et al. 2005). De Levia Moreno et al. (2000) proposed that one of the effects of eutrophication was to increase the ratio of biomasses of pelagic to benthic associated fishes, indicative of general system wide change from benthic to pelagic production. Indeed in the Chesapeake Bay, the ratio of pelagic to benthic fishery removals increased from 1.90 to 2.66 between the 1960's and the 1990s. Eutrophication and the change from a more pelagic to benthic ecosystem may cause alteration of diet patterns. Powers et al. (2005) found that the diet of Atlantic croaker shifted from clams to less nutritious food sources such as detritus and plant tissue after summer hypoxic events in the Neuse River estuary (NC, USA). Studies on other benthivores in Chesapeake Bay illustrated that the ability of a benthic predator to prey upon clams was reduced during periods of even sporadic low dissolved oxygen events (Seitz 2003).

An alternative explanation for the larger proportion of fish reported in the diet of croaker is the increasingly poor water quality in coastal areas where croaker live. There was no statistically significant correlation between dissolved oxygen and the amount of anchovy in croaker diet. However, croaker eat more anchovies in the summer when hypoxia is more common. In the summer of 2003, the middle and upper regions of the Bay experienced very low oxygen conditions, which is coincident with a high proportion of anchovy and fish in the diets of croaker in the same regions. However, the highest incidence of anchovy feeding was in 2002, when hypoxia was not as severe as 2003. Factors that influence diet were difficult to detect in this and other diet studies. Therefore, it is possible that a general shift from a

31

benthic to a pelagic Chesapeake Bay ecosystem may explain the higher incidence of anchovy in present day croaker diets.

It is more likely that the incidence of anchovy and fish in the diet of croaker were higher in this study because croaker are crepuscular predators on anchovy. This crepuscular feeding was identified in the nighttime midwater trawl samples, but was missed in other studies of croaker diet that have used bottom trawls during the day. The only other diet study where samples were collected at night probably did not capture this because it was conducted in shallow waters and there was a notable decrease in croaker catches at night presumably because croaker moved to deeper water at night (Homer and Boynton 1978). In this study, there was a higher weight of anchovy in croaker stomachs following sunset indicating crepuscular feeding behavior. The adjustment in sight and behaviors of many fish during the twilight period after sunset and before sunrise is thought to provide an opportunistic feeding time for some predators in aquatic environments. Indeed diel variations in diet have been detected in other studies (Clark et al. 2003, Johnson and Dropkin 1993). Taylor et al. (2007) also found that swimming speeds of bay anchovy were lower and less variable at night than during the day, which may enable a demersal fish such as croaker to feed upon prey that is much more mobile than its traditional benthic prey. While some consumption of anchovy could be from net-feeding in the midwater trawl, this is unlikely. The relative degree of digestion was recorded in 2004 and 2005 and all stages of digestion were present, indicating that the consumption of anchovy is not simply a result of net feeding.

The distribution of croaker varied seasonally and annually and is reflected in the maps of probability of occurrence and in the two stage GAMs. Croaker occurrence and abundance fluctuated annually so that the effect of year was included in all but two of all the first and second stage GAMs produced. Temperature and salinity and/or their interaction were also consistent contributor to predict croaker distribution. I hypothesized that presence of croaker would be predicted by physical properties of the water column because the presence of croaker should be bounded by its tolerance to water chemistry. However, croaker was tolerant of a wide range of salinity, temperature, and dissolved oxygen. Furthermore, the prey field seemed to be important in determining croaker occurrence. Anchovy was a consistent predictor of croaker occurrence in these models.

I secondarily hypothesized that croaker would be more abundant where prey resources were high. However, the second stage of the GAMs indicated that both abiotic and biotic factors were important in predicting abundance. In fact, anchovy biomass was not included in any of the second stage models and grain size was included only in the second stage GAM pooled over seasons. These results do not mean that prey field is not important in determining croaker distribution. Grain size was used as a proxy for benthic food resources, but it would have been better to use actual abundance estimates of benthic organisms upon which croaker frequently feed. Estimates of benthic biomass are available but do not overlap temporally with our sampling scheme. Furthermore, the estimates of grain size were obtained from the 1980s and there may have been changes in sediment characteristics since that time. However, the overall trends in grain size are probably similar. While anchovy was a

consistent predictor of croaker presence it is possible that anchovy abundance is influenced by the same factors as croaker and these factors may or may not have been incorporated into the model.

While pooling data across all seasons provided a large number of data points to fit the GAMs, seasonal GAMs predicted the abundance of croaker much better. The two stage GAM did predict general trends in croaker abundance, but was unable to capture the wide range of estimates of croaker biomass. In particular, GAMs were unable to capture the number of stations with zero values. GAMs have been used to predict the spatial distribution in much of the marine ecology literature (Hedger et al. 2004, Jensen et al. 2005, Stoner et al. 2001). While it is possible to create spatially explicit maps of croaker abundance based on abiotic and biotic factors, in this application GAMs were used to identify factors that influence croaker presence and secondarily abundance. GAMs allowed the incorporation of many possible explanatory variables, different distributions of data (Poisson in the first stage and Gaussian in the second stage), and the ability to fit curvilinear relationships to predict distribution, which is more biologically realistic.

Here, I have documented clear trends and levels of variability in the distribution and diet of Atlantic croaker in Chesapeake Bay. While the patterns were clear, the consequences of these patterns to the fitness of individual fish remain uncertain. For example, does the variability in croaker diet observed at the regional and interannual levels have any fitness consequence for the individual croaker? Specifically, does a higher proportion of anchovy in the diet confer a growth advantage, or does it reflect changes in diet driven by exclusion of croaker from

preferred habitats, and therefore the presence of anchovy in croaker diets actually confers a fitness cost. To explore these and other potential hypotheses, it would be necessary to assess the condition of croaker with different observed diets. The challenge of such analyses will be matching the temporal resolution of indices of condition with that of the diet. Dietary information derived from analysis of stomach contents represents a "snapshot" of consumption, but do not necessarily represent what a fish is consistently eating and more importantly assimilating. Similarly, indices of condition also have characteristic response and latency times (Ferron and Leggett 1994, Suthers et al. 1992). Thus, addressing the consequences of the patterns in distribution and diet observed here will require additional studies that seek to match observations on diet and condition at appropriate spatial and temporal scales.

Table 2.1:  Description of prey categories used to analyze croaker diet

| Prey category | Description | %W | %O |
|---|---|---|---|
| Polychaetes | Many unidentified species, but include trumpet worms *Pectinaria gouldi*, clam worms, *Neries spp.* and terebellid worms Terebellidae | 61.5% | 83.6% |
| Anchovy | Mostly bay anchovy, *Anchoa mitchilli*, but may include striped anchovy *Anchoa hepsetus* | 8.9% | 13.2% |
| Mysids | Mostly *Neomysis americanus*, but may include *Mysidopsis bigelowi* | 8.2% | 36.5% |
| Amphipods | Many species including *Gammarus spp*, *Leptocheirus plumulosus*, *Corophium lacustre*, *Monoculodes edwardsi* | 5.2% | 21.0% |
| Other benthic | Hydroids, molluscs, gastropods, barnacles, cumaceans, isopods, *Cyathura spp.*, skeleton shrimp, other crustaceans, sea squirts, and ribbon worms | 4.3% | 20.2% |
| Bivalves | Unidentified bivalves, clams and seedling mussels | 3.5% | 12.7% |
| Fish | Unidentified fish and fish remains, and YOY weakfish *Cynoscion regalis* | 3.4% | 12.3% |
| Crabs | Unidentified crab remains and white fingered mud crab *Rhithropanopeus harrisii* | 1.8% | 4.5% |
| Shrimp | Unidentified shrimp remains, Caridean shrimps, *Pugeo spp.*, sand shrimp *Crangon septemspinosa*, and mantis shrimp *Squilla empusa* | 1.6% | 6.5% |
| Detritus and macroalgae | Unidentified algae, inorganic matter, and plant matter | 1.3% | 11.4% |
| Other pelagic | Squids, sea nettles, insects | 0.3% | 1.1% |

Table 2.2: Pearson correlations between explanatory variables used in the 1$^{st}$ stage of the GAM, all seasons and years combined. Pairwise comparisons were considered significant at the P=0.002 level to maintain an experiment-wise error rate of P=0.05 (Bonferroni adjustment P =0.05/21=0.002).

| | Salinity | Temperature | Dissolved Oxygen | Depth | Grainsize | Log Anchovy Biomass |
|---|---|---|---|---|---|---|
| Salinity | 1 | | | | | |
| Temperature | 0.099<br>0.0151 | 1 | | | | |
| Dissolved Oxygen | -0.18344<br><0.0001 | -0.679<br><0.0001 | 1 | | | |
| Depth | 0.129<br>0.0016 | 0.01934<br>0.637 | -0.082<br>0.0442 | 1 | | |
| Grainsize | -0.611<br><0.0001 | -0.06962<br>0.089 | 0.112<br>0.0062 | -0.082<br>0.044 | 1 | |
| Log Anchovy Biomass | 0.319<br><0.0001 | 0.01038<br>0.8 | -0.173<br><0.0001 | 0.0075<br>0.855 | -0.105<br>0.011 | 1 |
| Log Croaker Biomass | 0.19928<br><0.0001 | 0.075<br>0.0673 | -0.036<br>0.377 | 0.014<br>0.733 | -0.134<br>0.001 | 0.0825<br>0.044 |

Table 2.3:  The percentage of simulations (number out of 100 iterations obtained from bootstrapping) where each explanatory variable was significant in 1$^{st}$ and 2$^{nd}$ stage GAMs using data pooled over all years and seasons 1995-2005.

| Explanatory Variable | 1st stage | | 2nd stage | |
| --- | --- | --- | --- | --- |
| | No year effects | Year effect included | No year effects | Year effect included |
| Temperature | 100 | 16 | 100 | 92 |
| Salinity | 93 | 12 | 100 | 99 |
| Dissolved Oxygen | 0 | 0 | 0 | 0 |
| Depth | 3 | 9 | 0 | 0 |
| Grain size | 69 | 75 | 4 | 5 |
| Log Anchovy Biomass | 100 | 100 | 13 | 4 |
| Year | | 83 | | 56 |
| Temperature* Salinity | | 100 | | 78 |

Table 2.4: Significant variables used in the final two stage GAMs developed for all seasons combined and then for each season separately.

| Explanatory Variable | 1st stage | | | | 2nd stage | | | |
|---|---|---|---|---|---|---|---|---|
| | All seasons | Spring | Summer | Fall | All seasons | Spring | Summer | Fall |
| Temperature | X | | X | | X | X | | |
| Salinity | | | X | | X | X | X | |
| Dissolved Oxygen | | | | | | X | | |
| Depth | X | X | | | | X | | |
| Grain size | X | X | X | | X | | | |
| Anchovy Biomass | X | X | | X | | | | |
| Year | X | X | | X | X | X | | X |
| Temp*Salinity | X | X | | X | X | | X | X |
| Deviance Explained | 18.7% | 36.60% | 20.4% | 24.3% | 43.2% | 65.4% | 34.60% | 46.6% |
| Adjusted $R^2$ | 0.195 | 0.351 | 0.188 | 0.262 | 0.383 | 0.602 | 0.272 | 0.417 |
| N | 1258 | 396 | 415 | 447 | 446 | 120 | 122 | 204 |

Figure 2.1: An example of the TIES and CHESFIMS survey design using the stations from the spring of 2001. Fixed stations are indicated with stars. Random stations are indicated with circles. The three strata of Chesapeake Bay (Upper, Middle, and Lower Bay) are separated with horizontal lines and labeled accordingly.
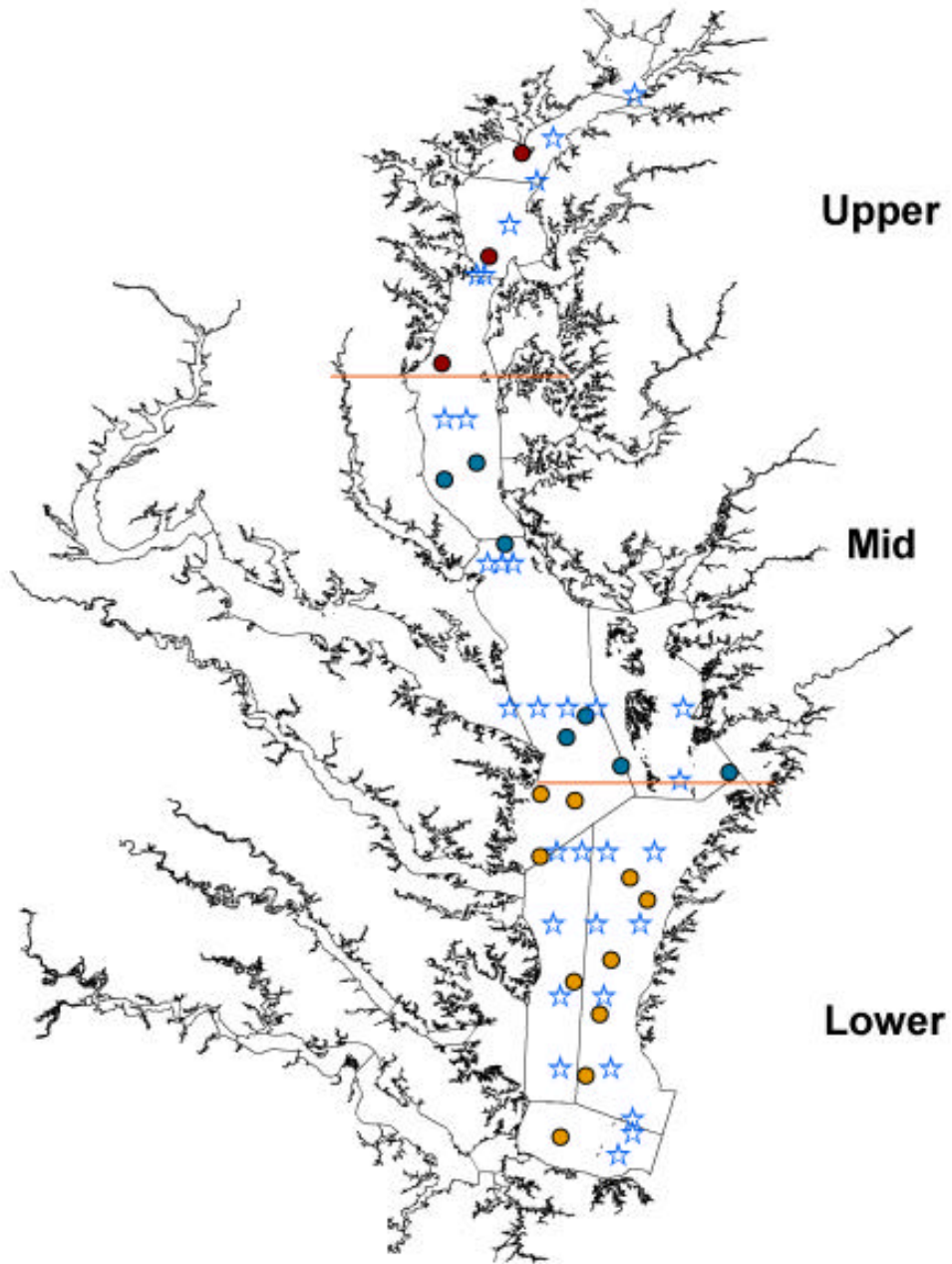
Figure 2.2:  Maps of the probability of occurrence of Atlantic croaker in Chesapeake Bay as estimated by indicator kriging for a) 2001, b) 2002, c) 2003 and d) 2004.  Numbers in parentheses indicate the number of stations sampled in that particular seasonal cruise.
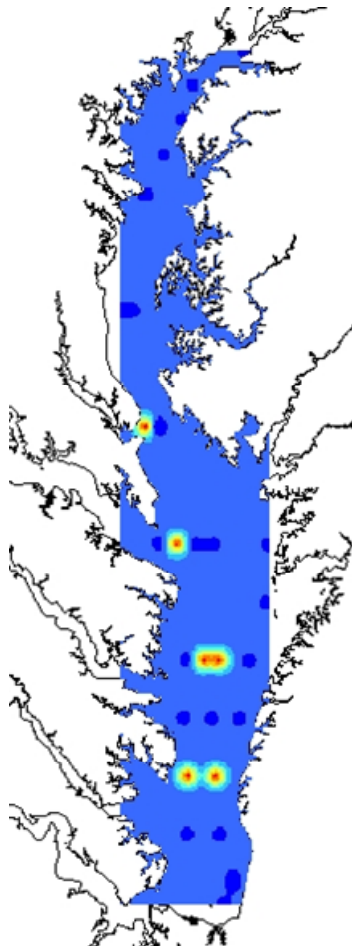
# May 2001 (31)    July 2001 (48)    September 2001 (15)
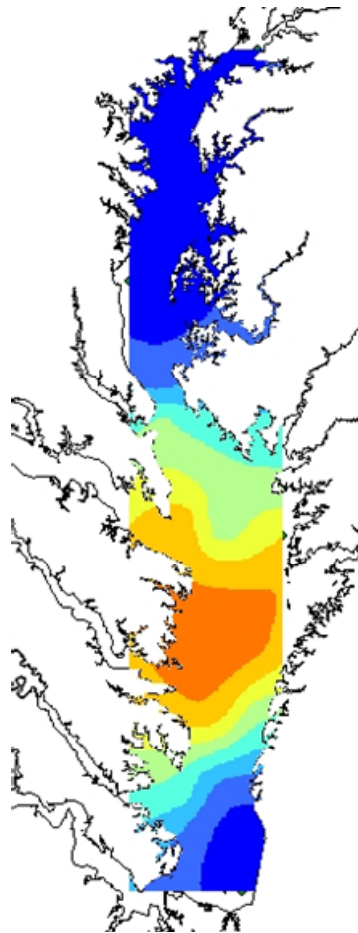


Probability of
occurrence

| | |
|---|---|
| ■ | 0.00 - 0.11 |
| ■ | 0.12 - 0.22 |
| ■ | 0.23 - 0.33 |
| ■ | 0.34 - 0.44 |
| ■ | 0.45 - 0.55 |
| ■ | 0.56 - 0.66 |
| ■ | 0.67 - 0.77 |
| ■ | 0.78 - 0.88 |
| ■ | 0.89 - 0.99 |
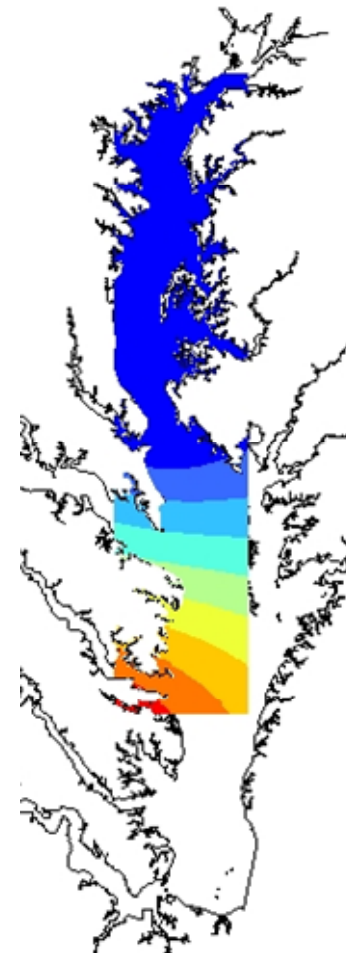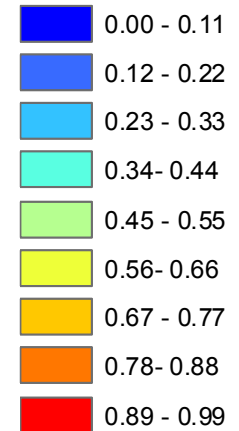
2.2b)
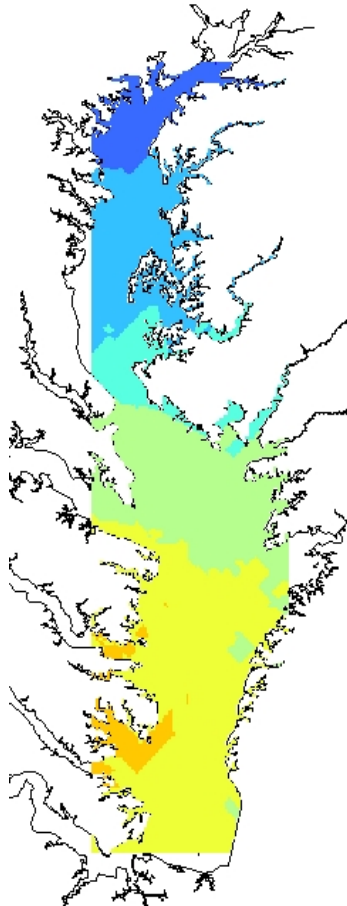
**May 2002 (46)**  **July 2002 (50)**  **September 2002 (51)**

Probability of
occurrence

| | |
|---|---|
| | 0.00 - 0.11 |
| | 0.12 - 0.22 |
| | 0.23 - 0.33 |
| | 0.34- 0.44 |
| | 0.45 - 0.55 |
| | 0.56- 0.66 |
| | 0.67 - 0.77 |
| | 0.78- 0.88 |
| | 0.89 - 0.99 |

2.2c)



**May 2003 (51)**　　**July 2003 (51)**　　**September 2003 (29)**

Probability of
occurrence

0.00 - 0.11
0.12 - 0.22
0.23 - 0.33
0.34- 0.44
0.45 - 0.55
0.56- 0.66
0.67 - 0.77
0.78- 0.88
0.89 - 0.99
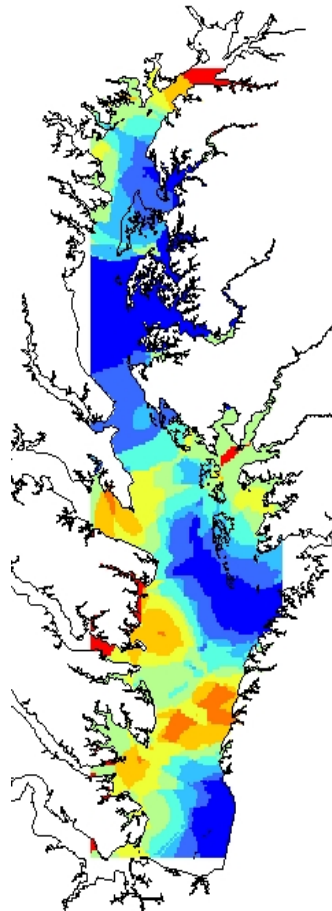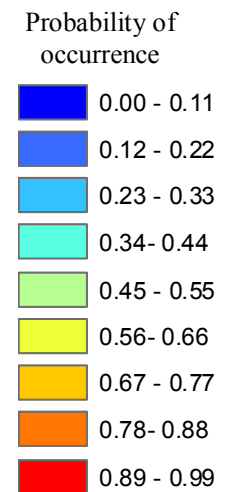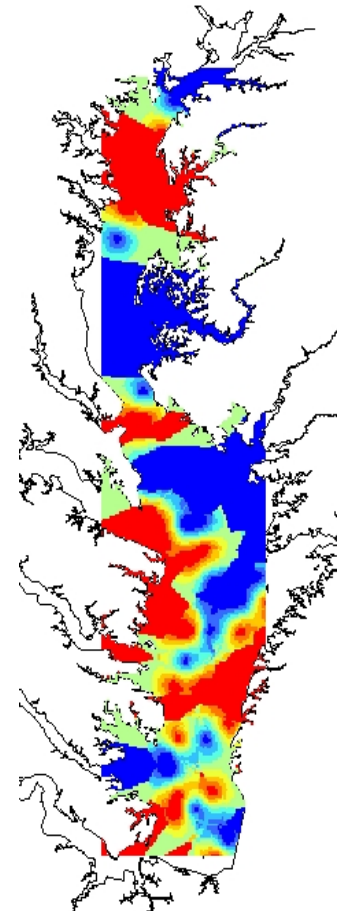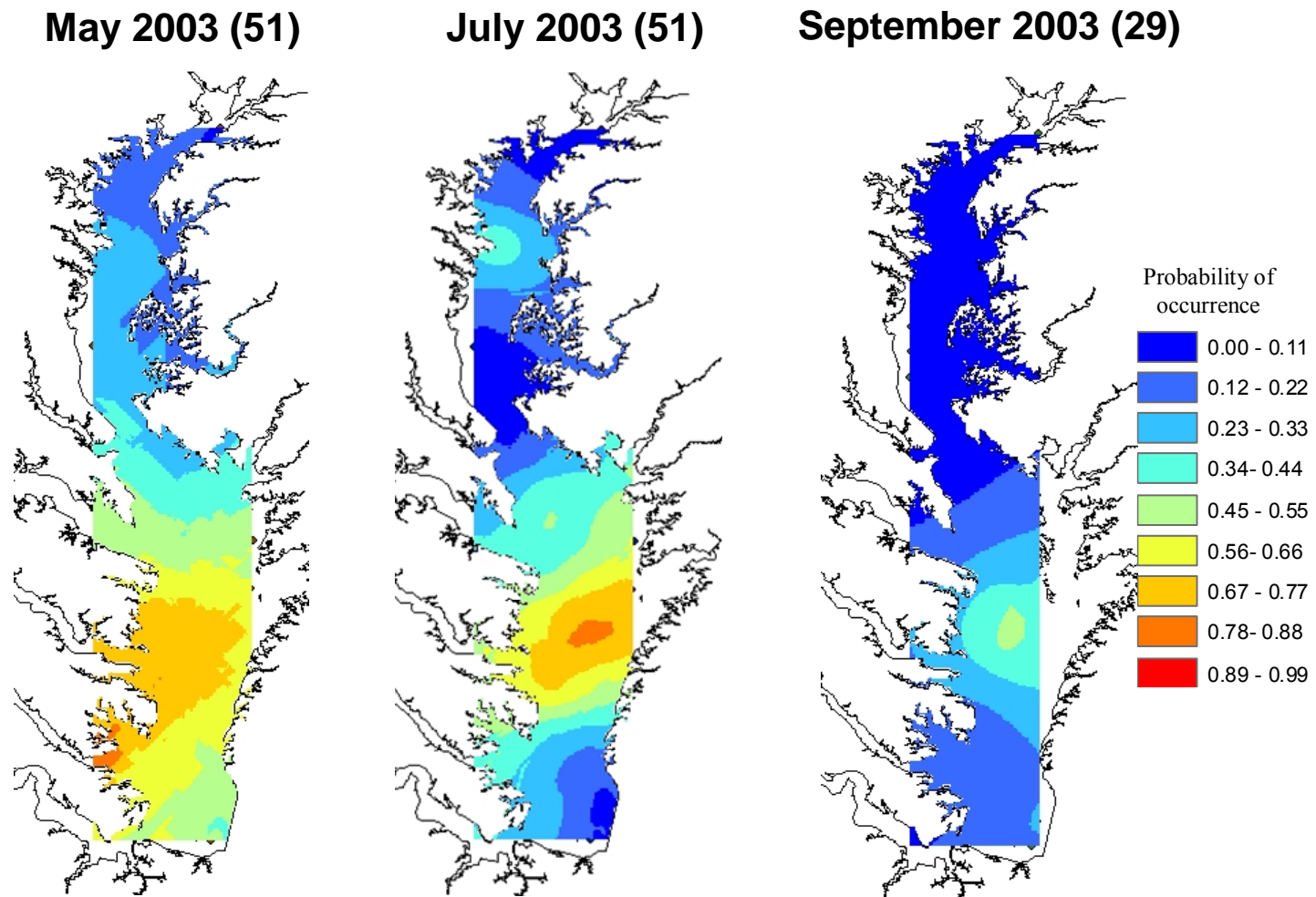
2.2d)
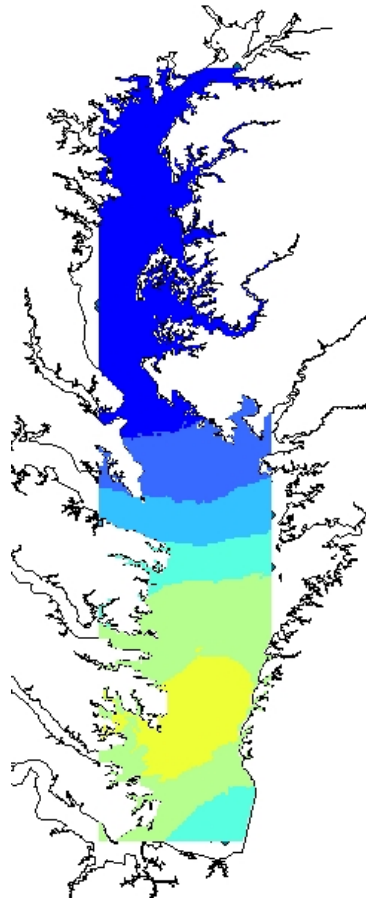


**May 2004 (50)**     **July 2004 (51)**     **September 2004 (47)**
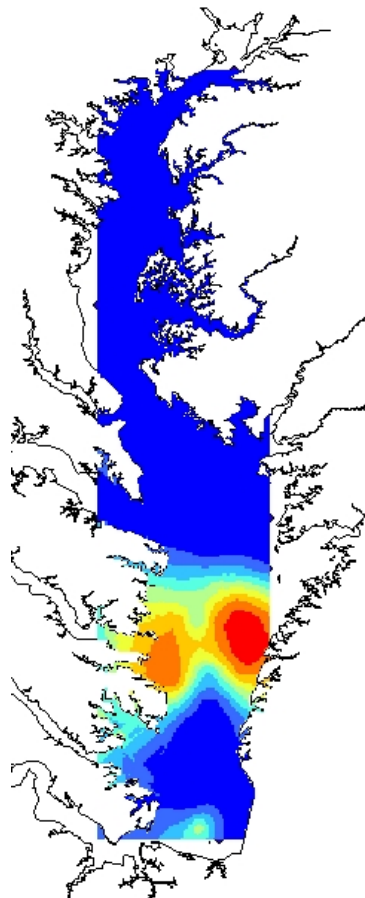
Probability of occurrence

0.00 - 0.11
0.12 - 0.22
0.23 - 0.33
0.34 - 0.44
0.45 - 0.55
0.56 - 0.66
0.67 - 0.77
0.78 - 0.88
0.89 - 0.99
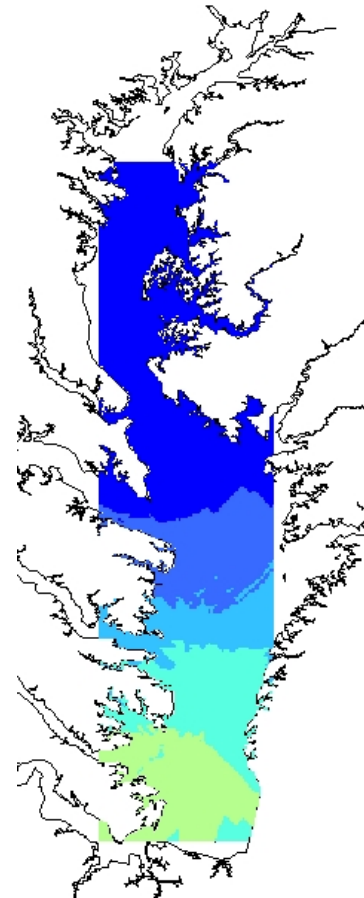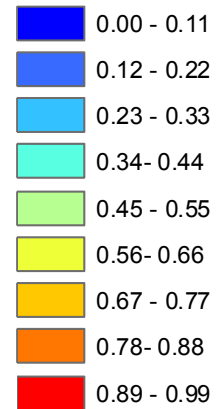
Figure 2.3: Diet of Atlantic croaker (proportion by weight) by year, season, and strata of the Bay a) 2002 Spring, b) 2002 Summer, c) 2002 Fall, d) 2003 Spring, e) 2003 Summer, f) 2003 Fall, g) 2004 Spring, h) 2004 Summer, i) 2004 Fall, j) 2005 Spring, k) 2005 Summer, and l) 2005 Fall. Panels where a figure is missing indicates that no croaker were collected in that sampling period.

# 2002



a)

Lower Bay

Middle Bay

Upper Bay

b)

c)

**2003**



d) Lower Bay | Middle Bay | Upper Bay
e)
f)
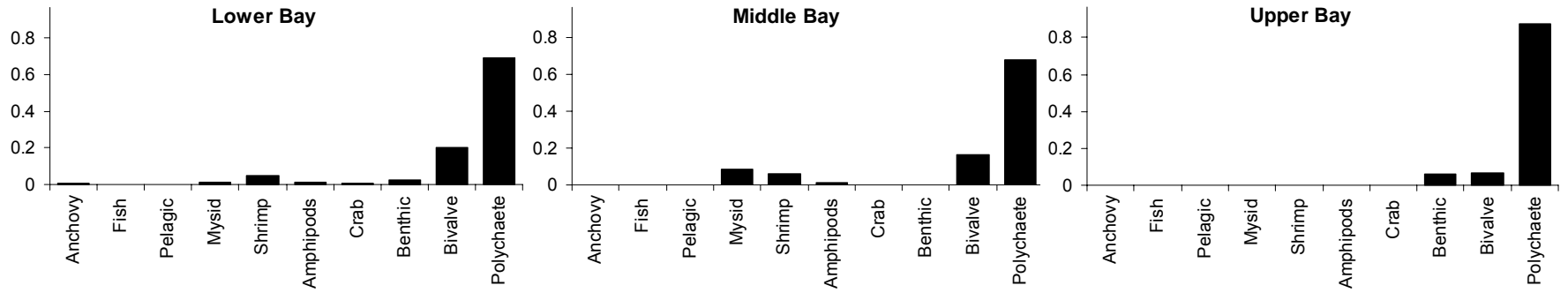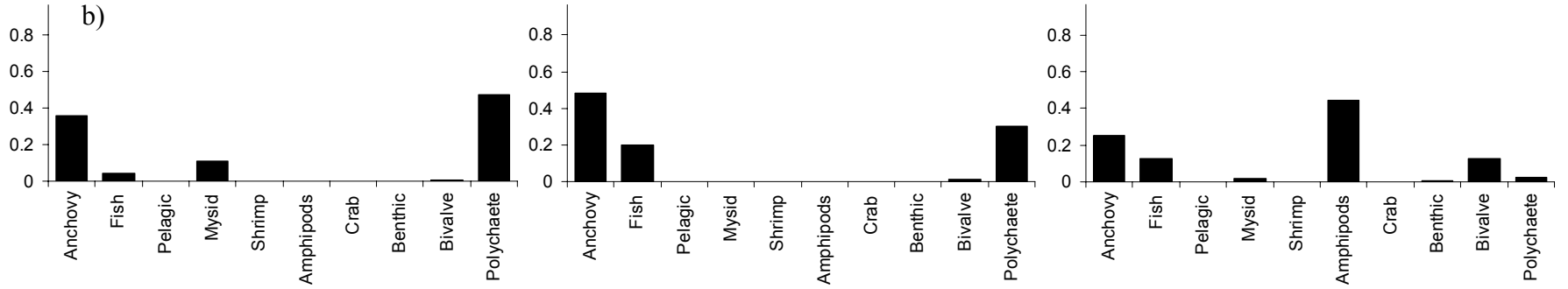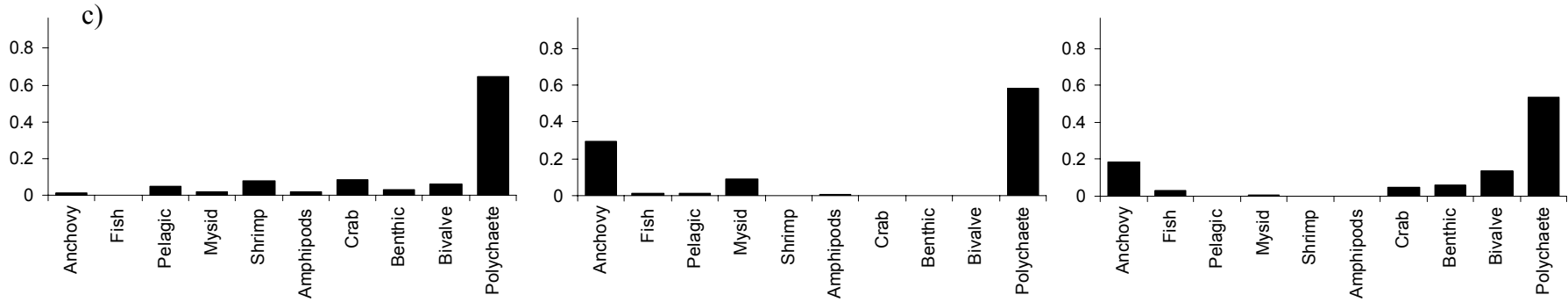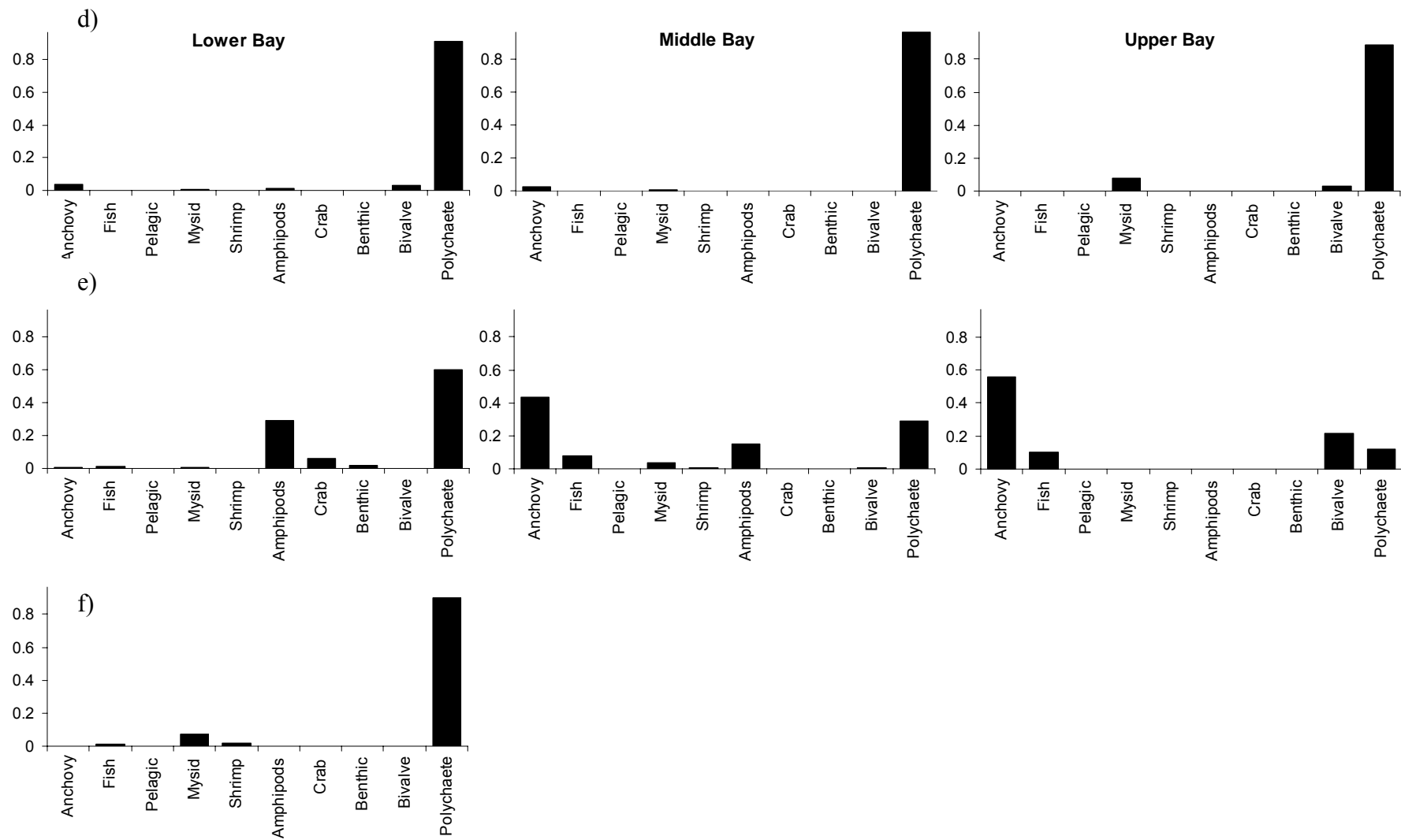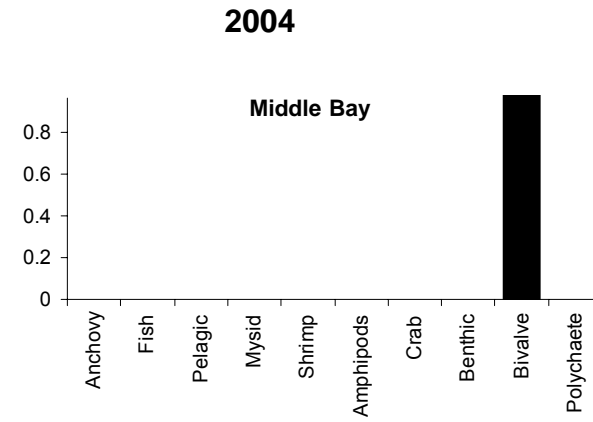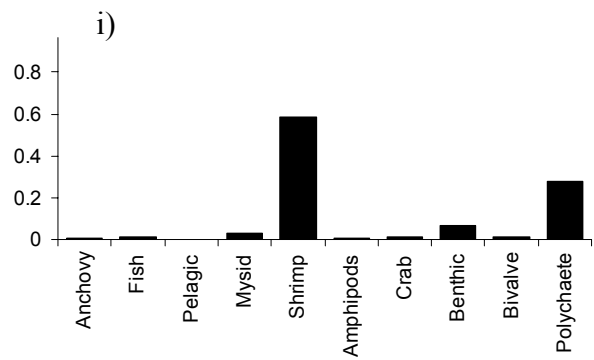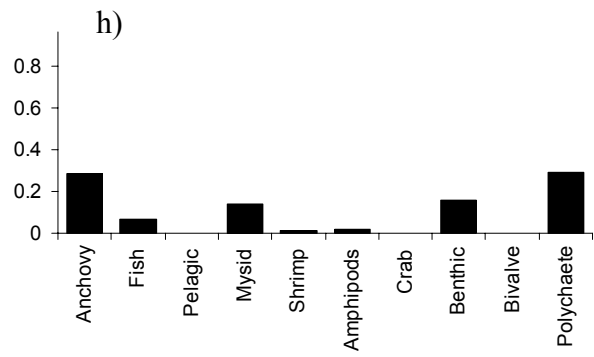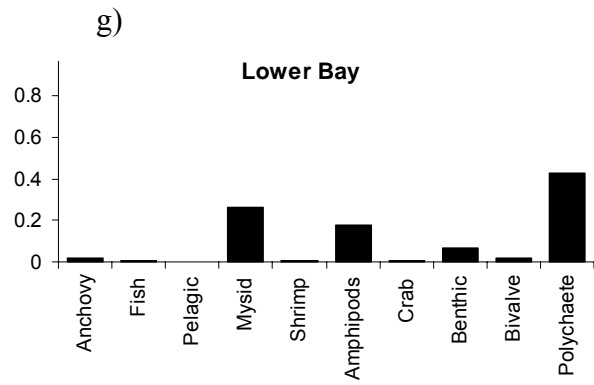
**2005**
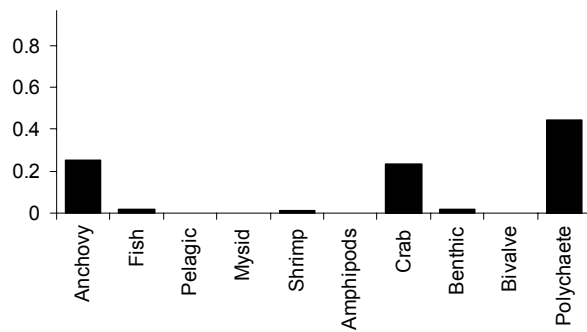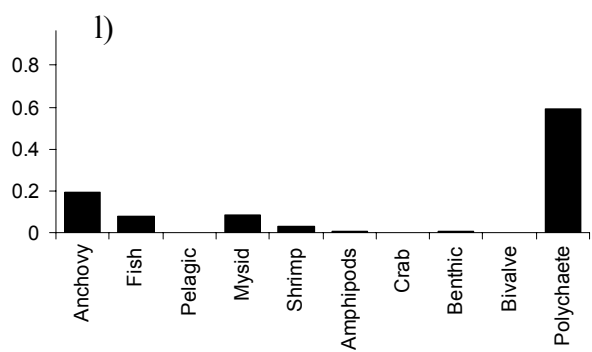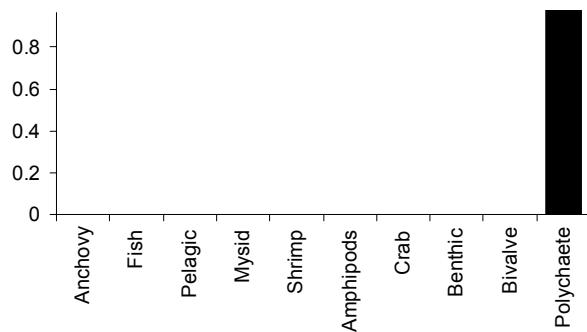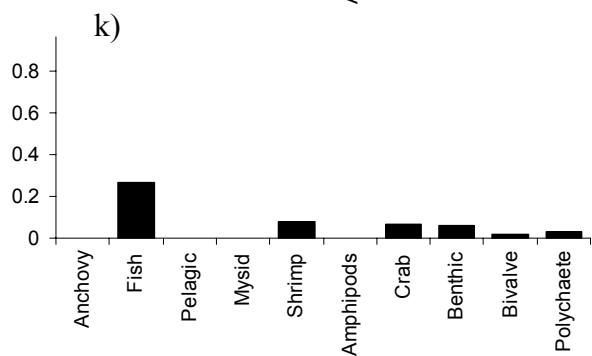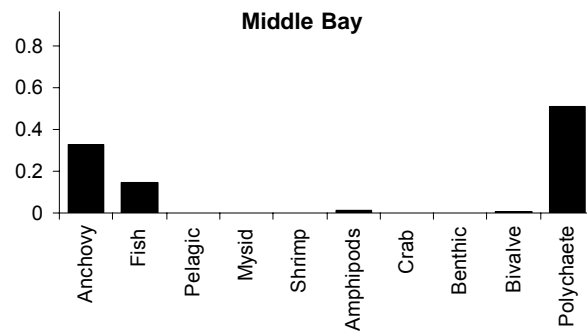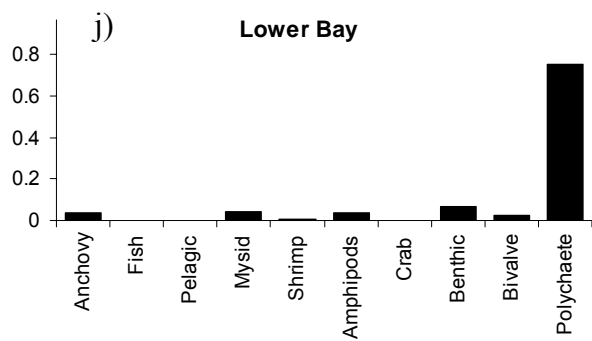
Figure 2.4: Biplot from Canonical Correspondence Analysis of the factors influencing diet composition of Atlantic croaker. Arrows represent factors while labels in blue are centroids of scores for the prey species.
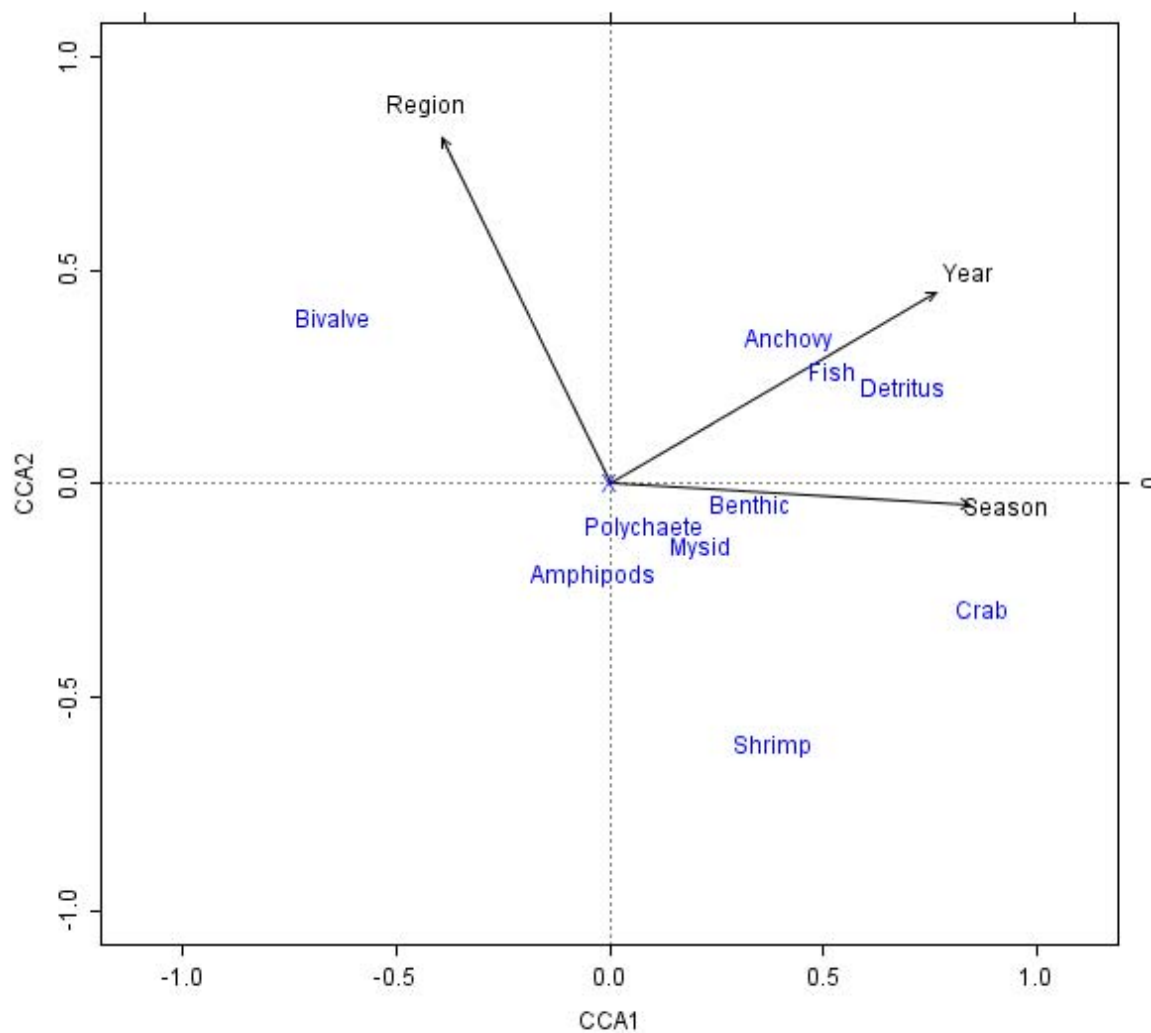
Figure 2.5: Diet composition by weight for each 10mm size class of Atlantic croaker examined 2002-2005. Fish <100mm and >390mm were pooled due to low sample size.
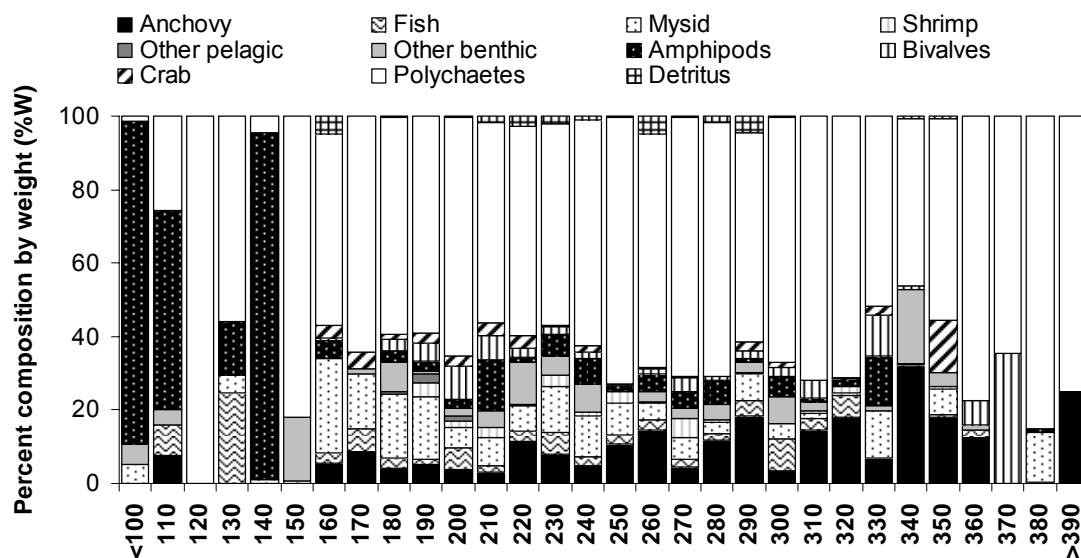
Figure 2.6: Total weight (g) of polychaetes and anchovies in croaker stomachs by one hour time periods. X-axis labels represent the beginning of each time interval (i.e. 19:00 indicates the time period from 19:00-20:00). Arrows indicate sunset.
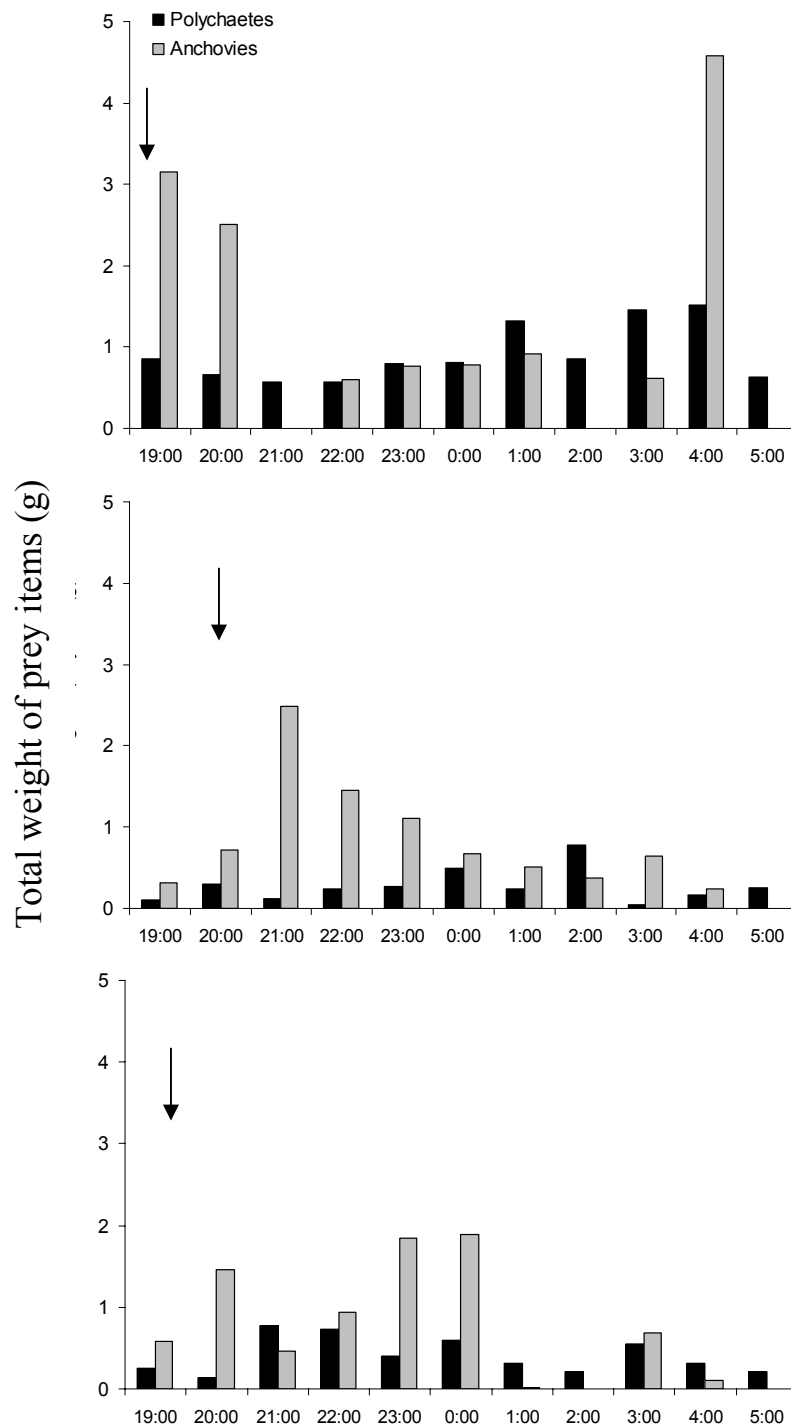
Figure 2.7: Relationship of the log of croaker biomass with explanatory variables used in the two stage GAMs.
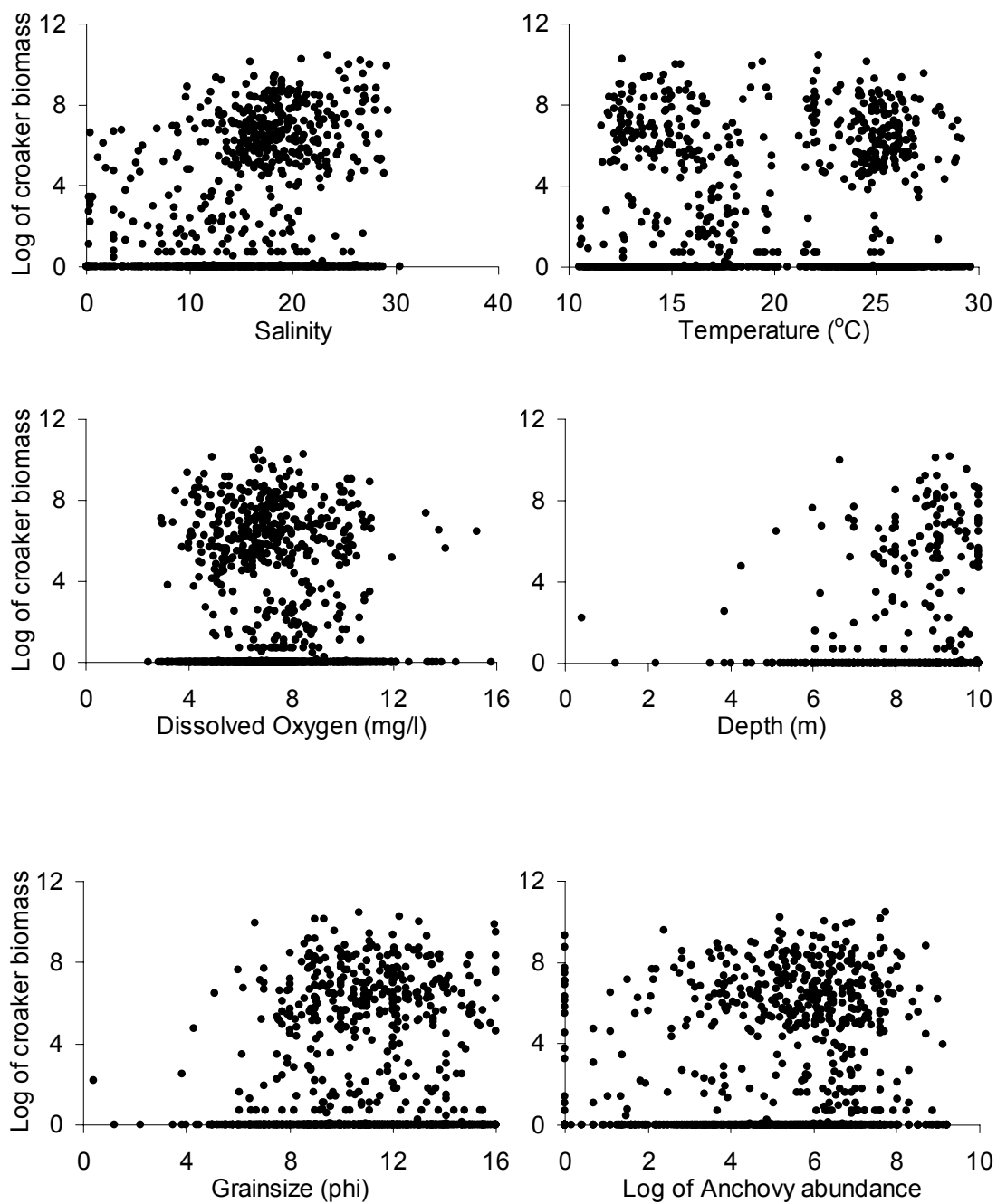
Figure 2.8: Comparison of general trends in a) salinity in the summer months and b) grain size (phi).
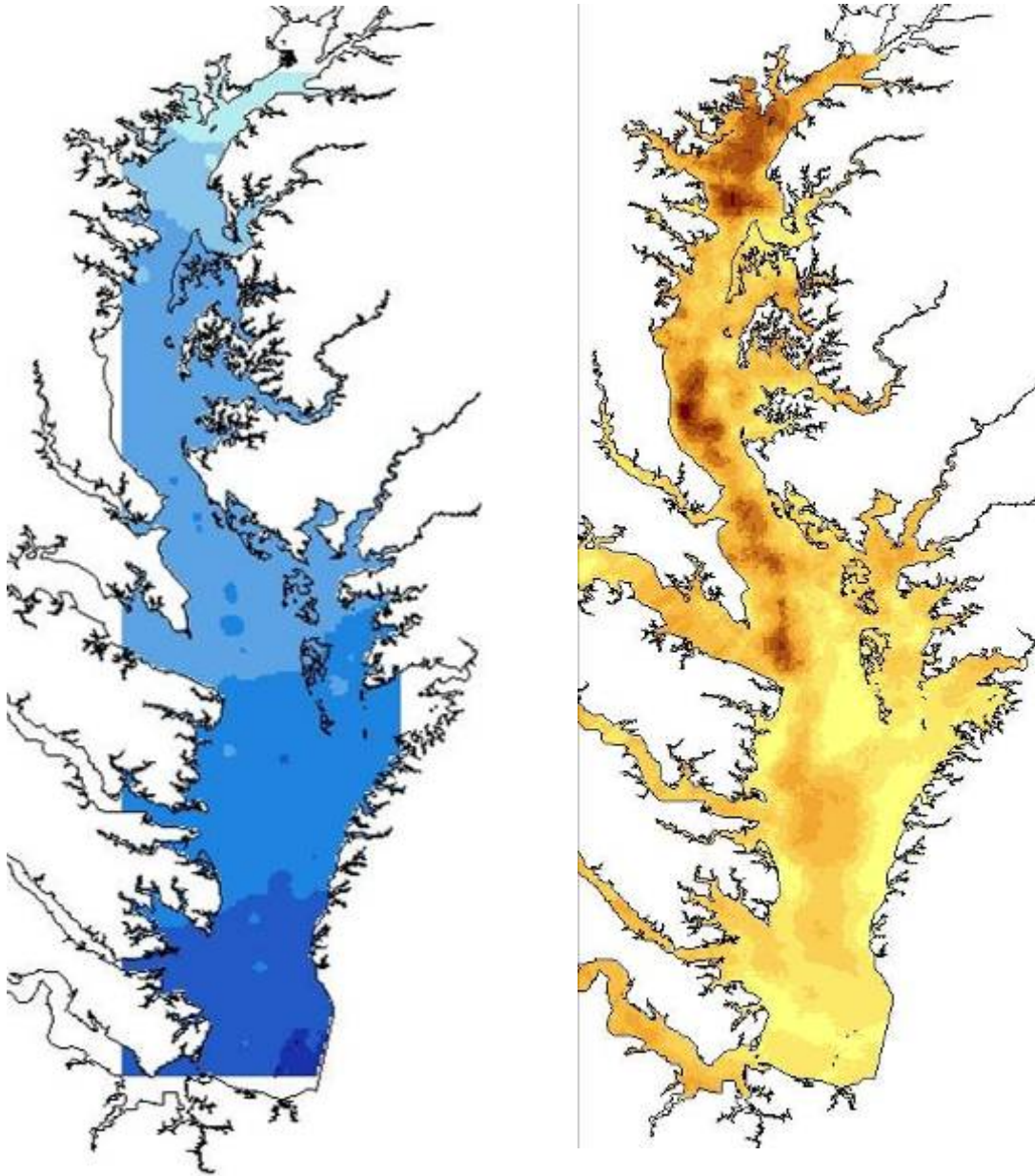
Figure 2.9: Smooth functions from 1<sup>st</sup> stage of GAM pooled over years and seasons. Y-axes represent the effect of the explanatory variable on croaker occurrence.  Tick marks (or rugs) on the x-axis indicate sampling intensity.  Points are residuals for each observation and dashed lines are twice the standard error.
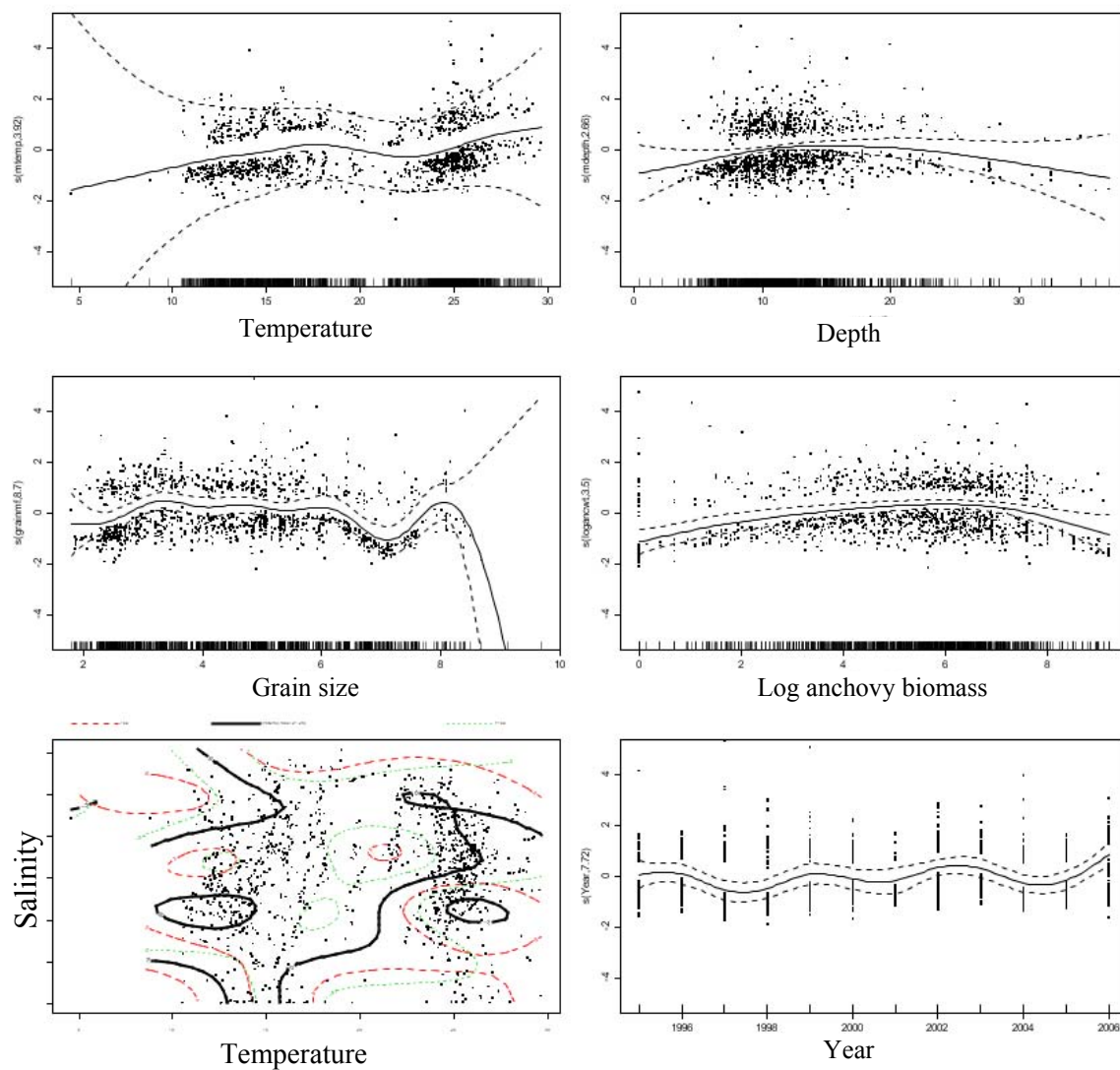
Figure 2.10: Spline functions for significant terms in the second stage of the GAM pooled over years and seasons. Y-axes represent the effect of the explanatory variable on croaker occurrence. Tick marks (or rugs) on the x-axis indicate sampling intensity. Points are residuals for each observation and dashed lines are twice the standard error.
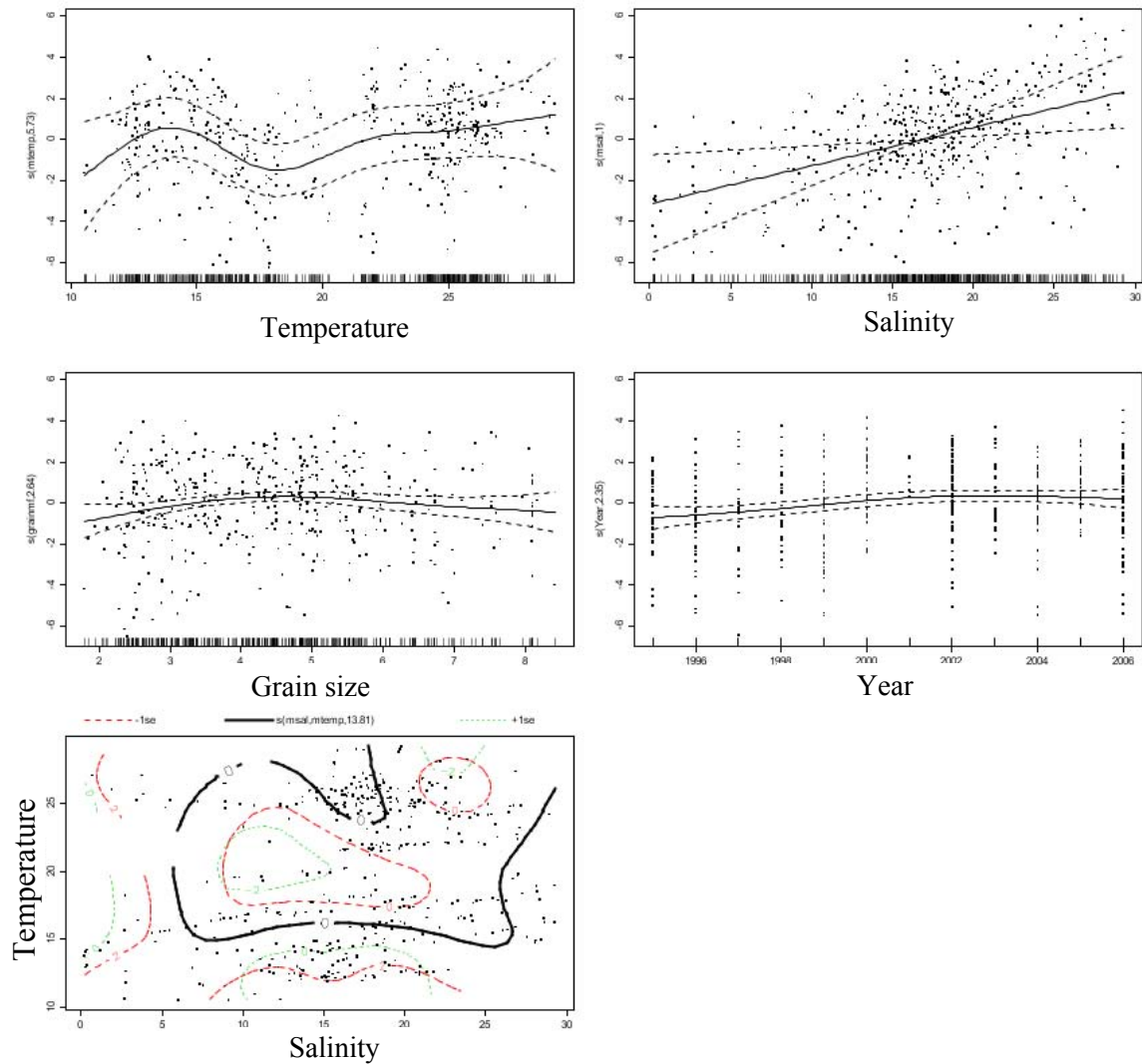
Figure 2.11: Prediction of croaker biomass obtained by multiplying the two stages of the GAM (●) and by the second stage of the GAM alone (▲). The dashed line is the 1:1 line for reference and regression lines are shown for both predictions.
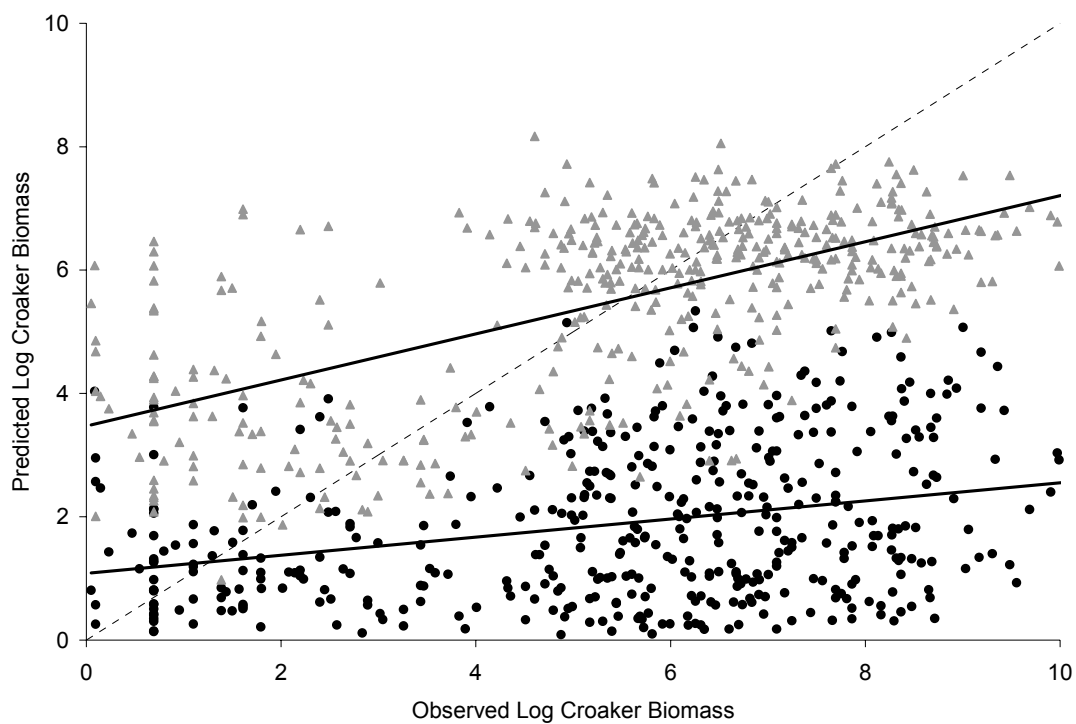
Figure 2.12: Spline smoothed plots of Atlantic croaker presence generated by the first stage spring GAM. Y-axes represent the effect of the explanatory variable on croaker occurrence. Tick marks (or rugs) on the x-axis indicate sampling intensity. Points are residuals for each observation and dashed lines are twice the standard error.
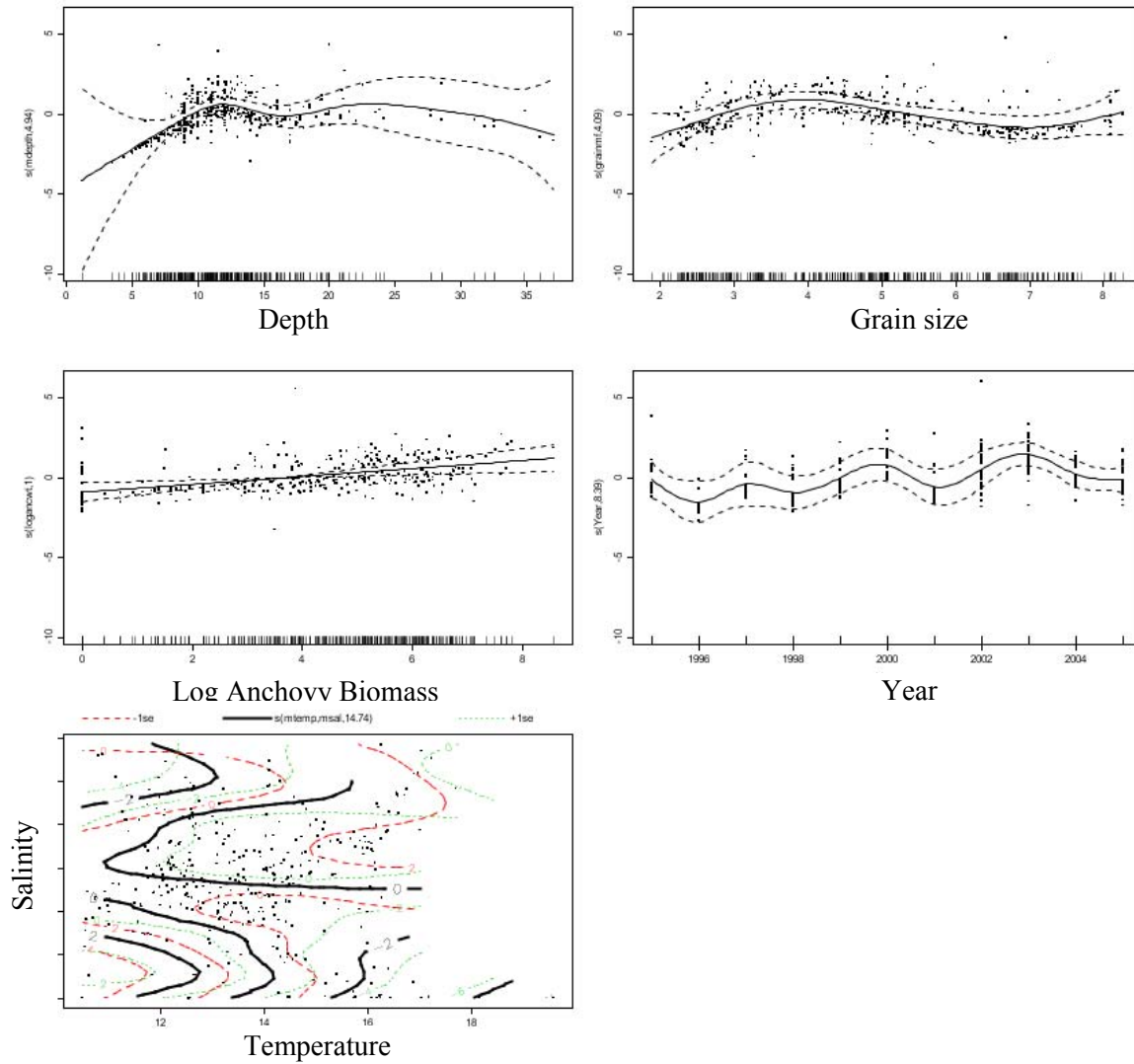
Figure 2.13: Spline smoothed plots of Atlantic croaker abundance generated by the second stage spring GAM. Y-axes represent the effect of the explanatory variable on croaker abundance. Tick marks (or rugs) on the x-axis indicate sampling intensity. Points are residuals for each observation and dashed lines are twice the standard error.



Temperature

Salinity

Dissolved Oxygen

Depth

Year
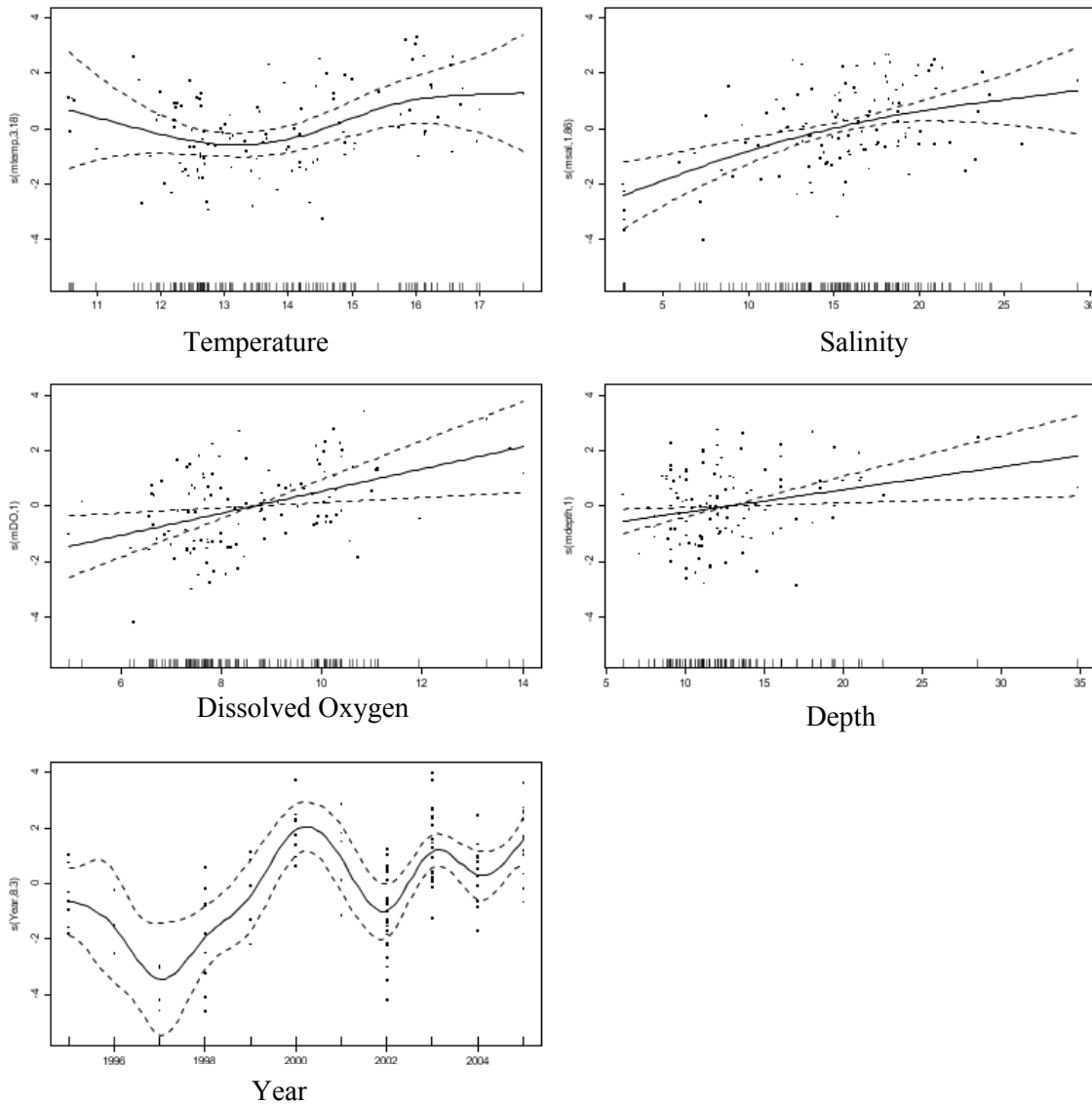
Figure 2.14: Spline smoothed plots of Atlantic croaker presence generated by the first stage GAM in the summer. Y-axes represent the effect of the explanatory variable on croaker occurrence. Tick marks (or rugs) on the x-axis indicate sampling intensity. Points are residuals for each observation and dashed lines are twice the standard error.

Temperature

Salinity

Grain size

Year

Year

Salinity
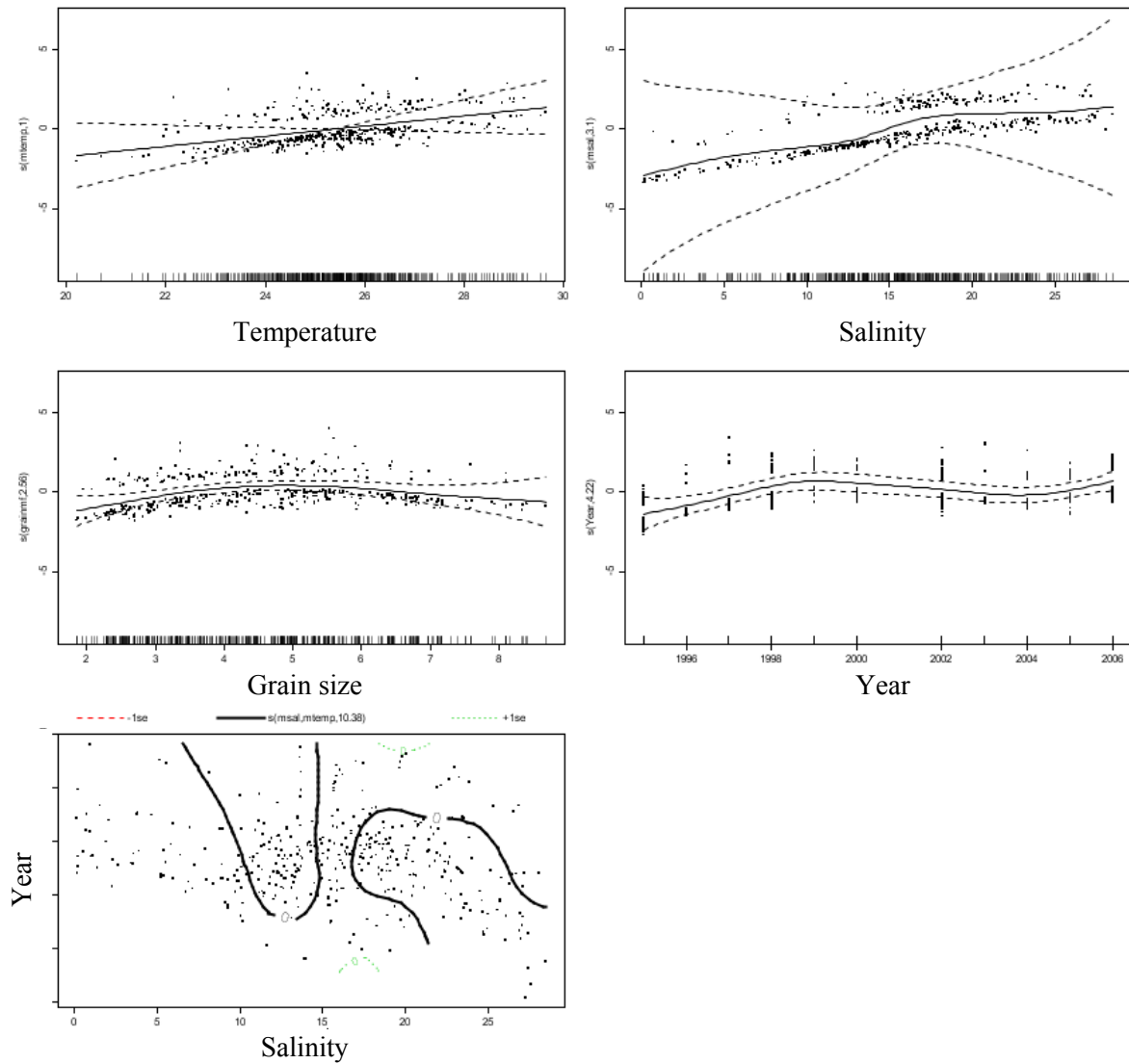
Figure 2.15: Spline smoothed plots of Atlantic croaker abundance generated by the second stage GAM in the summer. Y-axes represent the effect of the explanatory variable on croaker abundance. Tick marks (or rugs) on the x-axis indicate sampling intensity. Points are residuals for each observation and dashed lines are twice the standard error.
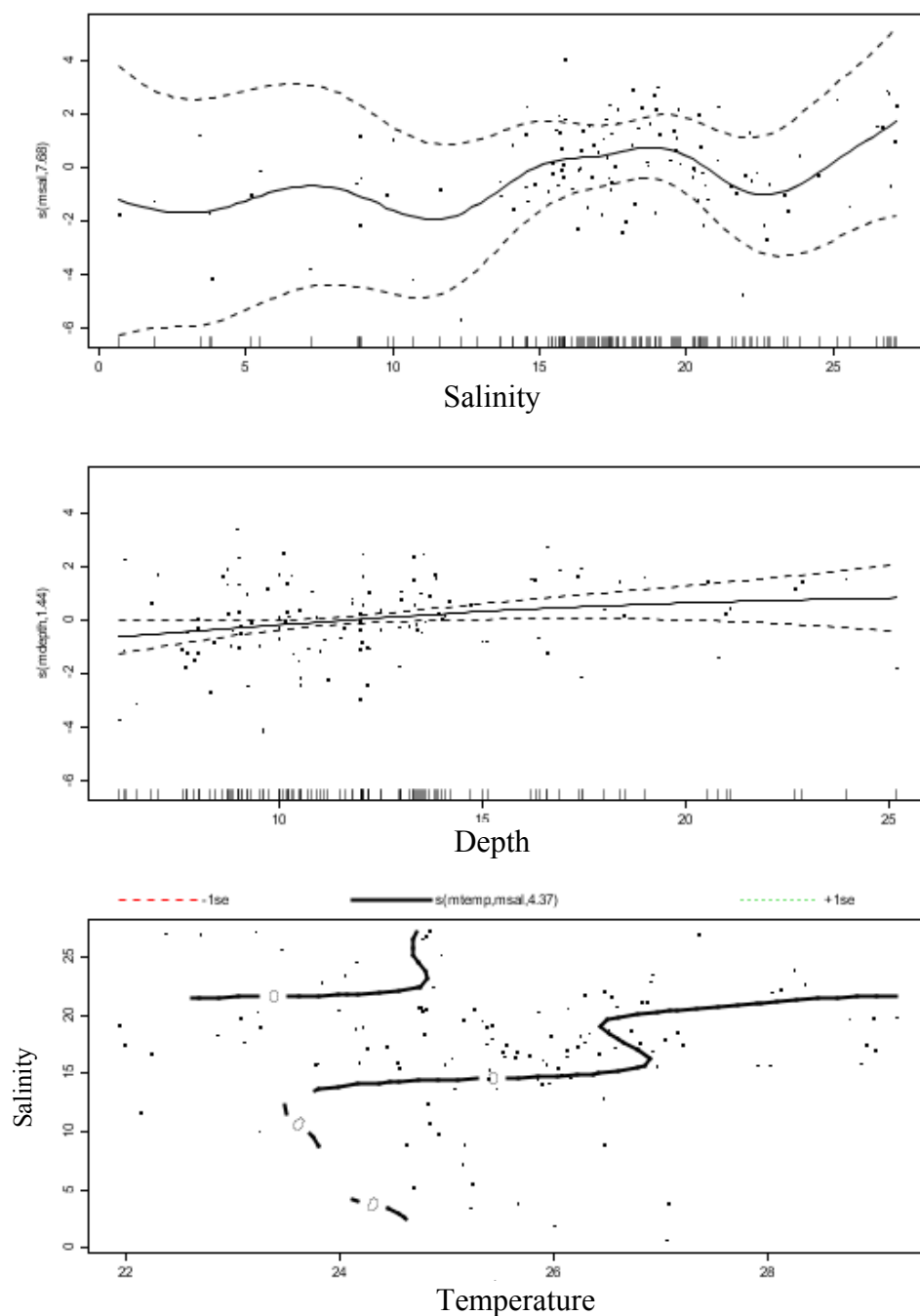
Figure 2.16: Spline smoothed plots of Atlantic croaker presence generated by the first stage fall GAM. Y-axes represent the effect of the explanatory variable on croaker occurrence. Tick marks (or rugs) on the x-axis indicate sampling intensity. Points are residuals for each observation and dashed lines are twice the standard error.
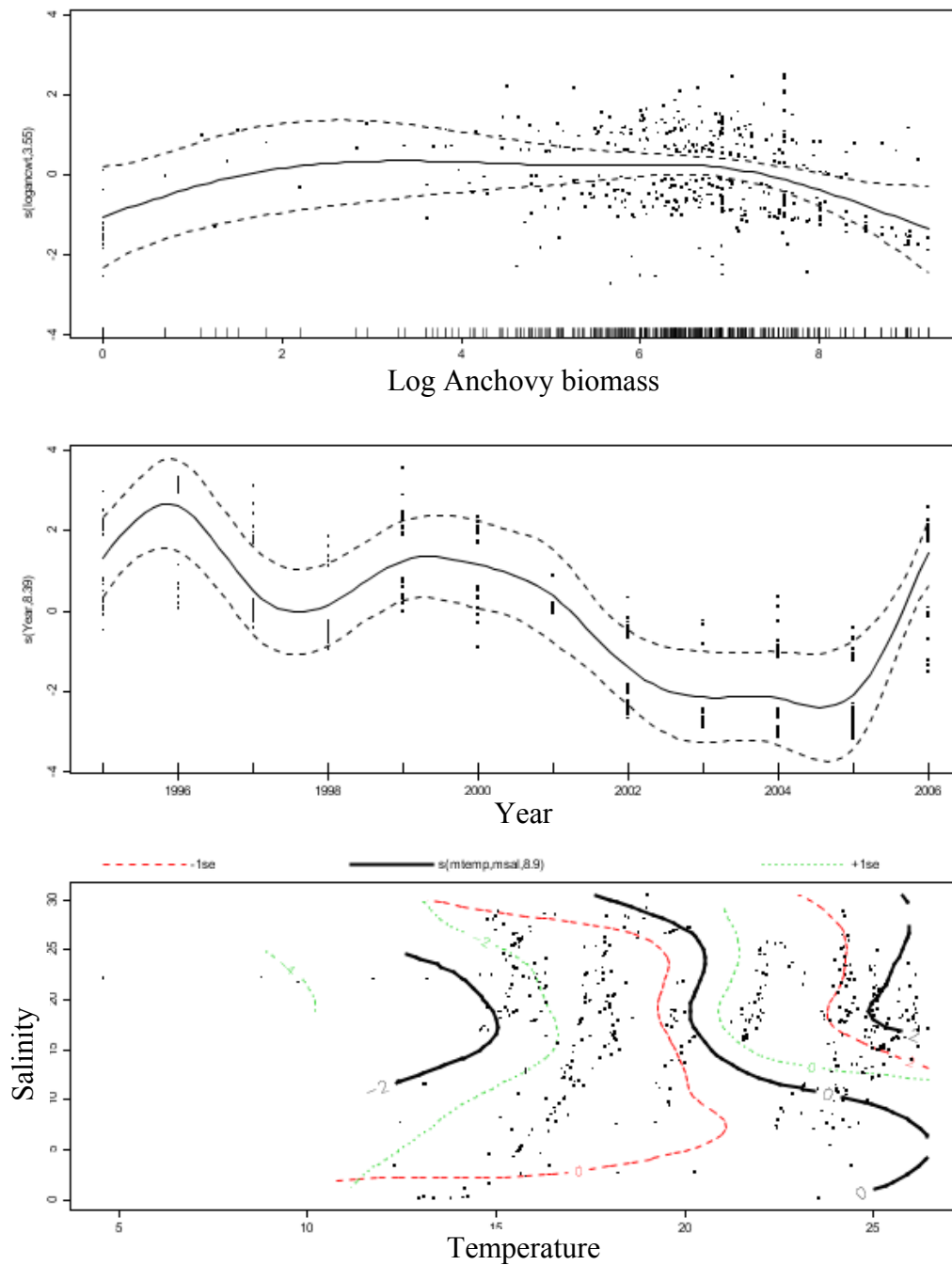
Figure 2.17: Spline smoothed plots of the distribution of Atlantic croaker biomass generated by the second stage fall GAM. Y-axes represent the effect of the explanatory variable on croaker abundance. Tick marks (or rugs) on the x-axis indicate sampling intensity. Points are residuals for each observation and dashed lines are twice the standard error.



64
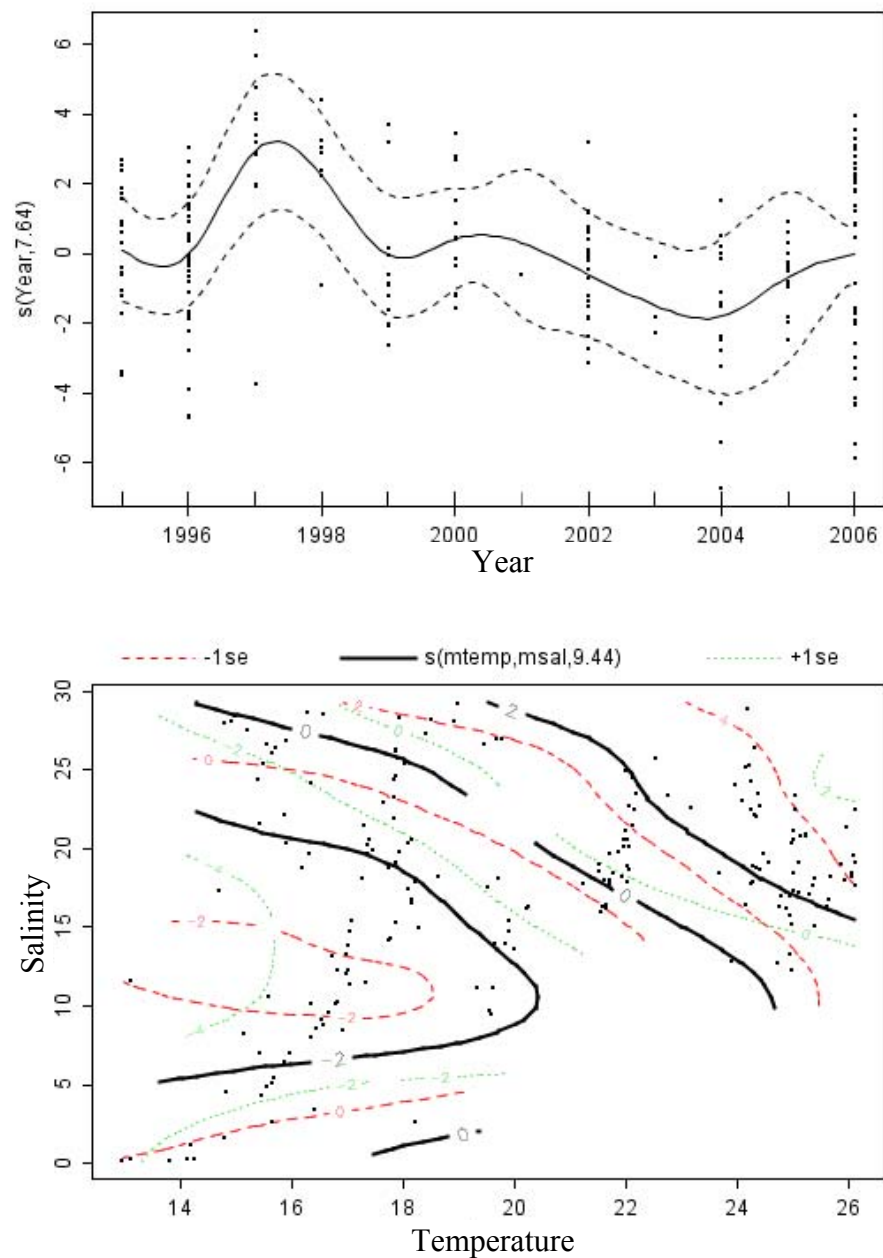
Figure 2.18: Comparison of observed biomass with biomass predicted by the two stage GAMs for a) spring, b) summer, and c) fall. Regressions and equations are provided to quantify model fit.
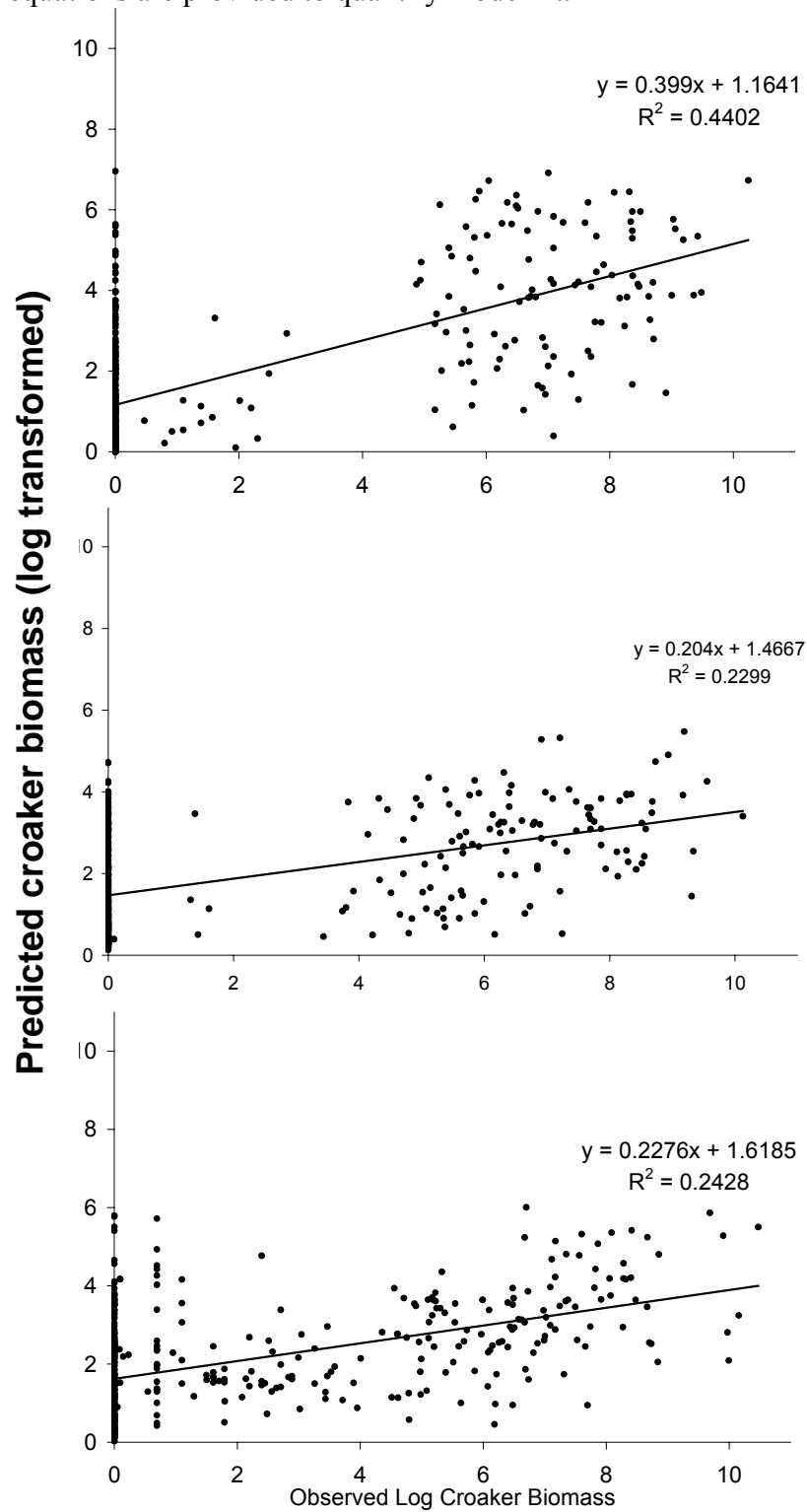
# CHAPTER 3: THE EFFECT OF DIET VARIABILITY ON CONDITION OF ATLANTIC CROAKER *MICROPOGONIAS UNDULATUS*

## INTRODUCTION

Many fish species exhibit prey switching in addition to ontogenetic, seasonal and annual changes in diet composition (Brabrand 2004, Mittelbach et al. 1992, Persson and Hansson 1998, Pihl 1994). For example, in the Chesapeake Bay Atlantic croaker *Micropogonias undulatus* (hereafter croaker), exhibits diet variability at ontogenetic, seasonal and annual scales (Chapter 1). I documented ontogenetic trends in croaker diets involving a shift from a diet dominated by amphipods to one dominated by polychaetes. Similarly, there were clear seasonal and annual trends in croaker diet. During summer months, approximately 20% of croaker diet by weight comprised bay anchovy (*Anchoa mitchilli*). However, bay anchovy is not as abundant in croaker diets in Chesapeake Bay in either the spring or fall, and even in summer months the contribution of bay anchovy to overall croaker diets is variable. Consumption of fish, particularly bay anchovy has been documented but not emphasized in previous croaker diet studies (Nemerson 2002, Overstreet and Heard 1978, Sheridan 1979). Presumably, a diet component that represents such a large fraction of the overall diet must be important for growth and production of croaker in Chesapeake Bay. The ecological and evolutionary consequences of variation in diet have been a subject of considerable research (Bishop and Wear 2005, Mason et al. 1998, Stephens and Krebs 1986). For fish, it has been shown that variation in diet can have important implications on the

66

growth, condition and survival of individuals (Moellmann et al. 2003, Yaragina and Marshall 2000). Often changes in diet are believed to optimize growth (Mittelbach and Persson 1998b, Miller et al. 1990). However, the links between diet variability and growth, condition, and survival remain poorly understood in the field.

Piscivory is believed to be a life history pathway that permits evolution of increased body size more efficiently than through other means (Mittelbach and Persson 1998a). Keast (1985) distinguished primary piscivores, fish that adopt a piscivorous diet within the first few days to months of life (e.g. Pikes *Esocidae* in freshwater systems and mackerel and tunas *Scombridae* in marine systems (Shoji and Tanaka 2001) from secondary piscivores, which become fish eaters much later in life. Keast (1985) hypothesized that secondary piscivory is a way that species or individuals maintain energetic efficiency as they grow. Consuming fish may be energetically expensive if foraging and handling costs are high, but the ratio of prey to predator size has been found to favor piscivory in larger fish (Juanes et al. 2001). Additionally, energetic assimilation of fish prey in fish predators may be greater and may provide greater nutritional values than other food items (Mittelbach and Persson 1998b). These findings suggest that there are likely substantial fitness consequences to consumption of fish prey and that these consequences should translate into impacts on the growth and ultimately the fitness of individuals adopting piscivory.

In the fisheries literature, the term "condition" refers to a fish's health. For example, a fish in "good condition" may refer to the "plumpness" of an individual fish, relatively fast growth rates of individuals, or the storage of fats and lipids as energy. Bioenergetically, this means that the fish has surplus energy sources that can be

allocated to growth and reproduction beyond the energy required to meet basic metabolic and maintenance costs.  Implicit in the use of the term "good condition" is that individuals in good condition have higher growth, survivorship, and reproductive success, usually translating into greater fitness.  In contrast, poor condition may be an indicator of a stressed or food limited population.  The concept of condition implies that the current physiological state of an individual has future consequences, although the timescale over which these consequences accrue is rarely rigorously defined.

A range of indices of condition have been proposed that include morphometric, calorimetric and biochemical approaches (Anderson and Neumann 1996, Bolger and Connolly 1989, Ferron and Leggett 1994).  Each approach integrates the current physiological condition over different time scales, and thus likely reflects the consequences of differences in condition over similarly different time scales.  Historically, the most common measures of condition in fisheries science are morphometric indices using length and weight measurements, which are measures commonly taken in sampling programs.  Morphometric measures of condition typically integrate the physiological status of an individual over extended time scales (months to seasons).  Thus, morphometrically-derived condition indices also likely forecast relative fitness for extended periods into the future.  Two common morphometric measures of condition are Fulton's condition factor (K) and relative weight (Wr).  Fulton's condition factor (K) describes condition based on the principle that weight increases with the cube of length (Fulton 1904, Ricker 1975).  Relative weight, Wr, also uses species specific weight-length relationships to quantify the weight-length relationship in relation to other fish in the sample (Anderson and Neumann 1996).

However, these measures should be used with caution as the relationship of weight and length may change with different populations of fish and by season (Blackwell et al. 2000, Sutton et al. 2000).

Other measures of condition relate the mass of one tissue type to that of the overall body weight. Two of the most common are the gonadosomatic index (GSI) and the hepatosomatic index (HSI). GSI is the ratio of the weight of reproductive organs and gametes to total body weight and HSI is the ratio of liver weight to total body weight. Both indices have been used to understand how fish allocate and store energy such that fish with higher index values are considered to have allocated energy either to the gonad or the liver that can be used for reproductive effort. GSI is a direct estimate of the investment in reproductive effort, whereas HSI reflects lipid stores that may be invested in subsequent egg production. Although not a direct measure of reproduction, liver condition has been correlated to recruitment success in cod *Gadus morhua* (Marshall et al. 1998, Marshall et al. 2000, Yaragina and Marshall 2000). Both of these measures of condition involve weight measurements which are subject to variability of water content in fish tissues. Therefore, more direct calorimetric indices have been suggested including the energy density (J/g) of individual tissues measured by bomb calorimetry, proximate composition analysis (Brown and Murphy 1991, Lukaski 1987) and bio-electrical impendence (Cox and Hartman 2005, Duncan et al. 2007).

Most morphometric and calorimetric measures of condition are useful, but their response time is likely of sufficient duration to make them incapable of reflecting changes in feeding and habitat on a short time scale. Biochemical indices of condition, usually based on chemical composition of lipids (Fraser 1986), protein synthesis

(Caldarone 2006, Peck et al. 2003), the synthesis of specific enzymes (Ueberschar and Clemmesen 1992) or RNA:DNA ratios (Buckley et al. 1999) are more direct measures of the condition of an organism. All of these measures respond within hours- days of changes in the physiological status of the individual fish and thus reflect environmental and habitat impacts on condition over similar time scales. However, the link between these temporally sensitive measures and fitness is less well established. Lambert and Dutil (1997) have shown that chemical composition data can be related to HSI-based indices and RNA:DNA ratios have been shown to be accurate proxies for growth in copepods (Wagner et al. 1998), larvae of freshwater fish (Heyer et al. 2001), larvae of marine fish (Buckley 1984), juveniles of estuarine fish (Malloy and Targett 1994, Malloy et al. 1996, Rooker et al. 1997), and juvenile marine fish (Smith and Buckley 2003b, Stierhoff et al. 2006).

Here, I use a suite of condition indices to examine the consequences of variability in diet on the condition of croaker in the Chesapeake Bay. Specifically, I test the hypothesis that croaker with a higher proportion of bay anchovy in their diet are in better condition. To test this hypothesis I use both experimental and field data to link diet to appropriate measures of condition and growth and subsequently relate condition to patterns in stomach content analysis. The ultimate objective of this work is to evaluate the consequences of a variable diet in Atlantic croaker and determine whether certain food items are important to the condition of individual fish. I apply three approaches to quantify the energetic consequences of diet choice in croaker: nucleic acid-based condition (RNA:DNA), energy density using bomb calorimetry and four common morphometric measures of condition (K, Wr, HSI, and GSI). Each

approach provides insight into the consequences of dietary choice at different time scales and in different tissues. To quantify condition of croaker in the short term, I used nucleic acid-based indices to determine the relationship between recent growth of croaker fed different prey types and rations in controlled laboratory experiments. Subsequently, I predicted growth rates of wild croaker collected in Chesapeake Bay using the laboratory-based relationship of RNA:DNA to growth. I also used bomb calorimetry and morphometric measures to quantify condition. I then described the relationships between these metrics and stomach content analysis to determine whether long-term diet choice affects condition and growth.

**METHODS**

I conducted both laboratory experiments and field sampling to describe the effect of diet on condition of individual Atlantic croaker. Laboratory experiments were designed to provide data on the relationship between known diet composition and condition indices. Field sampling was designed to provide samples of the distribution of diets and associated condition in wild croaker. Samples from both the laboratory experiments and the field were processed in the same fashion.

*Laboratory Growth experiments*

In order to develop a predictive relationship between growth and RNA:DNA ratios, I conducted controlled laboratory growth experiments at $12^{o}C$, $20^{o}C$ and $27^{o}C$ in which ration was manipulated. All experimental work was conducted at the Chesapeake Biological Laboratory, Solomons, MD from 2005-2006. Trials were conducted in 189-liter square, flow through tanks provided with temperature controlled,

ambient river water from the Patuxent River.  Salinities were constant within a trial and varied from 10 – 14 between trials.

Croaker used in the laboratory experiments were collected in several ways. Juvenile croaker (~0.5-2 g wet weight, ~50-95 mm TL) were caught with midwater and bottom trawls in the Patuxent River in the fall of 2004 and 2005.  Tow lengths were 10 and 5 minutes with the midwater and bottom trawls respectively to minimize capture stress.  Fish were kept in the lab for several months to obtain a size of at least 18 grams before being used in any experiment.  Temperature, salinity and dissolved oxygen were measured daily.  Before each growth experiment, fish were held at the experimental temperature for at least one week.  Any fish that showed signs of injury or appeared to be in poor condition were not used in experiments.  All work was conducted under procedures approved by the University of Maryland Center for Environmental Science Institutional Animal Use and Care Committee.

To begin an experiment, croaker were measured, weighed and introduced to tanks on the evening before the experiment began to acclimate fish to the tanks.  In the 12 and 20$^{\circ}$C experiments, two fish ranging in weight from 14-27g and 35-50g respectively were added to each of 22 tanks.  In the 27$^{\circ}$C growth experiment, larger fish were used (50-124g) and there was only one fish in each tank rather than two.  Croaker were fed different rations and a variety of different prey types for 14 days. Commercially available freshwater mysids (Piscine Energetics, www.mysis.com) were used as a food source in all trials.  In the 27$^{\circ}$C experiment, chopped frozen bay anchovy were the alternative prey treatment.  However, small croaker (< 20 g) would not eat bay anchovy, and so polychaetes (*Nereis sp*) were substituted as an alternate food source for

these trials. In the 27°C experiment there was a low (4% of body weight) and high (*ad libitum*) ration. In the 12 and 20°C experiments, there were three ration treatments where fish were starved, fed 4% per day of total body weight, or fed *ad libitum*. Treatments were maintained for 14 days. Fish were starved on the final day of the trial and then on the next day, fish were removed and given a lethal dose of MS-222. Fish were weighed, measured, and a sample of white hypaxial muscle tissue was taken to analyze RNA/DNA ratios for comparison to field samples.

*Field collection*

Fish used in this comparative study of diet and condition were collected during the CHESFIMS program in 2004-2005. Details of the collection techniques employed during CHESFIMS are provided in Chapter 1, and are only summarized here. Briefly, research cruises of 5-7 day duration were conducted three times annually, in May, July, and September. An additional cruise was conducted in August 2005 to expand the temporal coverage of diet and condition data. The CHESFIMS sampling design consisted of both fixed and random stations with stations proportionally allocated to strata according to strata volume. A midwater trawl with an 18-m$^2$ mouth-opening with 6-mm cod end was deployed to collect primarily pelagic and benthopelagic fishes. Croaker was one of the most frequently caught species in this survey. Oblique tows of the net were fished from top to bottom, and were 20 minutes in duration. The net was deployed in 2-min stepped depth increments to insure that it fished the entire water column with the last 2-min interval fishing the bottom to sample benthic species. A minilog recorder was attached to the top line of the net to document depth, temperature,

and time during each tow.  At each station, a CTD was deployed to measure dissolved oxygen, salinity, and temperature in the water column.

Croaker caught in the midwater trawl were separated and kept alive in water buckets until further processing.  Just before processing, fish were killed by the addition of a lethal dose of MS-222.  Individual fish were then measured for total length (nearest mm), weighed with a spring scale (wet weight, nearest g), and muscle sample taken for RNA:DNA analysis.  White muscle tissue was taken from the hypaxial muscle above the lateral line using a separate, new, clean razor blade for each fish.  Muscle tissue was placed in separate cryovials and frozen in liquid nitrogen.  Up to 20 fish were processed for each station, ensuring that the time between the end of the tow and when the samples went into the liquid nitrogen was not greater than one hour. The time required to take samples for RNA:DNA was usually less than 45 minutes. After sampling for nucleic acid analysis, fish carcasses were frozen in individual bags in an onboard freezer.

*Sample processing*

Field-caught fish were thawed and were again weighed and measured to account for uncertainty in field measurements.  Otoliths, stomachs, livers, and gonads were excised from each fish.  Stomachs, livers, and gonads were weighed wet (g). Stomachs were preserved in ethanol.  Livers and gonads were placed in aluminum weigh dishes, weighed, and placed in either a drying oven or freeze drier to be dehydrated.  Intestines were stripped of feces and fish carcasses were then refrozen. Frozen fish were then passed through an industrial meat grinder.  The ground carcass

was collected in aluminum weight pans and then dried in a drying oven or in a freeze drier.

The dehydrated livers, gonads, and whole fish were weighed repeatedly until they reached a constant weight, indicating that they were void of all water. Tissue was then homogenized with a grinder and/or mortar and pestle. Scales and fin tissue were further cut up with scissors if necessary. Powdered fish tissues were placed in air tight containers to await calorimetry.

*Measures of Condition*

## 1) Morphometric Measures of Condition

Two whole-body measures of condition were developed for all croaker collected for stomach analysis from 2002-2005. I calculated both Fulton's condition index (K) and relative weight (Wr) using the following equations:

$$K = (TW/TL^3) \times 10^5 \qquad \text{Eq. 3.1}$$

$$TW = aTL^b \qquad \text{Eq. 3.2}$$

$$Wr = (Wi/Ws) *100 \qquad \text{Eq. 3.3}$$

where TL is the total length in mm, TW is the total wet weight in grams, and a and b are fitted constants. To determine if the relationship between total weight and total length changed with season, I performed an ANCOVA on log transformed values using season as a covariate. To calculate Wr, first the length-weight relationship was developed using Eq. 3.2 for each season. A predicted weight, Ws, was predicted from these equations given the observed length of the individual fish. Wr was calculated as the ratio of the observed weight of the individual fish (Wi) to the length specific weight predicted by the length weight equation (Ws) (Anderson and Neumann 1996).

I used two measures of condition based on the relative importance of different body tissues for fish in 2004-2005 (n=368). Liver and gonad weight in relation to body weight (hepatosomatic and gonadosomatic indices) have long been used as measurements of body condition and reproductive state. They are calculated for each individual using:

Hepatosomatic index (HSI) = [liver wet weight/TGW] x 100          Eq. 3.4

Gonadosomatic index (GSI) = [gonad wet weight/TGW] x 100.          Eq. 3.5

where TGW is the total weighted minus stomach, liver, and gonad weight.

## 2)      RNA:DNA Analysis

RNA/DNA ratios were quantified for laboratory and field-caught croaker using a modified protocol from Calderone et al. (2001). Frozen 10-25 mg samples of hypaxial muscle tissue were placed in 2% sarcosil solution, shaken for thirty minutes, and then sonicated for 20 seconds to dissociate nucleoproteins. Samples were shaken for an additional hour and in the rare case that muscle tissue did not dissociate, the sonication and shaking process was repeated. Total nucleic acid levels (TNA) were quantified for each sample after adding ethidium bromide as a fluorochrome. Subsequently, RNA and DNA were quantified after addition of RNase and DNase respectively. Concentrations of individual nucleic acids were determined by difference. Addition of DNase was necessary to determine whether there was significant background fluorescence in juvenile and adult croaker tissue. Two to three replicate subsamples were analyzed for nucleic acid content and the mean value of all subsamples was used in statistical analysis.

## 3) Bomb Calorimetry

Because fish weight is highly dependent on water content, morphometric measures of condition are only crude estimates of condition. Therefore, bomb calorimetry of homogenized tissue samples was employed to quantify energy density. Croaker from laboratory experiments and those collected in the field in 2004-2005 were weighed to a constant weight, as detailed above. The dried tissues were ground in a commercial coffee grinder and the resultant powder was formed into pellets weighing approximately 0.5g using a pellet press (Parr Calorimeter, Moline IL). The energy density of the pellets was determined in a bomb calorimeter (Model 6200, Parr Instruments, Moline, IL). Two pellets, each representing separate subsamples of each fish were combusted in the bomb and the average of the two was reported as the energy content. If the percent difference between these two samples was greater than 10%, a third subsample was measured for energy content in the bomb and the closest of the three values were averaged to get the mean energy content.

*Stomach Content Analysis*

Preserved stomach contents were examined and quantified under a dissecting microscope using successful protocols established in Chapter 1. Briefly, full stomachs were weighed, and the contents were dissected out. The remaining tissue was reweighed to provide an estimate of total stomach contents. Prey items were identified to the lowest taxon feasible. Each prey item was weighed and individuals were counted. When whole fish were found in the stomach, the total length of the fish was measured. Diet was quantified using percent composition by weight (%W) for each individual fish.

*Statistical analyses*

For the experimental analysis, differences in growth rate, RNA:DNA ratio, and energy density were tested using a separate two-way ANOVA for each experimental temperature where the factors were food type and ration. Subsequently, pairwise comparisons were made between the treatments (food type and ration combinations). The distribution of RNA:DNA ratios were not normally distributed, but only slightly skewed. Therefore, for ease of interpretation and to be able to use RNA:DNA as a predictor of growth in field-caught fish, I used RNA:DNA ratios directly as the response variable rather than some combination of the concentrations of these nucleic acids in the ANOVA and regression analysis. In the laboratory experiments, I used multiple linear regression to model the relationship between daily specific growth rate (dependent variable) and RNA:DNA, temperature, and fish mass (independent variables).

For field collections of croaker the six measures of condition were tested for correlations using nonparametric Spearman rank correlation to evaluate their usefulness. The significance value was adjusted for multiple comparisons using the Bonferroni adjustment ($P_B=0.05/15=0.0033$) to maintain an experimentwise Type I error rate of 5%. These condition indices were then compared with the total weight of the stomach contents and with the two prey types that constituted most of croaker diets by weight, polychaetes and anchovies. I did not test for correlations between condition and other prey items because many prey items were rare and to do so would increase the risk of finding a spurious correlation. Because the diet data were not normally distributed, I used the non-parametric Spearman's rank correlation coefficients to

understand the relationships between condition indices and total weight of all stomach contents, %W of anchovy, and %W of polychaetes in the diet.

**RESULTS**

*Laboratory growth experiments*

In laboratory experiments, croaker fed at different ration levels induced differences in growth rates (Figure 3.1). However, there appeared to be no effect of growth in fish fed different food types. At none of the temperatures tested was there a significant effect of food type on daily specific growth rate ($F_{1,16}=0.83$, P=0.3762; $F_{1,13}=0.60$, P=0.4511; $F_{1,8}=0.31$, P=0.5926 for $12^{o}$C, $20^{o}$C and $27^{o}$C respectively). However, there was a significant effect of ration on daily specific growth rate in the 12 and $20^{o}$C growth experiments ($12^{o}$C: $F_{2,16}=12.85$, P=0.0005; $20^{o}$C $F_{2,13}=6.56$, P=0.0107). At these temperatures, pairwise comparison indicated that the differences in growth occurred between the starved and fed fish, but there was no statistical difference in growth between the high and low ration treatments. At $27^{o}$C, there was only a high and low ration treatment and no significant difference in growth rate among ration treatments ($F_{1,8}=0.01$, P=0.9242). Furthermore, growth rates in this experiment were negative.

RNA:DNA in laboratory growth experiments did not exhibit the same trends as growth (Figure 3.2). There was no statistically significant effect of ration or food type on RNA:DNA ratios. However, RNA:DNA was lower on average in starved fish in both the 12 and $20^{o}$C experiments. Multiple linear regression indicated that RNA:DNA was significantly related to daily specific growth rate. However, temperature and fish

weight were not significant factors in predicting growth. These analyses indicated that daily specific growth (DSGR) could be predicted by:

$$DSGR = 0.097 \cdot RNA{:}DNA - 0.41 \qquad (\text{Figure 3, } R^2 = 0.28) \qquad \text{Eq. 3.6}$$

Subsequently, RNA:DNA ratios were quantified in field fish caught on the July cruises only (n=73). RNA:DNA ratios were compared with other measures of condition in field caught fish.

The utility of energy density as a predictor of daily growth rate was evaluated for the 14 day growth experiments at $12^{\circ}C$ and $20^{\circ}C$ experiment. There was very little difference in energy density between all treatment combinations and no statistical difference between fish fed different prey types or rations in the $12^{\circ}C$ and $20^{\circ}C$ experiment (Figure 3.4).

*Field Collection*

Mean energy density of laboratory fish was higher than that of field caught fish. The distribution of energy content values was also much wider in field fish, indicating that energy density might be a better predictor of condition in field fish with more variable feeding histories than laboratory fish (Figure 3.5). There were seasonal differences in several measures of condition. Fish weight was significantly related to length (Fig. 3.6), but statistical analysis of length-weight relationships indicated a significant effect of season on the overall relationship (ANCOVA, $F_{[3,894]}=6.37$, P=0.0003). Indeed, weight at length was slightly higher in summer than other seasons, yet within-season relationships were very similar in all seasons (Figure 3.6). Although there were differences in the weight-length relationship by season there appeared to be no difference in mean Wr by season (Figure 3.7). Weight and length were also used to

calculate Fulton's K values, which ranged from 0.070 to 0.50.  There was no seasonal

trend in Fulton's K (Figure 3.7).  As expected, GSI increased as the fall spawning

season approached (Figure 3.8).  Interestingly, HSI decreased from spring to fall

(Figure 3.8).  Both of these measures appeared to be higher on average in 2005 than in

2004.  Mean energy density increased slightly from spring to fall (Figure 3.7).

Data on multiple indices of condition from individual fish were correlated

(Table 3.1, Figure 3.9).  Fulton's condition factor was significantly correlated with all

morphometric measures of condition measures, but showed no relationship with

RNA:DNA ratios.  The highest correlations were between K and Wr (r=0.76) and

between K and GSI (r=0.61).   Relative weight was correlated with energy density, K,

and GSI.   HSI was correlated with K only.  Energy density and K were significantly

positively correlated with the %W of anchovy in croaker diets (Table 3.2).  No

measures of condition were significantly correlated with %W of polychaetes in diet.

The total weight of food in stomachs was significantly positively correlated with K and

HSI.  No other measures of condition were related to diet composition.  For clarity,

only the correlations between %W of anchovy and polychaetes are shown in relation to

K (Figure 3.10), but scatter plots are similar between diet and condition variables.  The

correlation between energy density and %W in the diet is not clear.


**DISCUSSION**

In croaker, many morphometric measures of condition were correlated with

each other, but there was a lack of strong coherence between all measures of condition.

This finding is similar to studies in several species of fish that also reported a similar

81

lack of coherence among different measures of condition (Gilliers et al. 2004, Lambert and Dutil 1997, Suthers et al. 1992). One reason for this discrepancy is the different assumptions made by each measurement. Fulton's condition factor (K) is often considered a poor measure of condition because it assumes isometric growth and many studies have shown that growth in fish varies with ontogeny (Finn et al. 2002, Osse et al. 1997, Peck et al. 2005). However, Fulton's K was correlated with all other measures of condition except RNA:DNA ratios indicating that K may be a sensitive measure of changes in condition in adult croaker. Wr was highly correlated with K, which is to be expected because both are based on the same length-weight measurements. However, unlike K, Wr was not correlated with HSI, nor with any measure of diet. Both energy density and K were correlated with %W of anchovy in croaker diets. Because determination of energy density is such a time consuming process, K is a good candidate to assess condition in croaker because of its simplicity.

Ferron and Leggett (1994) and Suthers (1998) both hypothesized that the apparent discrepancies between measures of condition can be explained by understanding that the temporal resolution and responsiveness of the individual condition indices differ. If their hypothesis is correct, one would predict that indices that respond over similar time frames are more likely to respond similarly than are those that respond at substantially different time frames. I intentionally chose measures of condition that respond over different time scales to find the condition measure that would be most closely correlated with diet. In particular, RNA:DNA ratios have been shown to respond to changes in feeding and growth on the order of hours to days, the time scale on which stomach contents represent diet.

Stomach content analysis gives a snapshot of consumption habits in fish and reveals what an individual fish was eating in the past day or less depending on the type of prey (Jackson et al. 1987). While simple conceptually, interpretation of stomach contents can be problematic. Specifically, differential gut passage times can cause the diet to be overrepresented by prey items that are slow to digest. Jackson et al (1987) found that crustacean and fish muscle was digested in *in vitro* simulation experiments in about 12-17 hours, whereas gelatinous zooplankton were digested in only 20 minutes. Larval fish are digested in less than one hour (Able et al. 2007, Jackson et al. 1987). Thus if a fish were to eat a diet containing equal proportions of crustaceans and larval fish, stomach contents analysis would indicate that the diet was actually strongly biased toward crustacean prey purely as a result of differential prey digestibility.

Like measures of diet, indices of condition also operate on characteristic time scales. Studies indicate that the temporal response of RNA activity occurs at a time scale such that the condition of the fish at the time of capture reflects the recent feeding environment (Ferron and Leggett 1994). The quick response of RNA/DNA ratios has two advantages for estimating fish condition: no assumption regarding diet beyond current stomach contents is needed, and it removes the need to make assumptions about prior movement. In contrast, classic measures of condition, (e.g., Fulton's K, Wr) rely on relationships between weight and length. Accordingly, these measures of condition respond much more slowly and integrate over longer time periods. One would expect the snapshot of stomach contents to be most correlated with RNA:DNA ratios which are responsive on a similar time scale of days. However, there was no correlation with growth predicted by RNA:DNA ratios and stomach contents.

Here I quantified correlations between condition of individual fish and their most recent diet. I found significant positive correlations between the fraction of anchovy in the diet of croaker and the energy density and K of these fish, suggesting that anchovy is an important source of nutrition in some individual croaker. The correlation coefficients between condition and incidence of anchovy were weak and closer examination of the relationship does not show a strong relationship between these two measures. However, the correlation between anchovy consumption and both energy density and K is supported by the fact that croaker are in better condition in summer months, when the proportion of anchovy in their diet is highest (Chapter 1). An alternative explanation for this correlation is equally possible - that croaker in higher condition are able to feed on more mobile prey such as anchovy.

This study suggests that prey type, rather than simply overall food availability affects condition in fish. This result is not conclusive but is important as evidence increases that anthropogenic effects and climatic forcing dramatically alter food webs (Knowlton 2004, Pandolfi et al. 2003). Recent studies document the relationship between fish production and poor environmental conditions (Alheit and Niquen 2004, Page et al. 2007). However, little research has been conducted to understand the trophic linkages between the condition of fish and specific prey types (Gendron et al. 2001). To understand the role of prey type on condition in fish, more specific indicators of diet such as stable isotopes or lipid biomarkers (Sargent et al. 1997, St. John and Lund 1996) should be utilized to effectively track prey chemical signatures to predator chemical composition and condition, in addition to correlating diet with condition indices as I have done here.

In studies of larval and juvenile fish growth, RNA:DNA ratios were found to be highly predictive of condition or growth.  Many studies have related RNA:DNA ratios to recent feeding and growth (Clemmesen 1994, Malloy and Targett 1994).  For example, Caldarone et al. (2003) reported a multiple regression model that predicted specific growth based on RNA:DNA ratios that explained over 40% of the variation in the data.  In my laboratory experiments, RNA:DNA ratios were useful predictors of recent growth.  However, RNA:DNA ratios could only explain 28% of the variability in growth.  Although in previous studies temperature has been an important factor in predicting growth rates from RNA:DNA ratios (Caldarone 2006, Melzner et al. 2005, Peck et al. 2003, Stierhoff et al. 2006), including temperature in this model to predict daily specific growth rate of croaker did not explain any additional variability in the data.  There are several possible explanations, the first being that growth rates were relatively low in experiments at all temperatures, and much lower than expected at 27$^o$C.  Secondly, the RNA:DNA technique has been used frequently in larval and to a lesser extent juvenile fish, but the application herein is the first attempt to estimate recent growth in sub-adult and adult fish using this technique.

Although I was able to alter growth by varying rations in laboratory experiments, I was not able to induce statistically different RNA:DNA ratios in these laboratory growth experiments.  One reason for the poor performance of RNA:DNA ratios in this study is that growth rates in general are much lower in juvenile and adult fish than in larval fish, suggesting that it might be more difficult to detect differences in growth using RNA:DNA ratios when the level of the response variable (growth) is very low.  Furthermore, when quantifying RNA:DNA ratios for larval fish, the entire larva is

used so that any variability in protein synthesis within the larva is accounted for. However, it would be impossible to quantify nucleic acids for whole adult croaker, forcing us to analyze portions of tissue. Protein synthesis is variable among types of tissue and even within tissue types sampled at different areas of the fish (Mukherjee and Jana 2007, Smith and Buckley 2003a). Thus, using small subsamples of tissue may not yield RNA:DNA values that are representative of the whole adult fish. However, with advancement in molecular techniques and the success of RNA:DNA ratios in assessing larval condition, these techniques should not be ruled out entirely. The potential application of RNA:DNA ratios to evaluate condition and growth in adult fish should be further developed.

This work suggests that the *quality* of food eaten by fish, not just the *quantity* of food is important in determining condition in fish and that certain prey items may be important to the growth and reproductive success in adult fish. Thus, secondary piscivory, which is common in aquatic environments where food webs are strongly size structured, might be an important phenomena that has often been overlooked. Able et al. (2007) documented piscivory, in particular cannibalism and scavenging, in *Fundulus heteroclitus,* another estuarine fish like croaker that is not a traditional piscivore. They suggested that this source of food could be important to individual fish and to the ecosystem. The relationship between particular food sources, condition, and reproductive success has rarely been studied (but see Marshall et al. 1998, Marshall et al. 2000, Marshall et al. 1999, Yaragina and Marshall 2000). However, as ecosystems and trophic relationships change with increasing anthropogenic influence on estuaries and coastal environments, the role of weak trophic interactions in food webs should be

more closely examined.

Table 3.1: Correlations between six measures of condition in Atlantic croaker. Numbers in parentheses are sample sizes. Significance at the P=0.0033 level (Bonferroni adjustment, P=0.05/15) indicated by *.

| | RNA:DNA | Energy density | Fulton's K | Wr | HSI |
|---|---|---|---|---|---|
| Energy density | -0.030 (63) | | | | |
| Fulton's K | -0.097 (69) | 0.34* (277) | | | |
| Wr | 0.0067 (72) | 0.30* (296) | 0.76* (355) | | |
| HSI | -0.063 (69) | -0.12 (278) | 0.31* (355) | 0.099 (355) | |
| GSI | -0.13 (69) | 0.31* (278) | 0.61* (355) | 0.22* (355) | 0.11 (355) |

Table 3.2:  Spearman rank correlation coefficients between the percentage of anchovy and polychaetes in diets of Atlantic croaker with six measures of condition. Significance at P=0.0042 (Bonferroni adjustment, P=0.05/12) indicated by *.

| | % W Anchovy | % W Polychaetes | Total weight of stomach contents |
|---|---|---|---|
| RNA:DNA | -0.06 | -0.13 | 0.013 |
| Energy density | 0.20* | -0.12 | -0.10 |
| Fulton's K | 0.24* | -0.13 | 0.24* |
| Wr | 0.069 | 0.019 | 0.007 |
| HSI | -0.0075 | -0.0018 | 0.17* |
| GSI | 0.12 | -0.044 | -0.057 |

Figure 3.1: Daily specific growth rate (DSGR, % body weight per day) for food and ration treatment combinations in a) 12°C, b) 20°C, and c) 27°C growth experiments.
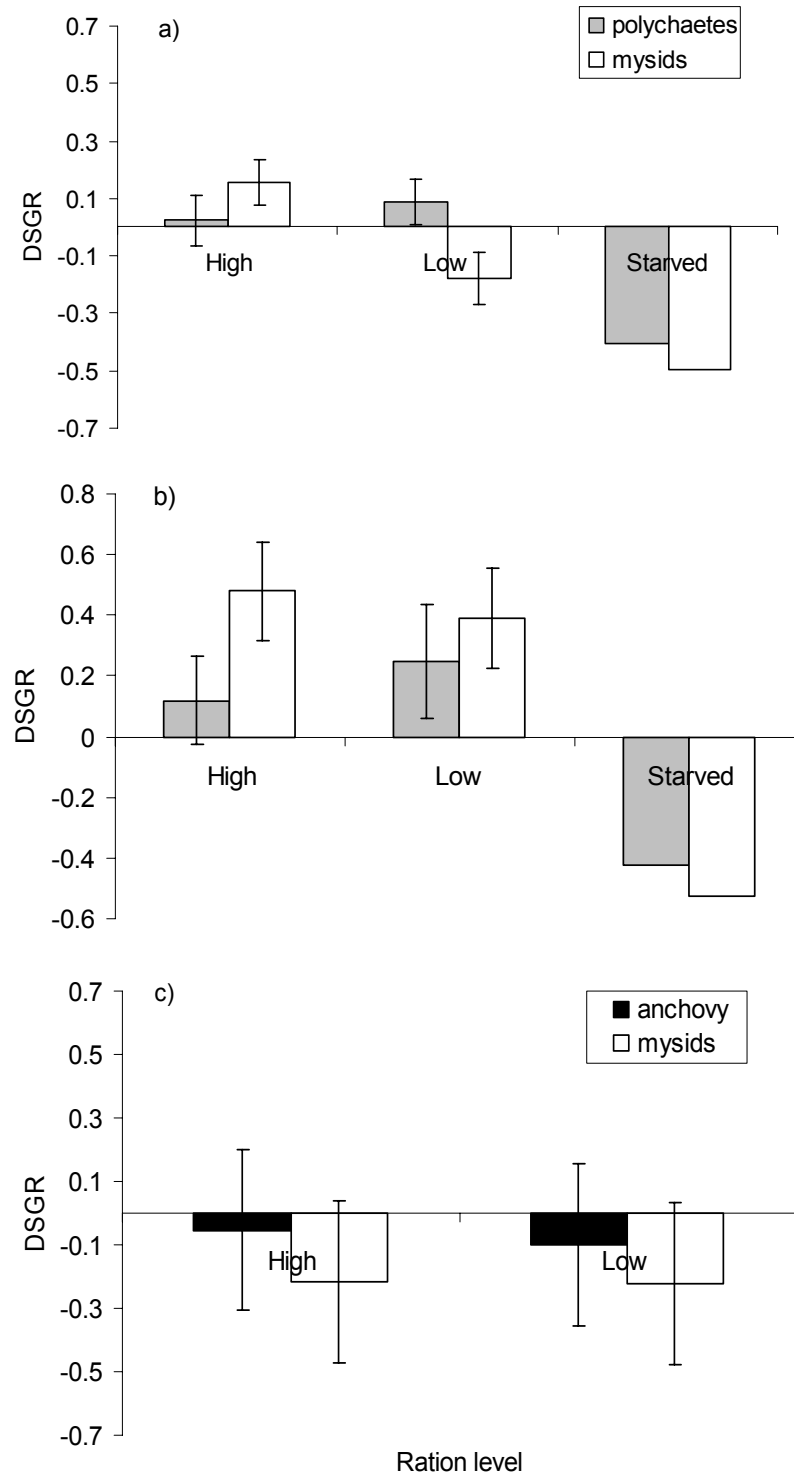
Figure 3.2: RNA:DNA for growth experiments conducted at a) 12$^{o}$C, b) 20$^{o}$C, and c) 27$^{o}$C
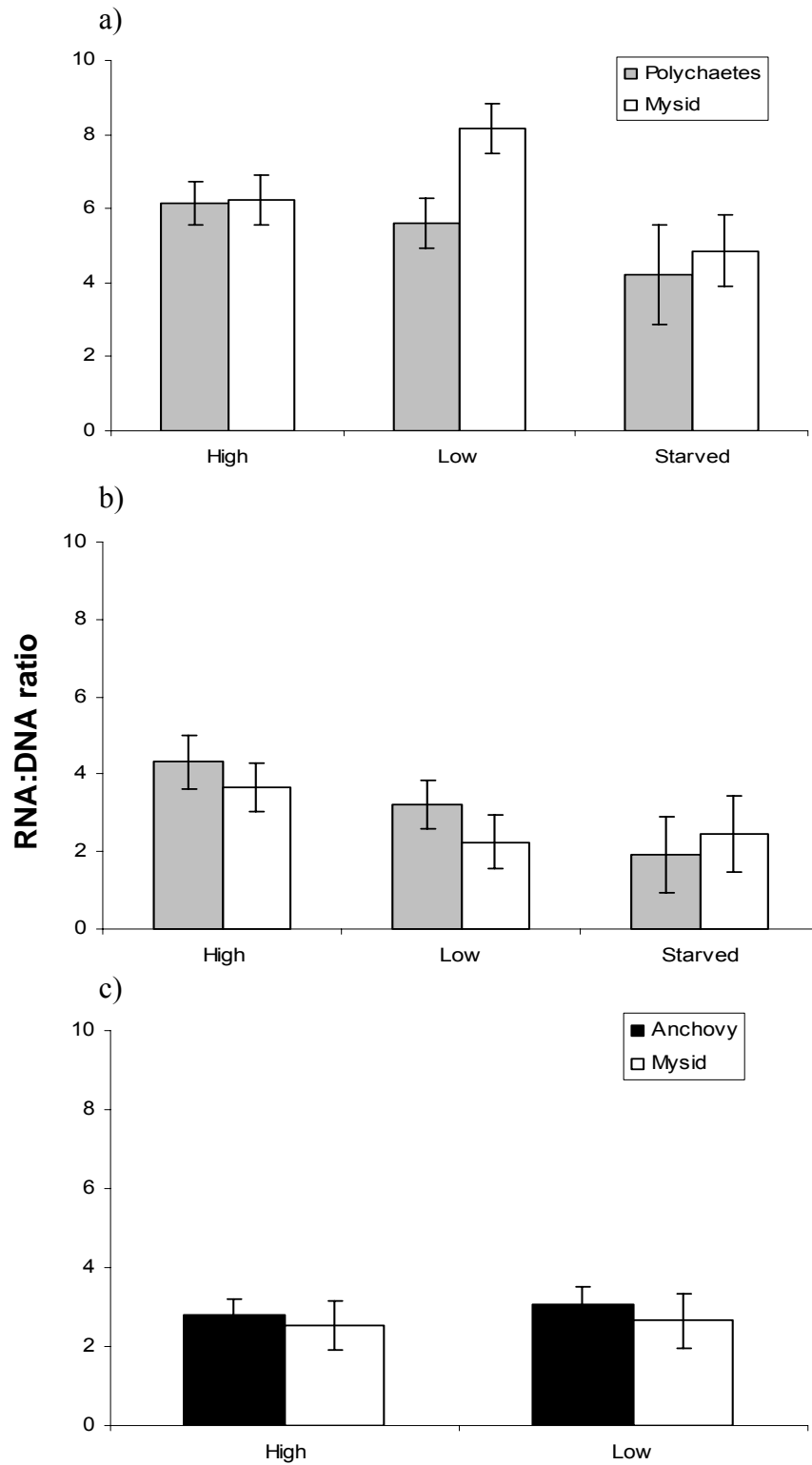
Figure 3.3: Daily specific growth rate predicted by RNA:DNA ratio. Regression line for all temperatures combined was DSGR=0.09665 (RNA:DNA)-0.41331, $R^2$=0.28).
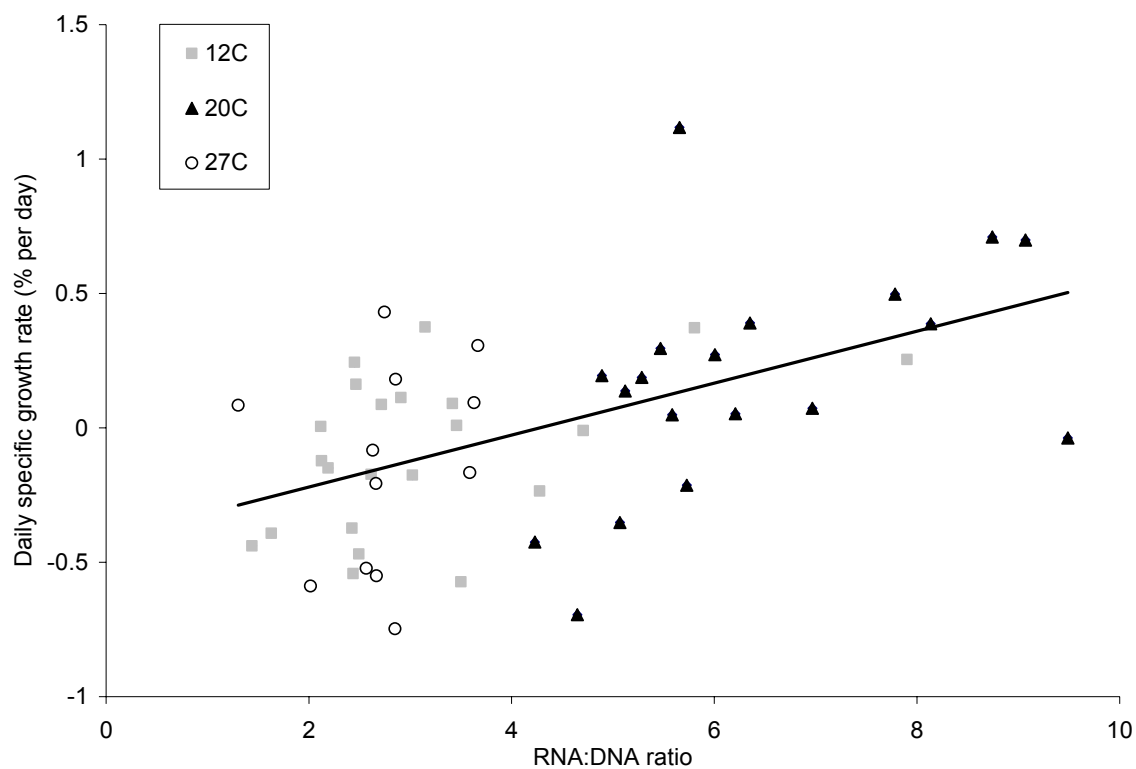
Figure 3.4: Energy content of homogenized fish (Kilojoules per gram dry weight) as determined by bomb calorimetry for fish from a) 12$^o$C and b) 20$^o$C growth experiment.

a)



b)
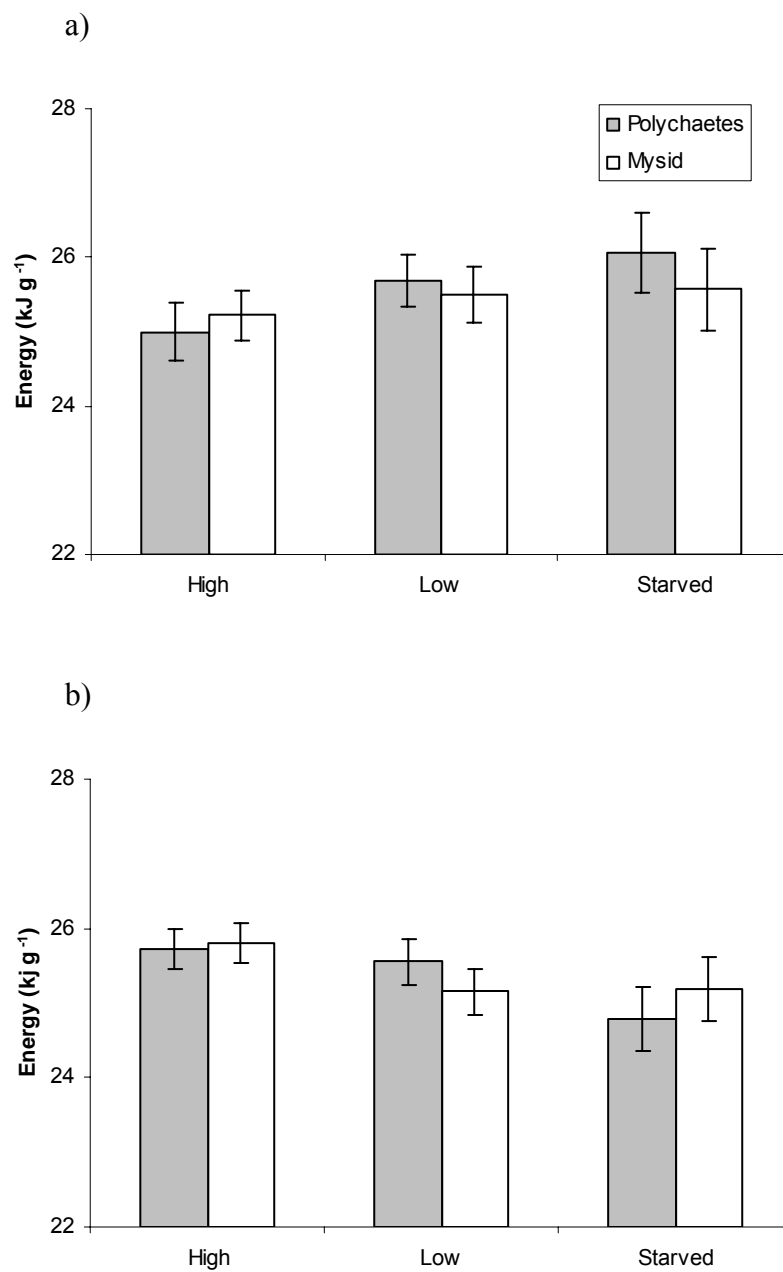
Figure 3.5: Distribution of energy density observations (1 kJ/g bins) for fish in growth experiments versus field-caught fish.
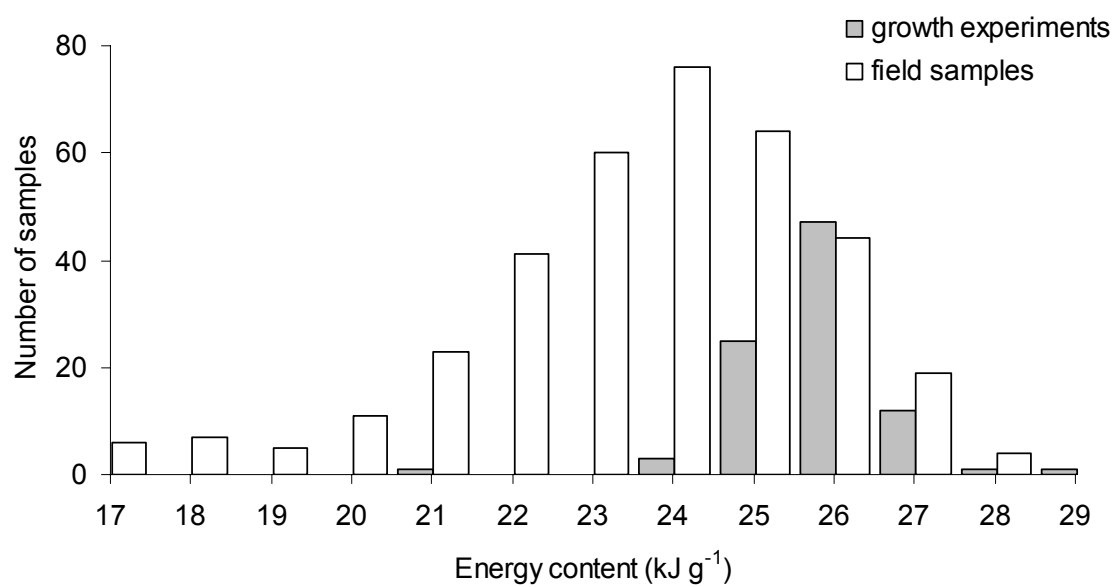
Figure 3.6: Seasonal relationships of total weight to total length in Atlantic croaker 2002-2005.
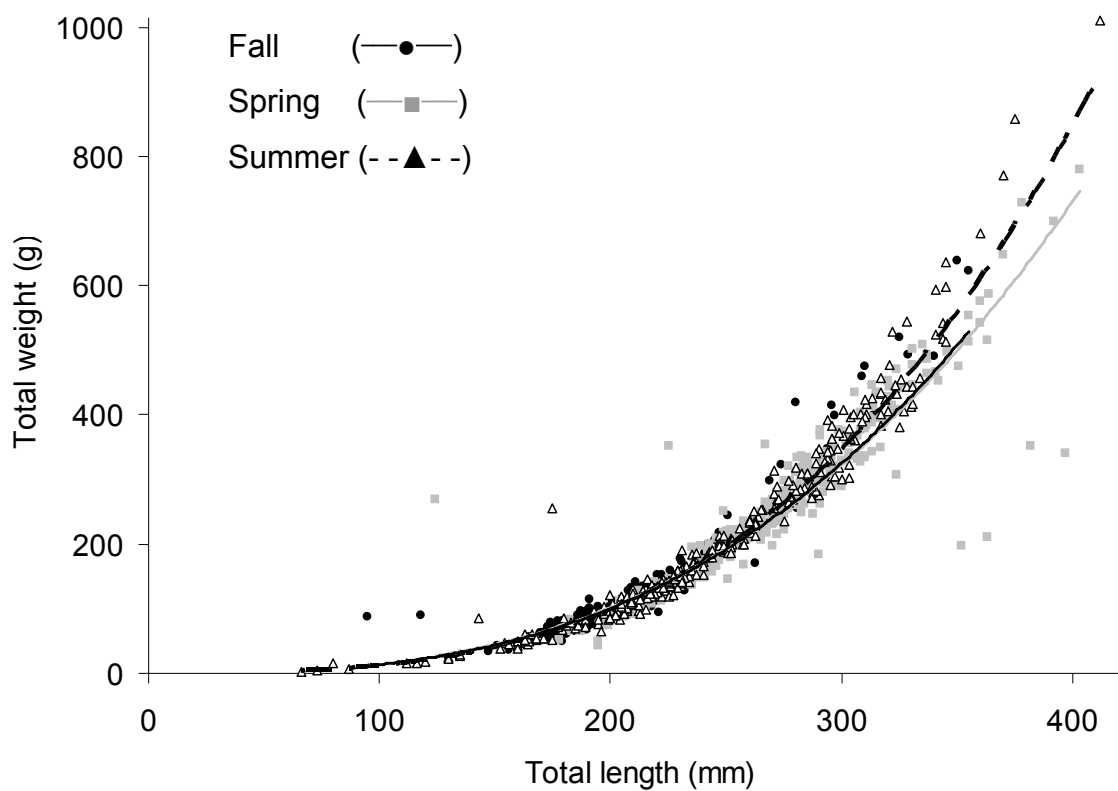
Figure 3.7: Seasonal means (+/- SD) of a) Wr, b) Fulton's K and c) Energy density in Atlantic croaker caught in 2004-2005.
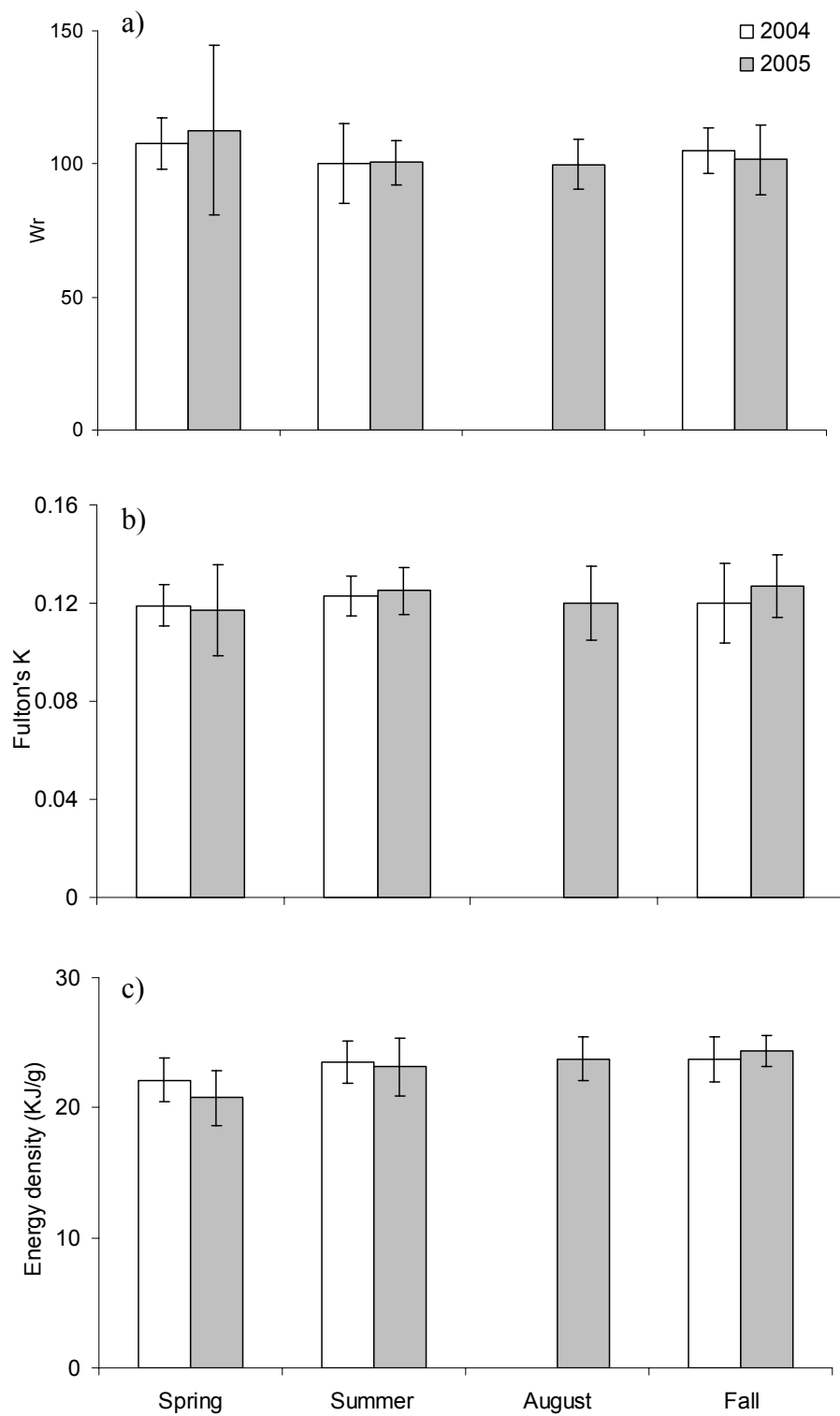
Figure 3.8: Seasonal means (+/- SD) of a) HSI and b) GSI in Atlantic croaker caught in 2004-2005.
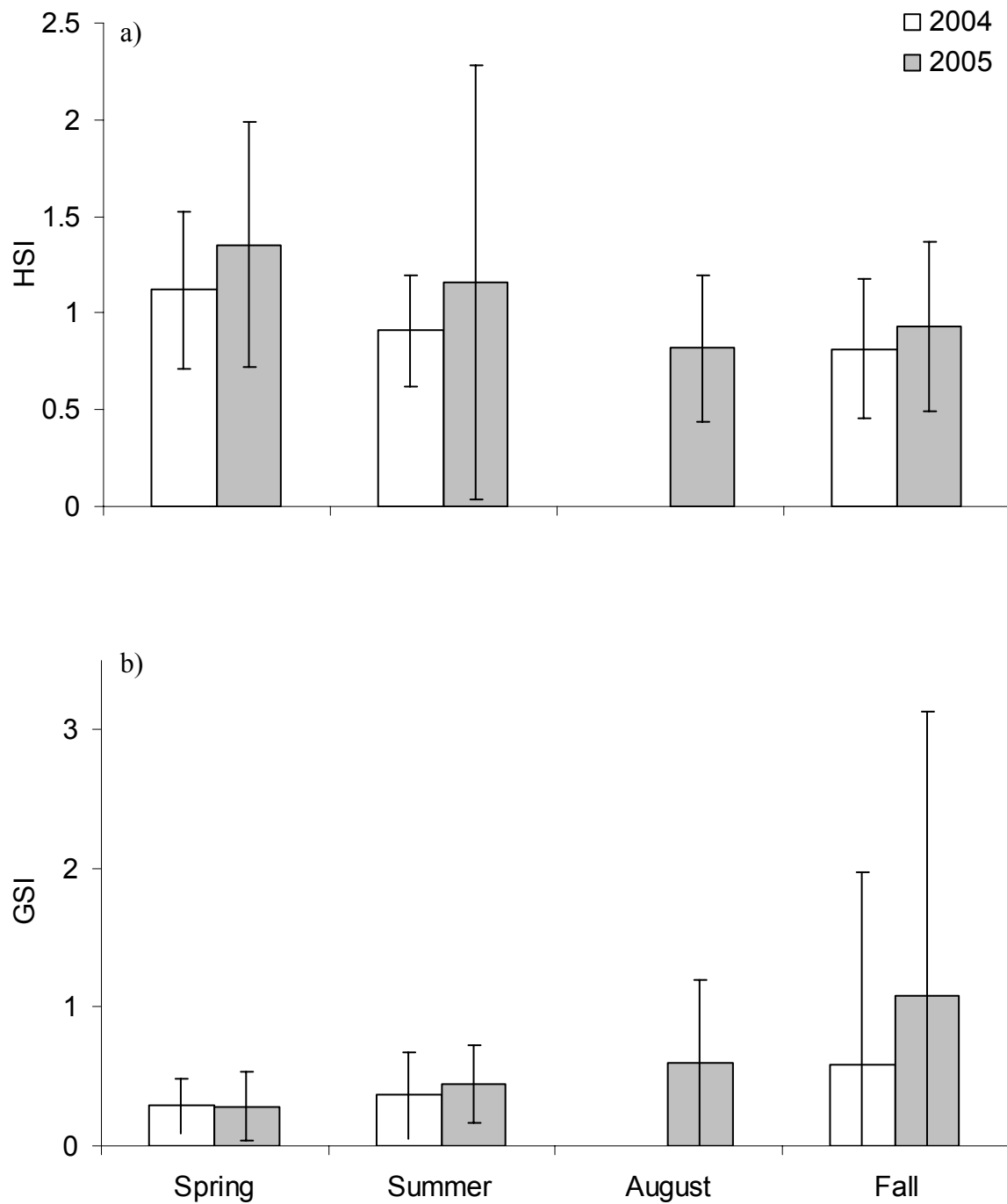
Figure 3.9: Scatterplot matrix showing correlations between different measures of condition in Atlantic croaker. For each measure the distributions are shown followed by the scatter plot with each subsequent condition measure.
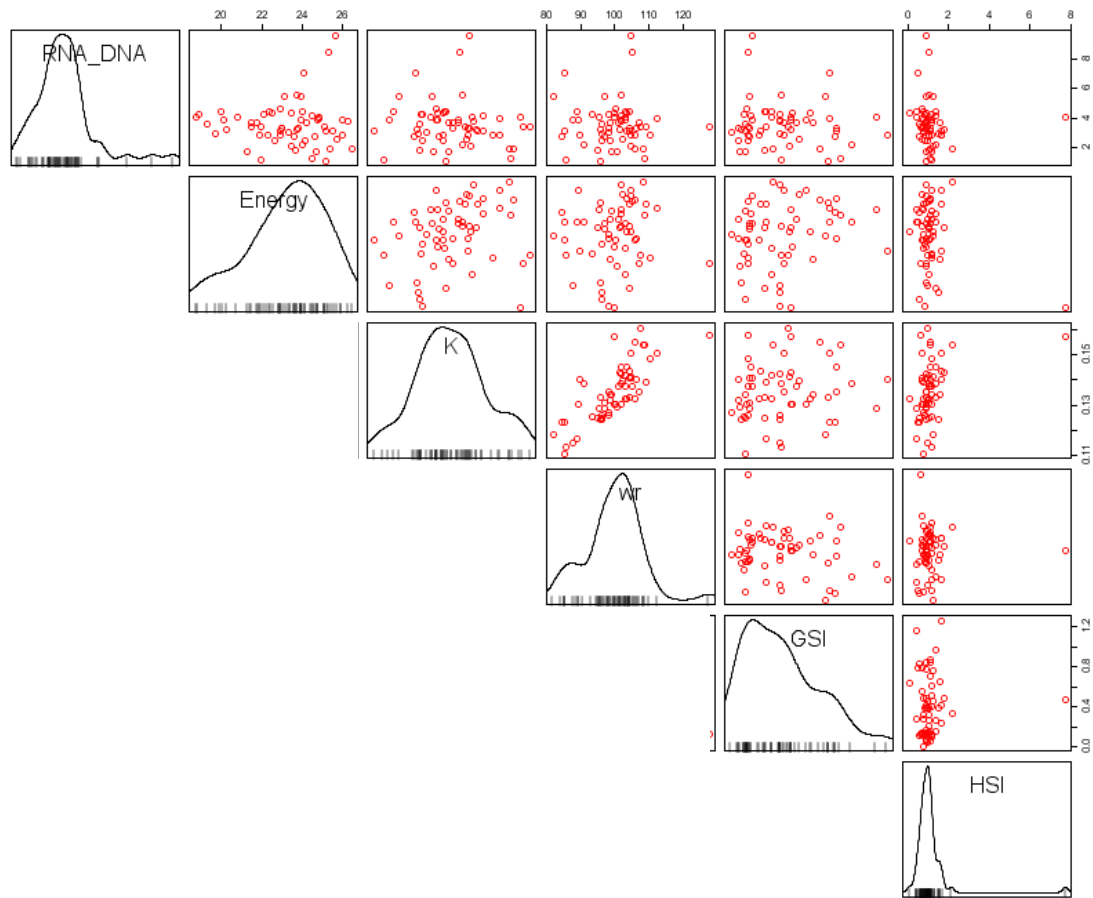
Figure 3.10: Relationship of Fulton's condition factor (K) with the proportion by weight (%W) of anchovy and polychaetes in the diet of Atlantic croaker.
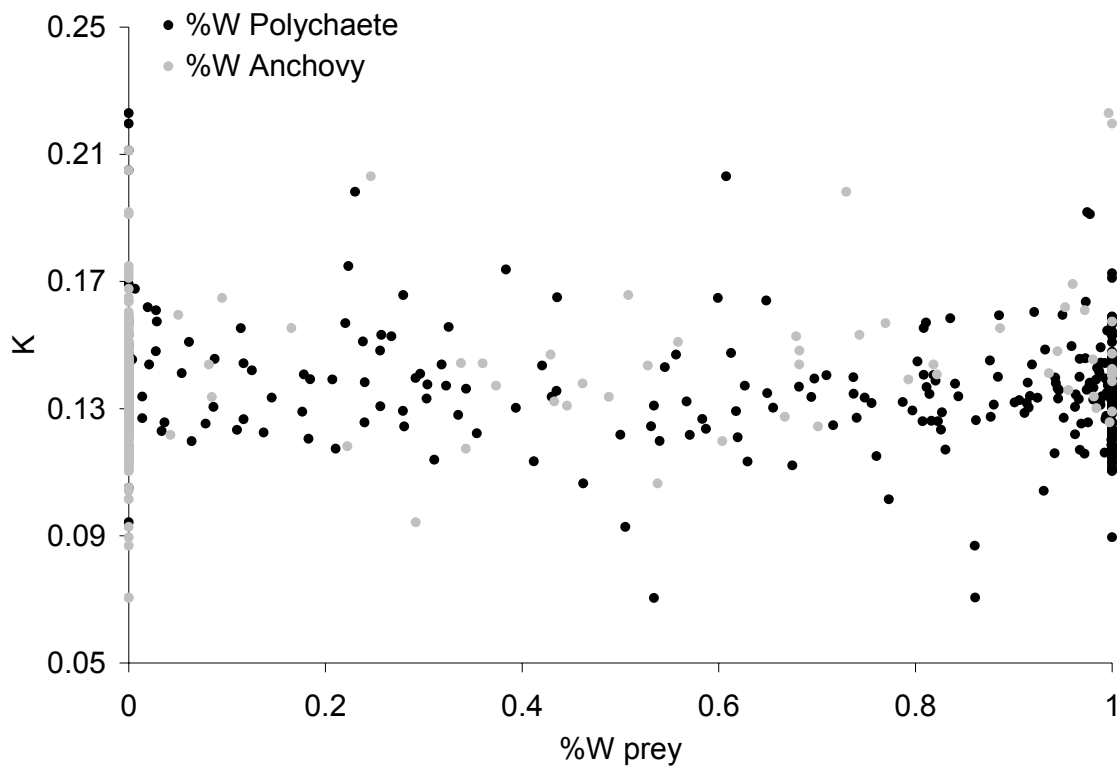
# CHAPTER 4: DEVELOPMENT AND VERIFICATION OF A BIOENERGETIC MODEL OF ATLANTIC CROAKER *MICROPOGONIAS UNDULATUS*

## INTRODUCTION

Quantification of bioenergetic patterns in individual species of fish provide insights into their life history (Roff 1983), growth and reproductive potential (Chipps et al. 2000, Luo and Brandt 1993), dietary demands (Hartman and Brandt 1995b, Trudel and Bosclair 1994) and habitat selection (Limburg 1996, Niklitschek 2001, Nislow et al. 2000). When linked with estimates of abundance, bioenergetic models can estimate trophic demand of the population, be used to infer the extent of potential competition among species (Hartman and Brandt 1995b, Labar 1993), and guide stocking levels in managed ecosystems (Rand and Stewart 1998a, b). Bioenergetic-based population dynamic models have also been developed (Megrey et al. 2007b). To answer ecological questions, bioenergetic models have been used to predict nutrient regeneration (Kitchell 1979, Durbin and Durbin 1983), contaminant accumulation (Trudel and Rasmussen 1999), and stable isotope signatures (Harvey et al. 2002). More recently, these models have been used to provide spatially explicit estimates of growth and consumption when environmental data is available for the area of interest (Luo et al. 2001, Nislow et al. 2000).

The concept underlying bioenergetic models is relatively simple, in that all the physiological processes relating to fish growth can be quantified and used in the mass balance equation:

$$G = C - R - F - U \qquad \text{Eq. 4.1}$$

where G=growth, C=consumption, R=metabolism, F=egestion and U=excretion. A selected component of this equation can be predicted by measuring the other components of the equation. Furthermore, these physiological components can each be modeled as functions of environmental factors, and the subsequent mass-balance equation can then be used to predict growth or consumption as functions of these environmental factors. Temperature is believed to be the most important environmental factor controlling physiological rates in fishes (Fry 1971).

Other than temperature, fish size is the other most important factor determining physiological rates. In general, as fish grow, size-specific consumption and metabolism rates decrease (Winberg 1956). Metabolism and consumption can also change ontogenetically, the functional relationship between physiological rates and both fish size and temperature can be characteristically different at different stages of development. Thus, the parameterization of a bioenergetic model requires laboratory experiments conducted at different sizes and temperatures to quantify the functional relationships with these factors and physiological rates. The bioenergetic model itself is the combination of these functional relationships in the mass balance equation (Eq 4.1). Once these parameters are estimated, the model must be evaluated to determine if it accurately represents growth processes in the species of interest. Ideally, bioenergetic models should be verified using laboratory experiments and then validated

using field studies where consumption and growth are measured simultaneously (Rice and Cochran 1984).  Verification by laboratory growth experiments tests how well the model works under controlled conditions whereas validation indicates how well the model predicts in the "real world."  A full evaluation can indicate where bias in the model exists and identify its strengths and weaknesses.

Bioenergetic modeling has been frequently undertaken for freshwater fishes (Bevelheimer et al. 1985, Fox 1991, Kitchell et al. 1977, Whitledge et al. 2003), but models are becoming increasingly common for marine and estuarine fish.  Bioenergetic models exist for some larval and juvenile marine fishes (Houde and Schekter 1982, Laurence 1977), adult estuarine fishes (Durbin and Durbin 1983, Hartman 1993, Houde and Madon 1995) and adult marine fishes (Boggs 1991, Kerr 1982, Megrey et al. 2007).  Bioenergetic models exist for three commercially important species in Chesapeake Bay: weakfish, bluefish, and striped bass (Hartman 1993, Hartman and Brandt 1995a).   However, no model currently exists for Atlantic croaker *Micropogonias undulatus* even though it is one of the most abundant fish in Chesapeake Bay and along the Atlantic coast.  Atlantic croaker is ranked not only as one of the top ten commercial fisheries on the East and Gulf coasts (www.st.nmfs.gov), but is the number one recreational fishery in Chesapeake Bay in terms of numbers and biomass of fish harvested.  Furthermore, the diet of croaker exhibits annual, seasonal, spatial, and ontogenetic variability that has bioenergetic consequences (Chapters 1 and 2).  Thus, a bioenergetic model for croaker could be applied to understand growth dynamics of individuals, evaluate ecosystem interactions and to provide management advice.

The purpose of this chapter is to develop and evaluate a bioenergetic model for Atlantic croaker. While this model will have many possible applications, it was developed to quantify population consumption of Atlantic croaker while resident in Chesapeake Bay. In particular, it was developed to be used in conjunction with the laboratory based models of striped bass and weakfish (Hartman 1993, Hartman and Brandt 1995b) to understand the trophic demand and potential competition between croaker, weakfish, and striped bass. Following development of the model in the lab, additional independent laboratory growth experiments were conducted to verify the model, identify sources of error, and to assess the strengths and weaknesses in applying the model.

**METHODS**

Croaker used in laboratory experiments described herein were collected in several ways. Juvenile croaker (~0.5-2 g wet weight, ~50-95 mm TL) were collected with midwater and bottom trawls in the Patuxent River in the fall of 2004, 2005, and 2006. Tow lengths were 10 and 5 minutes with the midwater and bottom trawls respectively. Adult croaker (~60-800 g wet weight, ~180-300 mm TL) were caught primarily with hook and line. In August 2004, approximately 15 adult croaker were caught near the Rappahannock River in the Chesapeake Bay. In the summers of 2005 and 2006, the remaining adult croaker were caught from the Chesapeake Biological Lab pier near the mouth of the Patuxent River. In the winter of 2005, several juvenile croaker were caught in the Rhode River to complete trials.

Croaker were kept in the lab for at least one week before undergoing any experimentation. Temperature, salinity and dissolved oxygen were measured daily.

Fish were held at the experimental temperature for at least one week prior to respiration, consumption, or growth experiments.  Any fish that showed signs of injury or appeared to be in poor condition were not used in experiments.  All work was conducted under procedures approved by the University of Maryland Center for Environmental Science Institutional Animal Use and Care Committee.

*Consumption*

Maximum consumption was quantified for croaker ranging from 0.5-975 grams (50-395 mm TL) at temperatures from 7.1 to 30.6$^{o}$C (Table 4.1).  Several different sizes of tanks were used in experiments.  Experiments were conducted in 40-liter, 200-liter, and 900-liter tanks for fish <20g, 20-100 grams, and >100 grams respectively.  For the majority of trials, tanks were established as flow-through seawater systems using filtered, conditioned and temperature-regulated estuarine water drawn from the Patuxent River at Solomons, MD.  Where necessary, temperature was regulated by heaters immersed into the water.  For trials involving fish <20 grams at temperatures of 7.5, 25, and 30$^{o}$C, some experiments were conducted in controlled-temperature rooms in a modified flow through system where the water in each tank was replaced each day. A preliminary experiment revealed that croaker <20 grams consumed significantly more with two fish in a tank as compared to tanks with either one fish or five fish ($F_{7,1}$=17.27, P=0.0057).  Because the goal was to quantify maximum consumption and large fish would not feed when placed in tanks individually, maximum consumption experiments for all fish < 60 grams were conducted with two fish in each tank and for fish > 60 grams with three to four fish in each tank.  Croaker of similar sizes were put into the same tank to the extent possible so that maximum consumption measurements

104

were not skewed by large disparities in the size of other fish, since other studies have shown that large fish can out-compete smaller fish for food (Cutts et al. 1998, Jobling 1983). In subsequent analyses, consumption was related to the mean weight of individual croaker in each tank.

Croaker < 100 grams were fed mysid shrimp and croaker >100 grams were fed bay anchovy. In all cases, fish were starved at least 24 hours before they were introduced into experimental tanks. Fish were weighed, measured and placed in experimental tanks at least one day before the induction of the experiment. Fish were fed, *ad libitum*, twice daily for several days and their total daily consumption estimated. Prey items were thawed and weighed wet prior to addition to the tanks. At least one hour after addition, the food remaining in the tanks was siphoned out and weighed wet again. Experiments at all temperatures >10 $^{\circ}$C were conducted for 3-5 days so that consumption estimates were averaged over several days. Experiments at 7-10$^{\circ}$C lasted 7-14 days to determine if fish did not feed at these low temperatures or if they fed at very low rates that would not be detected in experiments of shorter duration. Recovery experiments were conducted for both mysid and anchovy prey in which weighed portions of prey were introduced into tanks without croaker present and retrieved an hour later. In these experiments, the weight of food retrieved was regressed against weight of food introduced to estimate a recovery rate that accounted for error in both weighing the wet prey items and the technique for recovering the food. Approximately 73% of the wet weight of mysids introduced was recovered and approximately 100% of the wet weight of anchovy was recovered. Thus, adjustments to estimated consumption were made only to the experiments where mysids were fed to croaker.

*Respiration*

Routine metabolism was estimated for croaker from 0.18 to 1075 grams (25-408mm TL) at temperatures from 7.1-30.9$^{\circ}$C (Table 4.2). The methodology for estimating respiration rates varied according to croaker size. Routine metabolism in fish < 10 g was quantified using a computer-controlled, closed-circuit microrespirometer, hereafter called the Oxymax (MicroOxymax; Columbus Instruments, Columbus, OH). The Oxymax measures the oxygen in the headspace of the container in µl/min at regular intervals depending on the number of chambers in the Oxymax for 24-48 hours. Respirometry chambers of two different sizes were used in the Oxymax: 500ml or 1000ml containers. Fish were weighed and measured before being added individually to respirometry chambers. The chambers were then sealed and placed into a dark incubator where temperature was maintained. For each trial, one chamber filled with seawater only served as a blank to measure background microbial oxygen consumption. As an additional control, a medical battery was placed in one chamber that consumed a known amount of oxygen per minute. Routine metabolism was calculated by averaging oxygen consumption measured at each time interval by the Oxymax. Before the average was used as a measure of routine metabolism, the data were tested for skewness to ensure that the average was an appropriate measure of routine metabolism. Inspection of the data from this set of experiments revealed that no correction for skewness was needed. Oxygen consumption in the bottles containing fish was corrected by subtracting the value of the blank from the values of the experimental bottles.

Respiration rates of croaker ranging from 1-50 g were measured in plastic 20-L cylindrical respirometers, 31 cm in diameter and 37 cm high. A Sensorex (Garden Grove, CA) dissolved oxygen probe was suspended in each chamber with the tip of the sensor approximately 20 cm from the top of the chamber. Before fish were introduced, chambers were filled with new, filtered, clean water at the experimental water temperature. Fish were introduced into the chamber at least 14 hours before the start of the experiment and the screw-on lid was tightened. An aerator was placed in the chamber through the bleeder hole to oxygenate the container as the fish acclimated. After acclimation, the aerator was removed, the remainder of the chamber was filled with water and the bleeder hole closed with a rubber stopper and plumber's putty to ensure that the respirometer was airtight. To maintain temperature, these respirometers were held in a water bath. Temperature in each respirometer was measured before and after the experiment. Oxygen consumption was measured as described for the larger respirometers below.

Croaker > 51g were tested in large, plastic cylindrical 189-liter respirometers, 58.5 cm in diameter and 91 cm high. Experimental procedures were similar to those for the 20L chambers. Briefly, a Sensorex probe was suspended approximately 40cm from the top of the chamber. Before each trial, chambers were drained at least half way and almost completely filled with clean filtered water. Fish were acclimated to the aerated chamber at least 14 hours before the experiment. After acclimation, the lid of the chamber was fastened closed with a metal lever lock. The chamber was filled with water through a bleeder hole in the lid. After filling the chamber and checking that all

air bubbles were removed, the bleeder hole was screwed shut and covered with plumber's putty to insure the chamber was airtight.

Oxygen consumption measures for the 20-L and the 189-L chambers were similar. Signals from the Sensorex probes were converted from mA to oxygen concentrations (mg $L^{-1}$) and recorded every 5 seconds by a computer-controlled data collection system (Daqbook and Dasylab v9, Iotech Inc, Cleveland, OH). The oxygen readings were monitored and the experimental trial was stopped when the oxygen values dropped by at least 0.9 mg $L^{-1}$ from the initial reading. This process took anywhere from 45 minutes to 7 hours depending on the temperature and the size of the fish.

For each trial, the slope of the linear regression of dissolved oxygen (mg $L^{-1}$) versus time (day) was converted to respiration rate in $mgO_2$ $day^{-1}$ by multiplying by the volume of the respirometer. In some cases, the oxygen measurements taken over the first few minutes were erratic or the initial slope differed from the slope during the remainder of the time that oxygen was measured. This anomaly could be caused by fish movement or because the oxygen sensor was equilibrating. Therefore, rather than subjectively eliminating some data points, I deleted the first 25 minutes of readings from each respirometry trial. In most cases, this did not change the slope or $R^2$ value, but in some it greatly improved the fit of the linear regression model. All slopes were significantly different from zero and the lowest $R^2$ value was 0.36. Several measurements at a range of temperatures were taken in both respirometers with no fish in the chambers in order to adjust for background microbial respiration or local depletion of the oxygen around the oxygen sensor. However, both positive and

negative slopes were obtained in these measurements and there was no trend with temperature. Therefore, I did not adjust for any background microbial respiration or oxygen depletion in calculating respiration rates. Oxygen sensors were calibrating approximately every three weeks to ensure that they were functioning properly.

*Energy content*

Energy content (Joules.g$^{-1}$ dry weight) of prey items and of Atlantic croaker was assessed using a bomb calorimeter (Parr 6200, Calorimeter, Moline IL). Prey items or whole croaker from growth experiments were weighed wet and then placed in a 70$^{\circ}$C drying oven. Items were considered dry when weight was maintained over two successive days. A wet weight to dry weight relationship was established for each species of prey and for laboratory-raised croaker. The dried prey or fish was then ground using a tissue grinder and/or mortar and pestle. Dried, homogenized prey and fish were then made into small pellets (~0.25-0.60g) and burned in an oxygen rich bomb. Duplicate trials, each representing separate subsamples of each fish were combusted in the bomb and the average of the two was reported as the energy content. If the percent difference between these two samples was greater than 10%, a third subsample was measured for energy content in the bomb and the two closest of the three values were averaged to get the mean energy content.

*Statistical fitting*

Parameterization of the temperature- and size-dependency of individual components of a bioenergetics model was conducting using non-linear optimization methods within Solver (Microsoft Excel 2002). In all cases, the sum of squares was

minimized to determine the optimum combination of parameter values to maximize

model fit. Many starting parameters were used iteratively to fit each function to avoid

selecting a model because of local minima. In the cases where multiple models were

arrived upon depending on the starting parameters, the model with the lowest sum of

squares was selected for use in the full bioenergetic model.

Both consumption and respiration were modeled as functions of temperature

and fish weight. Before curve fitting, I tested for interactions between temperature and

fish size to determine the number of models that should be developed using ANOVA.

A significant interaction indicated that the relationship between temperature and the

response variable (either consumption or respiration) was different for different size

classes of fish and that these functions should be modeled differently for each size

class. Total weight was log transformed in order to perform the parametric analysis on

consumption data.

The maximum specific daily feeding rate was related to fish mass (W) using the

allometric equation,

$$ Cmax = CA * W^{CB} \qquad\qquad Eq. 4.3 $$

where Cmax ($g \cdot g^{-1} \cdot d^{-1}$) = maximum rate of consumption and CA and CB are fitted

constants (Kitchell et al. 1977). Once the relationship between Cmax and fish weight

was established, the proportion of maximum consumption (P) was calculated for each

observation as the ratio of observed consumption to the expected maximum

consumption predicted by Equation 4.3. The specific consumption rate ($g \cdot g^{-1} \cdot d^{-1}$), C, is

then related to temperature using:

$$ C = Cmax * P * f(T) \qquad\qquad Eq. 4.4 $$

where T=temperature ($^{\circ}$C). For Atlantic croaker, the relationship of Cmax with temperature f(T) was fit using the Thornton and Lessem equation:

$$F(T) = KA * KB \qquad \qquad \text{Eq. 4.5}$$

where KA= (CK1*L1)/(1+CK1*(L1-1))

L1 = e $^{(G1*(T-CQ)}$

G1= (1/(CTO-CQ))*ln((0.98*(1-CK1))/ (CK1*0.02))

KB= (CK4*L2)/(1+CK4*(L2-1))

L2 = e$^{(G2*CTL-T)}$

G2 = (1/(CTL-CTM))*ln ((0.98*(1-CK4))/(CK4*0.02))

and CK1 is the overall maximum consumption rate, CTO is the water temperature corresponding to 98% of the overall maximum consumption rate, CK4 is some fraction of the maximum consumption rate, CTL is the temperature at which dependence is some reduced fraction of the maximum rate (CK4), CTM is the water temperature at which dependence is 98% of the maximum rate, and CQ is the lower water temperature at which temperature dependence is a small fraction (Hanson et al. 1997). KA refers to the temperature increasing function and KB refers to the decreasing function.

Total metabolism for adult fish was modeled as a function of wet weight (W), temperature, and activity:

$$R = RA*W^{RB}*e^{T*RQ}*ACTIVITY \qquad \qquad \text{Eq. 4.6}$$

where R=oxygen consumption (gO$_2$ g$^{-1}$ day$^{-1}$), T=temperature, and RA, RB, and RQ are fitted constants. RQ is analogous to the Q10 or the rate at which the function increases with water temperature. The activity function was modeled assuming constant swimming speed of 1 cm s$^{-1}$ (Rice et al. 1983) where:

$$ACTIVITY = e^{(RTO*VEL)} \qquad\qquad \text{Eq. 4.7}$$

and where VEL=velocity=1cm s$^{-1}$ and RTO is the coefficient for swimming speed dependence on metabolism. In order for the model to operate in the Fish Bioenergetics 3.0 software, the respirometry data was used to solve simultaneously for RA, RB, and RQ and entered as such. Activity (ACT) was estimated separately (described below) and accounted for by setting RTO=ln(ACT). For very small croaker, metabolism was modeled as a function of temperature with an activity multiplier following Kitchell (1977):

$$f(T) = V^X \, e^{\,(X(1-V))} * ACTIVITY \qquad\qquad \text{Eq. 4.8}$$

where:

$$V = (RTM-T)/(RTM-RTO)$$

$$X = (Z^2 * \,(1+(1+40/Y)^{0.5})^2)/400$$

$$Z = LN(RQ)*(RTM-RTO)$$

$$Y = LN(RQ)*(RTM-RTO+2)$$

An activity multiplier (ACT) and specific dynamic action (SDA) are also respiration costs that must be included in the bioenergetic model. ACT, the activity multiplier component of the respiration term, was estimated after the bioenergetic model was developed using consumption, and initial and final weights taken for maximum consumption experiments. Total consumption, number of days, and the initial and final weight for the experiment were used as inputs into the bioenergetic model. ACT was then adjusted so that the predicted final weight was equal to the observed final weight. SDA was taken from the literature to be 0.172 (Hansen et al. 1997).

The full bioenergetic model was developed by inputting the parameters of consumption and respiration determined above as functions of temperature and fish size into Fish Bioenergetics 3.0 software. This software uses species specific physiological parameters of consumption, respiration, egestion, and excretion in the energy mass balance equation (Eq. 4.1). Growth is then calculated as the difference between daily consumption and all energetic costs. Once the weight and temperature specific functions of consumption, respiration, egestion, and excretion are combined into one model, energy budgets can be created as a function of temperature to determine scope for growth or amount of surplus energy available for growth. These energy budgets, standardized for fish size, can also determine the temperatures at which a species experiences lethal temperatures or are subject to starvation and weight loss. Once the balanced energy budget is obtained growth and consumption can be predicted using Fish Bioenergetics software.

*Validation of the bioenergetic model*

The croaker bioenergetic model was validated with three sets of growth experiments. For fish > 20g, I employed a 2x3x3 factorial growth experiment involving two different prey, three different ration levels and three different temperatures to validate the croaker bioenergetic model. For the bioenergetic model of fish <20g, previously published work on croaker physiology was used to verify the model (Lankford and Targett 2001a). I used Fish Bioenergetics software Version 3.0 to test the bioenergetic model in two ways: 1) by using the observed growth rates from each tank as starting parameters to predict consumption and 2) by using initial weight and observed consumption in the experiment to predict final weight.

The validation experiments were conducted at 12, 20, and 27$^o$C. Fish used in these experiments were not used in any of the respiration and consumption trials, but were collected and maintained in the same manner as described above. Trials were conducted in 189-liter square tanks established with flow through water. Fish were measured, weighed and introduced to tanks the evening before the experiment began to acclimate to the tanks. Fish were fed for 14 days, and then weighed and measured on Day 15 to calculate growth rates. For the 12 and 20$^o$C experiments, there were two fish in each tank and fish sizes ranged from 14-27 g and 35-50g respectively. There were two prey type treatments where fish were fed either the same mysid shrimp used in consumption experiments or diced polychaete worms, *Neries virens.* There were also three ration treatments where fish were fed *ad libitum*, 4% of total body weight per day, or were starved. For the 27$^o$C growth experiment, larger fish were used (50-124g) and there was only one fish in each tank rather than two. Fish were fed either chopped bay anchovy or mysid shrimp and at either a high (*ad libitum*) or low (4% of body weight) ration. Consumption was measured for 4, 14 and 12 days for the 12, 20, and 27$^o$C growth experiments respectively using the same method as the consumption experiments described above. In all experiments, the daily consumption rate was averaged and multiplied by 14 to get the total amount of food eaten over the duration of the experiment.

Feces were collected from individual tanks during growth experiments conducted at 12 and 20$^o$C and stored at -80$^o$C until analysis. To estimate absorption efficiency feces was first dried for at least 24 hours in a 70$^o$C drying oven until the dry

114

weight of feces remained constant.  Then feces were ashed in a muffle furnace at 450$^o$C

to calculate absorption efficiency (AE) using the following equation:

$$AE = 100 \times \frac{ash\ mass\ in\ food\ consumed - ash\ mass\ in\ feces}{ash\ mass\ in\ food\ consumed} \qquad \text{Eq. 4.2}$$

Ash mass in food was determined using the same process with weighed portions of

polychaetes and mysids.

All three growth experiments were used to evaluate the >20g model.  The 12$^o$C

experiment, was also used to evaluate the performance of the <20g model because the

range of fish sizes (14-27g) in this experiment straddled the 20g cutoff.  The <2.5g

model was evaluated with data reported by Lankford and Targett (2001a).  The >20g

and <20g models were evaluated for systematic biases using error analysis as described

by Rice and Cochran (1984).  Regressions were estimated for observed versus

predicted values.  Error analysis of both predicted growth and consumption for all three

growth experiments was conducted by partitioning mean square error (MSE) into the

mean component (MC), slope component (SC) and residual component (RC) using:

$$1 = MC + SC + RC = \frac{(\overline{P} - \overline{A})^2}{MSE} + \frac{(S_P - rS_A)^2}{MSE} + \frac{(1 - r^2)S_A^2}{MSE}$$

where P and A indicate the predicted and actual values of the mean ($\overline{P}$ and $\overline{S}$) and

standard deviation (S) and r is the correlation coefficient. Ideally majority of the error

should be in the residual component indicating that there are no systematic biases in the

model.

**RESULTS**

*Consumption*

I obtained 213 estimates of consumption over a range of temperature and fish size (Table 4.1, n=213). Maximum consumption exhibited a relationship with both temperature and fish size (Figure 4.1, 4.2). The relationship between size and maximum consumption was modeled by selecting the highest 10% consumption values for each of four size classes. The equation for this relationship was:

$$0.405 * W^{-0.342} \ (n=23, R^2=0.86) \qquad \text{Eq. 4.9}$$

This equation was used to calculate p-values that were used later to model the relationship of consumption with temperature. The relationship of maximum consumption to temperature differed for the two major size classes of fish (<20g, >20g) and was modeled as such (Figure 4.2). There was a significant interaction between weight and temperature ($F_{1,192}=36.79$, P<0.0001) indicating that consumption should be modeled differently by size class. Therefore, consumption was modeled separately for fish < 20g (hereafter juvenile) and fish > 20g (hereafter adult). There was no significant interaction between size and temperature for either the small size class ($F_{1,82}=0.06$, P=0.8120) or the large size class. ($F_{1,123}=2.31$, P=0.1310).

The Thorton and Lessem equation adequately predicted consumption for both size classes (Figure 4.3). The shapes of the Thorton and Lessem curves appear similar for both size classes of fish. Residuals for consumption were plotted against temperature to determine at what temperature the model may under- or over-estimate consumption (Figure 4.4). For both juvenile and adult fish, there is an increase in variance with an increase in temperature. However, there is less variability in the

116

relationship described for juvenile fish and the residuals appear equally positive and negative at all temperatures indicating that the model does not consistently over- or under-estimate consumption. For the adult fish, the model underestimates consumption at low temperatures as indicated by the positive residuals and overestimates consumption at very high temperatures as indicated by the negative residuals.

*Respiration*

Oxygen consumption rates were measured for 316 fish (Table 4.2) and also displayed non-linear relationships with temperature and fish weight (Figures 4.5, 4.6). After total weight, temperature, and respiration data were log transformed to meet assumptions of normality, there was a significant interaction between total weight and temperature for respiration ($F_{1,311}$=13.04, P=0.0004). The interaction among the size classes indicates that respiration must be divided into size classes and modeled separately. Thus, the respiration data were divided into three size classes to eliminate the interaction between size and temperature: <2.5g ($F_{1,91}$=0.40, P=0.2328), 2.55-20g ($F_{1,48}$, P=0.2635), and >20 grams ($F_{1,164}$=0.23,P=0.6326). Respiration was modeled as increasing exponentially with temperature (Figure 4.7) for both the 2.55-20g fish and the >20g fish, but modeled using the equation developed by Kitchell et al. (1977) for fish less <2.5g (Figure 4.8). Respiration rates appeared to decline at temperatures around 25$^{\circ}$C in juvenile fish (Figure 4.8). Residuals from the three respiration models were plotted against temperature. For both juvenile and adult fish the residuals are equally positive and negative and there is no apparent trend in residuals with temperature (Figure 4.9). This indicates that respiration is not consistently over- or under-estimated as a function of temperature.

ACT was estimated for fish at temperatures ranging from 14.9-30.6°C using growth and consumption data obtained in maximum consumption trials. Although only values of ACT >1 can be incorporated into the model, all values estimated for ACT are shown to illustrate the model fit (Figure 4.10). Values of ACT<1 indicate a trial in which the fish grew more than what was predicted by the model and values of ACT>1 indicate trials in which fish grew less than predicted. Values of ACT were more variable and of larger magnitude for small fish using the <20g model. In addition, ACT was higher at low temperatures, indicating that both the <20g model and the >20g model overestimate growth at these temperatures (Figure 4.10). Mean ACT (± standard deviation) was 3.29 (± 4.88) for fish 2.5-20g and 1.65 (± 1.62) for fish <20g.

After physiological parameters were incorporated into the Fish Bioenergetics software (Table 4.3), the balanced energy budget of croaker was examined and scope for growth estimated. Rates of consumption, respiration, egestion, and excretion were standardized by fish size and plotted as functions of temperature (Figure 4.11, 4.12). The optimum temperature for growth appears to range from 25-29°C for all fish sizes. Scope for growth is in general very high for Atlantic croaker at a wide range of temperatures, especially young croaker as illustrated by the graphs of a 1g and 10g fish (Figure 4.11). In large fish, respiration exceeds consumption at about 14°C for a 30g fish and at about 17°C for a 500g fish (Figure 4.12).

*Validation of the bioenergetic model*

Growth experiments were conducted to evaluate the model at three different temperatures. Fish were fed different prey types and rations to evaluate model performance with these variations. At 12°C, there was no statistical difference in

118

consumption ($F_{1,13}$=3.65, P=0.0783) or growth ($F_{1,16}$=0.83, P=0.3762) between fish fed

different prey items (Figure 4.13a).  However, there was a significant difference in

daily specific growth rate between fish fed different rations ($F_{2,16}$=12.85, P=0.0005).

The difference in growth rate and consumption was statistically significant between the

starved and fed treatments, but not between the low and high ration treatments (Figure

4.13, 4.14).  Note that there were many individual fish that lost weight, but there was

still positive growth at this temperature.

In the 20$^{o}$C growth experiment, there was no significant difference in daily

specific growth rate between fish fed different food types (Figure 4.13b; $F_{1,13}$=0.60,

P=0.4511), but there was a significant difference in fish fed different rations (Figure

4.13b; $F_{2,13}$=6.56, P=0.0107).  Similar to the 12$^{o}$C growth experiment, the differences

in growth occurred between the starved and fed fish, but there was no statistical

difference in growth between the high and low ration treatments (Figure 4.14b).

Absorption efficiencies were also calculated for each treatment in the 12 and

20$^{o}$C growth experiments.  Absorption efficiencies largely mirror the results of

consumption estimates for each experiment as these consumption estimates were used

in the calculation of AE (see Eq. 4.2).  For the 20$^{o}$C experiment, there were significant

effects of food type, ration, and the interaction of food and ration ($F_{1,28}$=39.70,

P<0.0001).  Fish fed the high ration of polychaetes had the highest AE and that value

was significantly different from all other treatments as shown by pairwise comparisons

(Figure 4.15).  Because there was a significant interaction between the food and ration

factors in this experiment it is not clear how ration and food type affected absorption

efficiency.  The AE values for croaker fed a low ration of mysids at 12$^{o}$C were all

negative, indicating that the fish absorbed more than they were fed.  These errors could be a result of erroneous consumption values used in calculating AE (see Eq. 4.2).  The values of AE do not explain the trends in growth and consumption for the 12 and 20$^{o}$C experiments and are similar regardless of temperature.  The average absorption efficiency for croaker was relatively low, 66%, over all temperatures and treatments.

Similar to the 12$^{o}$C and 20$^{o}$C experiments, at 27$^{o}$C growth rates were low and there was no effect of food type on growth rate (Figure 4.13c; $F_{1,8}$=0.31, P=0.5926). Unlike the other growth experiments, there was no significant difference in daily specific growth rate for fish fed different diet rations ($F_{1,8}$=0.01, P=0.9242) even though there was a significant effect of ration on mass specific consumption ($F_{1,12}$=26.76, P=0.0009).  The growth rates in all three experiments were very low in general which made evaluating how well the model predicted growth and consumption problematic (Figure 4.13c, 4.14c).  I documented high energy densities (10,000-12,000 kJ/g) and maturing gonads in fish used in all three experiments even though the fish used in the 12 and 20$^{o}$C experiments were less than 1 year old and just over 1 year for the 27$^{o}$C experiment.  However, I observed no spawning and no mature eggs in any of the fish.  I used a fixed value of 10,000 kJ/g in model validation simulations for experimental fish, but a value of 5,100 is recommended for field caught fish based on data from Chapter 2.

The bioenergetics model was validated in one of two ways using Fish Bioenergetics software and the independent data obtained from the three growth experiments.  First, final weights were predicted using initial weight and observed total consumption as starting parameters for each experimental unit in the growth

experiment. Secondly, consumption was estimated by the model using initial weights and final weights observed in growth experiments. The final weights predicted by the model from initial weight and observed consumption agreed well with the observed final weights in all three experiments (Figure 4.16). Highly predictive linear relationships between the observed and predicted final weights were developed at each temperature using the >20g model ($R^2$=0.94, $R^2$=0.92. $R^2$=0.64 for 12, 20, and 27$^o$C respectively). At 12$^o$C, estimates of final weight from the model were slightly higher than observed total weights using the >20g model. The tendency for the >20g model to overestimate growth at 12$^o$C is reflected in a high proportion of error in the mean component (34%), but majority of the error (65%) is in the random component of the model at this temperature (Table 4.4). Interestingly, the observed and predicted final weights agreed better using the <20g model at 12$^o$C for this range of fish sizes. The better fit of the juvenile model for fish ranging from 14-27g is further reflected by majority of the error residing in the random component (92%) in the mean square partitioning analysis of predicted final weight and a lower overall MSE (Table 4.4).

Estimates of final weight were also slightly lower at 27$^o$C indicating that the>20g model has a tendency to overestimate growth. While majority of the error is random, the proportion of error in the mean component is a bit high (Table 4.4). The percentage difference between observed and predicted values were low and ranged from 0.65-9.27%, 1.12-36%, and 1.12-10.58% for the 12, 20, and 27$^o$C growth experiments respectively.

The model did not predict consumption well when given the observed initial and final weights (Figure 4.17). Percent difference between the observed and modeled

consumption for all three experiments ranged from 1.63-1921% for all experiments. In contrast to the high $R^2$ values obtained in the relationships between observed and expected growth, there were no significant relationships between observed and predicted consumption. For the >20g model, the greatest proportion of MSE was in the residual component at 20 and 27$^{\circ}$C, indicating that that most of the error is from random error and not systematic (Table 4.4). Again, at 12$^{\circ}$C, the <20g model predicted consumption better than the >20g model. However, in both models, there was considerable error in the slope component of the (table 4.4). The MSE was in general higher for consumption predictions than for growth predictions.

The growth experiments had three ration treatments and two prey type treatments to evaluate how well the model performed with these variations to feeding conditions. The model performed equally well at different ration levels (Figure 4.18, 4.19). Similar to the results when individual observations were compared to model predictions, the model predicted total weight well. In contrast to the point estimates of consumption, when grouped by treatment, mean consumption estimates agreed better with the observed mean consumption values (Figure 4.19). Whether estimated by the model or measured during growth experiments, consumption was more variable than total weight, in part explaining the discrepancies in observed and modeled consumption values.

The <2.5g model developed for very small juvenile fish was tested using growth experiments conducted by Lankford and Targett (2001a). In these growth experiments, croaker were collected from three estuaries (North Carolina, Chesapeake Bay and Delaware Bay) and fed mysid shrimp *ad libitum*. Mean initial weights, feeding rates

122

and growth rates were reported for fish in each estuary so that final weight and consumption could be calculated and used as input parameters to test the croaker bioenergetic model. I compared observed and predicted final weights and consumption using the respiration model developed for fish <2.5g and the consumption function developed for fish <20g (Figure 4.20). Percentage difference between observed and predicted final weights for this experiment were 24%,17.3% and 24.2% for the Delaware, North Carolina, and Florida treatments respectively and for total consumption percent difference between observed and predicted final treatments were 16.8%, 9.8%, and 14.8% respectively (Figure 4.19). For this set of models, consumption and total weight was predicted equally well and was not consistently over- or under-estimated.

**DISCUSSION**

Laboratory experiments produced estimated functional forms for key bioenergetic processes that when integrated into a bioenergetic modeling framework could accurately predict growth patterns in Atlantic croaker, but poorly predicted their consumption. Many bioenergetic models predict growth better than consumption (Chipps et al. 2000, Kitchell et al. 1977, Rice and Cochran 1984), but I was unable to fully validate consumption estimates using this model because growth was very low in all three growth experiments even though consumption varied with ration treatments. Because there was little variation in growth in these experiments, the model predicted similar consumption rates even though I measured very different rates of consumption relative to ration treatments. Although growth was low, these fish may have been

converting food into energy stores rather than adding body mass. I observed very high energy contents for fish in these growth experiments (10,000-12,000 kJ/gram) and some fish had begun to mature even though they were <1 year old. Thus, it is likely that by incorporating changes in energy density of fish and prey into model predictions, the model would have predicted consumption better. Similarly, Hartman and Cox (2008) found that a brook trout bioenergetics model could be more properly validated when changes in energy density of predator and prey were incorporated into the model validation. When growth rates are sufficiently high, model performance is relatively insensitive to changes in energy density.

There are several other reasons to explain why consumption was poorly predicted in this and other models in general. In the model itself when feeding is estimated from observed growth rates, every component in the model is affected by any bias in temperature that may exist in the model (Rice and Cochran 1984). In contrast, when final weight is predicted with initial weight and observed consumption as starting parameters, the error in the temperature component of consumption, egestion and excretion are not present. Analysis of consumption residuals in the >20g model suggests that there is a bias in the consumption model where consumption is underestimated at low temperatures. Furthermore, consumption is empirically difficult to measure and estimate especially in fish such as croaker that feed on smaller-sized meals.

Consumption estimates in this study and in other studies are highly variable. Estimates in consumption may be inaccurate simply by the logistics of measuring the wet weight of food in these experiments. Furthermore, consumption estimates may be

affected by the duration of the experiment. When fish are fed *ad libitum* for many days, consumption will decrease over time and daily consumption may be underestimated. However, consumption experiments at low temperatures may need to be of longer duration to detect fish feeding. Thus, variation in the length of consumption experiments introduces error into consumption estimates. Consumption experiments of shorter duration may overestimate consumption, especially after fish are starved before the initiation of consumption measurements.

This bioenergetic model developed for Atlantic croaker should only be used to predict consumption and growth at temperatures above 14$^o$C for fish >20g. A major flaw with the model is its performance at low temperatures. This model predicts that starvation would occur if croaker are kept at temperatures 14$^o$C or lower for fish >20g because consumption is too low to support the costs of metabolism. Negative scope for growth at temperatures <14$^o$C is consistent with the migration patterns observed in croaker where adults enter estuarine waters typically when temperatures are greater than 14$^o$C. Very few adult croaker were caught at or below 14$^o$C on CHESFIMS surveys (Chapter 1). While the pattern in scope for growth is consistent with adult croaker life history, I observed positive growth in the growth experiment performed at 12$^o$C for fish ranging from 14-27g in size. The scope for growth at small sizes is consistent with previous studies that have documented significant mortality at water temperatures ≤ 7$^o$C, although large juvenile croaker are less susceptible to mortality at these temperatures (Lankford and Targett 2001). Analysis of the residuals of consumption for fish >20g indicates that this model underestimates consumption at low

temperatures, suggesting that scope for growth is likely higher at these temperatures than this model predicts.

The transition between the juvenile and adult physiology was modeled as an instantaneous change when a fish exceeds 20g. In reality, this transition is blurred imprecise because of individual differences in development and perhaps by interactions between the effects of size and temperature on physiological processes. This fact is evident in the performance of the models at 12$^{\circ}$C. Fish in this experiment ranged from 14-27g, straddling the observed statistical cutoff value. While most fish were >20g, the <20g juvenile bioenergetic model performed better for fish of all sizes at this temperature. There are several implications of the performance of the model at this temperature and for the ontogenetic shifts in physiological processes. First, it is recommended that at 12$^{\circ}$C and for fish ranging in the 10-30g size range, the "<20g" model should be used to model growth and consumption. Second, the transition between these two models should be examined more closely.

As evident by the energy budgets developed for fish of different sizes, the temperature at which respiration exceeds consumption increases with fish size. Respiration exceeds consumption at 14$^{\circ}$C for a 30g fish and at 17$^{\circ}$C for an 800g fish. There was indeed very little growth in the growth experiments performed at 10-12$^{\circ}$C, but positive rather than negative growth as the model predicts did occur at these temperatures. This discrepancy in the model could possibly be rectified if consumption had been measured for more fish in the 20-60g size range at 10$^{\circ}$C and below. The observations of fish consumption at 7.5$^{\circ}$C used to develop the relationship between consumption and temperature for fish >20g were adult fish greater than 500g.

126

Measuring consumption of fish in the 20-60g size range at temperatures below 10$^{\circ}$C would improve model performance because their consumption rates are likely higher at low temperatures than very large fish that rarely feed at temperatures below 12$^{\circ}$C.

Laboratory experiments revealed size- and temperature-dependent relationships for both croaker consumption and respiration. Croaker consumption was found to be a non-linear function of temperature. However, we did not detect a decrease in consumption at high temperatures as is predicted in some species using the Thorton and Lessem equation to describe consumption. Experiments at temperatures greater than 30$^{\circ}$C would clarify this relationship and may further refine consumption as a function of temperature, but are not advised as they would be stressful for croaker. Respiration exhibited clear ontogenetic differences so that fish <2.5g were modeled using a different equation than larger fish entirely, where respiration increased exponentially with temperature.

Ontogenetic differences in metabolism occur in other species such as striped bass where similarly, metabolism is modeled exponentially in adults, but modeled with a decreasing function at high temperatures in larvae (Johnson 1995, Hartman and Brandt 1995). Many bioenergetic models developed for larval and juvenile fish model metabolism use the relationship developed by Kitchell (1977). The relationship of respiration to temperature was difficult to discern for juvenile fish because many fish had elevated activity and respiration rates at 30$^{\circ}$C. Elevated respiration rates were a result of increased swimming activity to avoid this high temperature. For this reason, respiration should be measured at temperatures greater than 25$^{\circ}$C for juvenile croaker

to better discern the trends in metabolism at high temperatures and to determine the sizes at which respiration changes ontogenetically.

The bioenergetic model developed for croaker reflects the trade-offs between surplus growth and energy allocation that shape its life history. Adult croaker exhibited a high scope for growth at a wide range of temperatures, from 14-30$^\circ$C in this model. Optimum temperature for growth was between 28 and 29$^\circ$C for all life history stages. The high scope for growth at a wide range of temperatures and a relatively high optimum temperature in part explains the wide distribution of croaker from the Gulf of Mexico to Delaware Bay. Tolerance of relatively high temperatures explains the ability of croaker to migrate into estuaries such as Chesapeake Bay and Delaware in summer months where temperatures are optimal and high productivity can support their consumption needs. Atlantic croaker move out of the estuary as temperatures decline and are suboptimal for growth. While older croaker had negative growth at temperatures around 12-14$^\circ$C, young croaker have a positive scope for growth from 5-30$^\circ$C. This corresponds to the early life history of Atlantic croaker where they spend their first winter (<20g) in bays and estuaries that often reach temperatures of 5$^\circ$C and below. The northern distribution of several temperate fish species is essentially set by the temperature at which metabolism exceeds consumption, or the temperature at which starvation occurs (Shuter and Post 1990). Similarly, the northern distribution of croaker is Delaware Bay where temperatures more frequently drop below 4$^\circ$C (Lankford and Targett 1994). Winter water temperatures in Delaware Bay and Chesapeake Bay frequently reach 4$^\circ$C or lower and recruitment in these years is lower.

Thus, recruitment of croaker at its northern extreme is most variable (Joseph 1972, Lankford and Targett 2001b).

Because physiological rates in part determine life history, the bioenergetic parameters of croaker should be similar to other estuarine fish. The mass dependent coefficients for consumption, CA and CB were similar to many species including estuarine fish such as bay anchovy, weakfish, bluefish, and striped bass (Hanson et al. 1997). However, CQ estimated for croaker was higher than many species. CQ was in the range of values reported for bluefish and weakfish, both estuarine species, but CQ in striped bass was half the estimates of bluefish, weakfish, and croaker even though it is also a temperate estuarine-dependent fish. In the Thorton and Lessem model of consumption used in all consumption models of these estuarine species, CQ is the lower water temperature at which temperature dependence of consumption is a small fraction. Striped bass have a more northerly range than these other species, which may explain this discrepancy.

Values of the weight specific parameters of respiration for adult croaker were similar to many other bioenergetic models developed for other species (Hanson et al. 1997). In particular, RA and RB were similar to the closely related weakfish (*Cynoscion regalis*). For weakfish and croaker, RB was much more negative than the estimate of this parameter in other species. The parameter, RB, is the slope of the allometric function for metabolism so a highly negative value of RB indicates that respiration rapidly declines with fish weight for these species. This finding is interesting because it allows the scope for growth to be relatively high for young fish and may explain the young ages and small sizes at maturity for these species of

sciaenids (Roff 1983, 1984, Wootton 1998). In the bioenergetic model of croaker <2.5 grams, RB was not significantly different from zero. However, RB in most other bioenergetic models ranged from -0.2 to -0.4. The allometric equation of respiration for Atlantic croaker <2.5g was closest to yellow perch juveniles and bay anchovy. RTO and RQ for croaker >2.5g were similar to striped bass and bluefish, but most similar to smelt and coregonids for croaker >20g (Hanson et al. 1997). RTO was much higher in weakfish, bluefish, and striped bass than in croaker. RQ and RTO in croaker <2.5g were closest to values for sea lamprey and walleye pollock.

The bioenergetic model of croaker developed here is a representation of the physiological processes that regulate growth in this species as functions of the two most important factors influencing physiological processes, temperature and fish size. As with any model, improvements could be made by evaluating the impact of additional factors such as salinity and dissolved oxygen that have been shown in some cases to modify growth. While the measurement of these parameters may improve model performance in some applications, additional parameters in any model requires additional input parameters, which themselves have uncertainty. Additionally, overparameterized models can introduce more bias into the model that may be more difficult to isolate than in a more simple model. To improve this bioenergetic model of Atlantic croaker, rather than incorporate the effect of additional environmental factors on consumption and respiration, validation of the model with additional laboratory and with field estimates of consumption, evacuation rates and daily rations would improve the model a great deal more. The main issue with the model validation presented here is that fish did not grow enough in the three growth experiments conducted to evaluate

estimates of consumption.  Full evaluations of bioenergetic models require experiments at multiple temperatures, rations, and prey type (Hartman and Cox 2008). Consumption predicted by this model therefore, should be viewed as relative estimates of consumption and should not be used to set specific biological reference points for species of interest, but should be viewed as the relative impact of one species on another.

Table 4.1:  Number of replicates in each size class and temperature grouping to estimate maximum consumption of Atlantic croaker.

| Size class (g) | Temperature (°C) | | | | |
|---|---|---|---|---|---|
| | 7-12.5 | 12.6-17.5 | 17.6-22.5 | 22.6-27.5 | 27.6-31 |
| <20 | 18 | 13 | 24 | 18 | 14 |
| 20-60 | 9 | 23 | 11 | 9 | 4 |
| 61-300 | 5 | 5 | 3 | 5 | 7 |
| 301-600 | 4 | 15 | 7 | 13 | 6 |

Table 4.2:  Number of replicates used in each size class and temperature grouping to estimate routine metabolism of Atlantic croaker.

| Size class (g) | Temperature ($^{o}$C) | | | | |
|---|---|---|---|---|---|
| | 7-12.5 | 12.6-17.5 | 17.6-22.5 | 22.6-27.5 | 27.6-31 |
| <20 | 34 | 28 | 51 | 25 | 11 |
| 20-60 | 9 | 19 | 10 | 15 | 5 |
| 61-300 | 10 | 13 | 11 | 4 | 11 |
| 301-600 | 13 | 12 | 13 | 10 | 12 |

Table 4.3: Parameters used in bioenergetic models for Atlantic croaker by size class. The 2.55-20g model of consumption should also be used for fish <2.5g.  See methods for a description of the symbols and functional relationships.

| Component (Equation) | Symbol | Parameter value | | |
|---|---|---|---|---|
| | | <2.5g | 2.55-20.0g | >20g |
| Consumption (3) | CA | | 0.405 | 0.405 |
| | CB | | -0.342 | -0.342 |
| | CQ | | 12.26 | 10.04 |
| | CTO | | 29 | 35 |
| | CTM | | 39 | 35 |
| | CTL | | 28.82 | 36.019 |
| | CK1 | | 0.359 | 0.0144 |
| | CK4 | | 0.899 | 0.982 |
| Respiration (2,1) | RA | 0.0094 | 0.00425 | 0.00298 |
| | RB | -0.000001 | -0.527 | -0.102 |
| | RQ | 3.1377 | 0.0580 | 0.0401 |
| | RTO | 21.199 | 0 | 0 |
| | RTM | 38.613 | 0 | 0 |
| | RTL | * | 0 | 0 |
| | RK1 | * | 1 | 1 |
| | RK4 | * | 0 | 0 |
| | ACT | 1 | 1 | 1 |
| | BACT | * | 0 | 0 |
| | SDA | 0.172 | 0.172 | 0.172 |
| Egestion/Excretion (1) | FA | 0.1 | 0.1 | 0.1 |
| | FB | * | * | * |
| | FG | * | * | * |
| | UA | 0.1 | 0.1 | 0.1 |
| | UB | * | * | * |
| | UG | * | * | * |
| Predator density (field-caught fish) | | | 5,100 | 5,100 |

Table 4.4: Mean square partitioning of error between observed and predicted values of final weight and consumption for three growth experiments. The >20g model was validated using experiments at all three temperatures. However, the $12^o$C experiment was used to assess both the <20g and >20g model because fish size ranged from 14.5-27.3g  MC=Mean component, SC=slope component, RC=Residual component, and MSE=Mean square error.

|  | Experiment | MC | SC | RC | MSE |
|---|---|---|---|---|---|
| $12^o$C <20g | Final weight | 0.014 | 0.065 | 0.92 | 0.81 |
|  | Consumption | 0.00046 | 0.54 | 0.46 | 3.47 |
| $12^o$C >20g | Final weight | 0.35 | 0.0073 | 0.64 | 1.18 |
|  | Consumption | 0.01 | 0.74 | 0.25 | 16.90 |
| $20^o$C | Final weight | 0.026 | 0.16 | 0.81 | 6.98 |
|  | Consumption | 0.11 | 0.25 | 0.64 | 34.41 |
| $27^o$C | Final weight | 0.36 | 0.07 | 0.57 | 65.15 |
|  | Consumption | 0.040 | 0.191 | 0.77 | 357.33 |

Figure 4.1: Consumption rate as a function of fish size and by 5 degree temperature classes. The curve represents the relationship between consumption and fish size at temperatures for the 90th percentile consumption rates in each of four size classes.
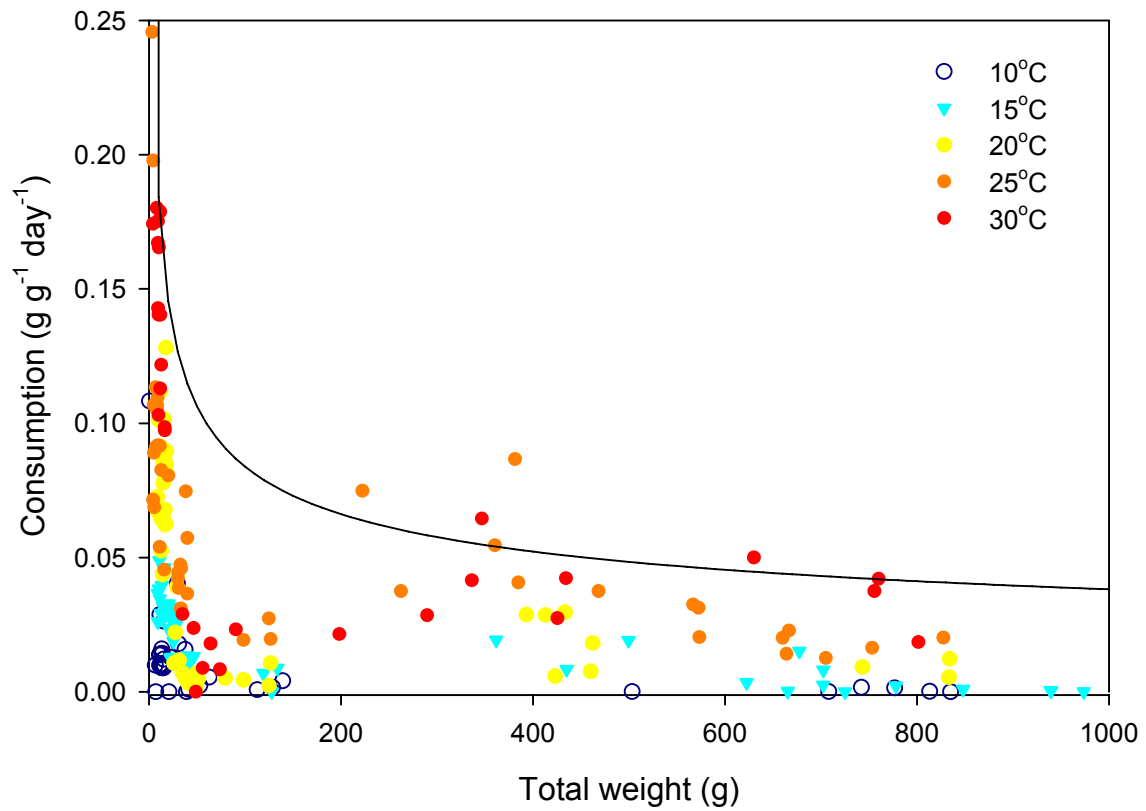
Figure 4.2:  Consumption as a function of temperature for fish less than 20 grams and fish greater than 20 grams.
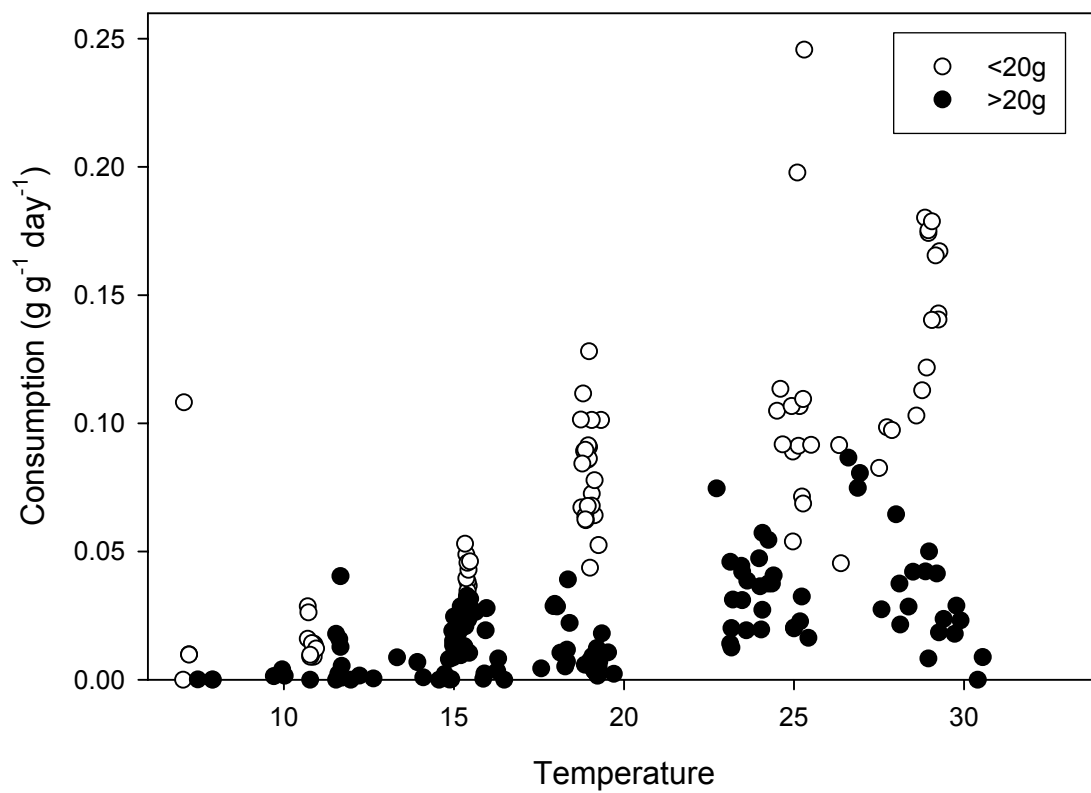
Figure 4.3: Thorton and Lessem curves developed to model the proportion of maximum consumption (P-value) as a function of temperature for a) fish less than 20g and b) fish greater than 20g.
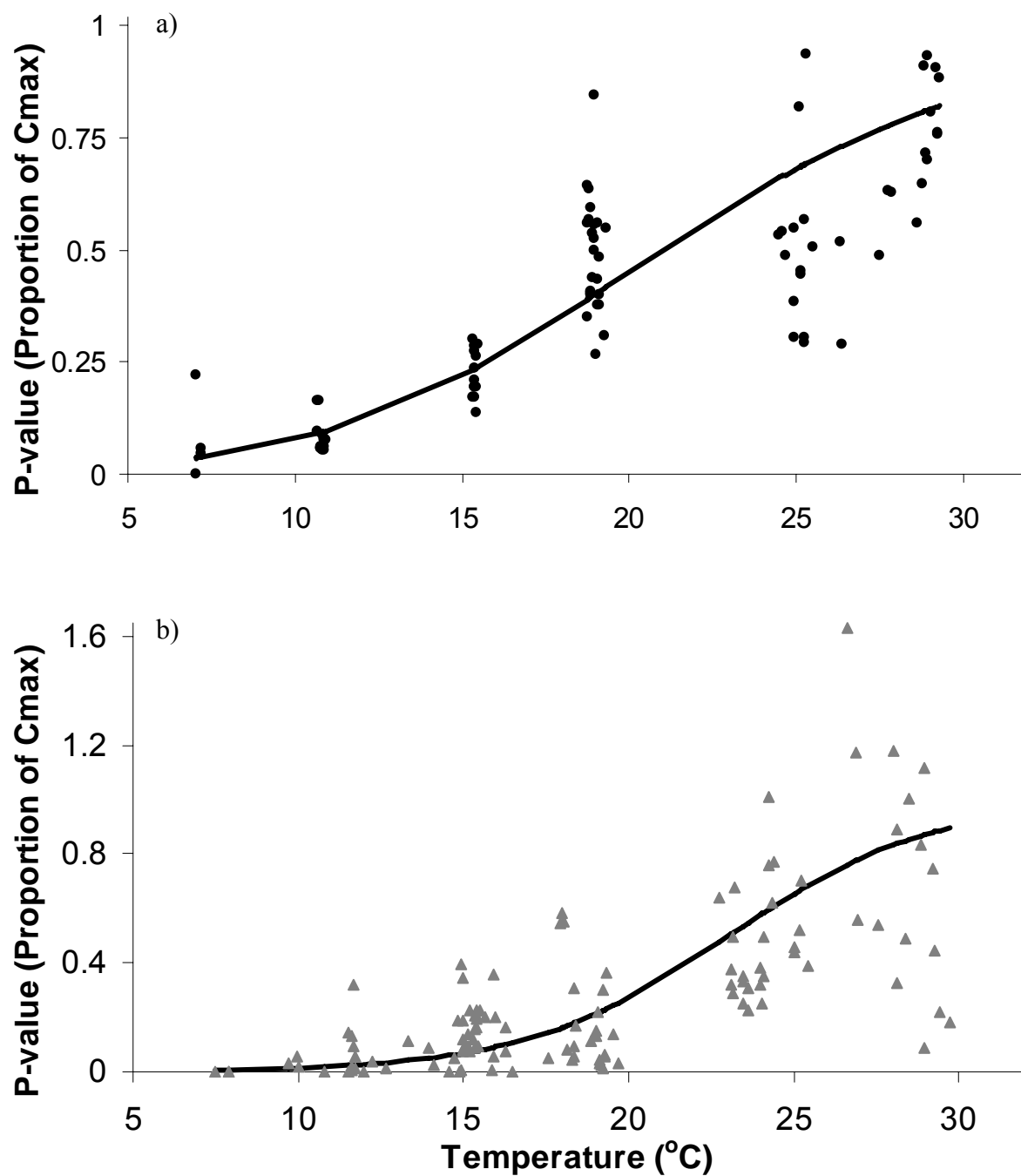
Figure 4.4: Residuals by temperature for consumption models developed for fish less than 20g (●) and fish greater than 20g (▼).
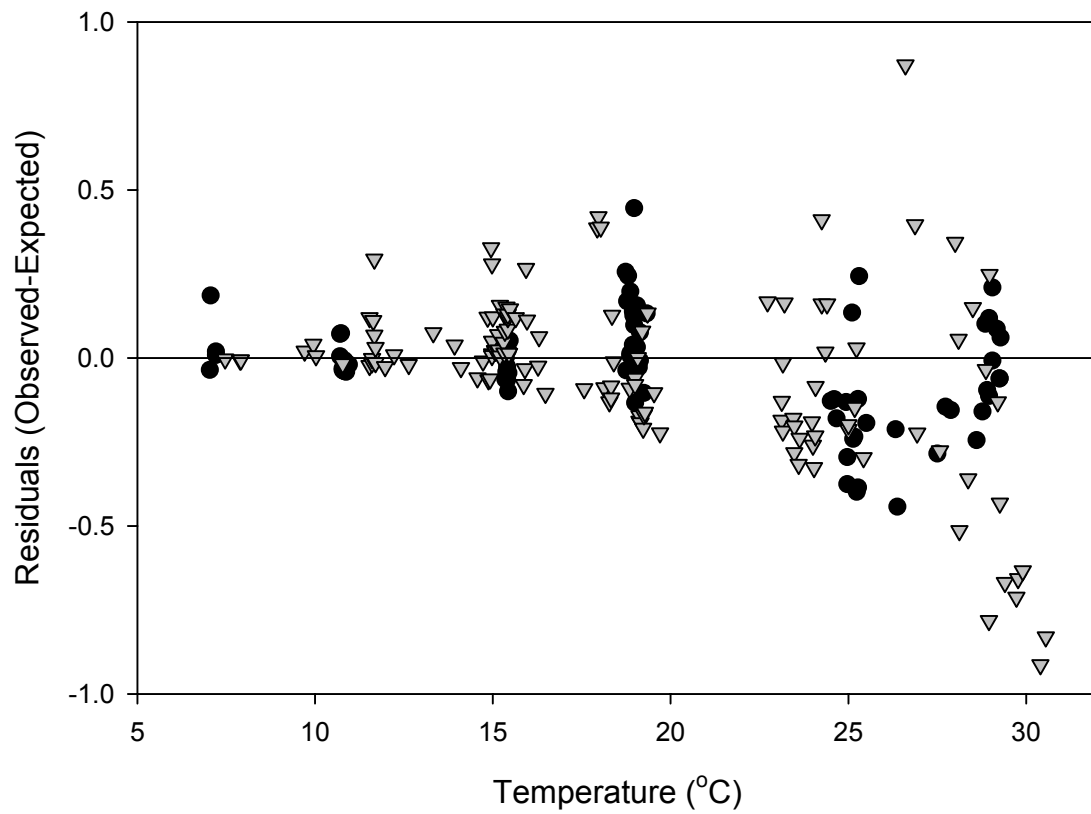
Figure 4.5: Routine metabolism of Atlantic croaker as a function of weight. Nonlinear regressions were fit with data combined into five temperature classes.
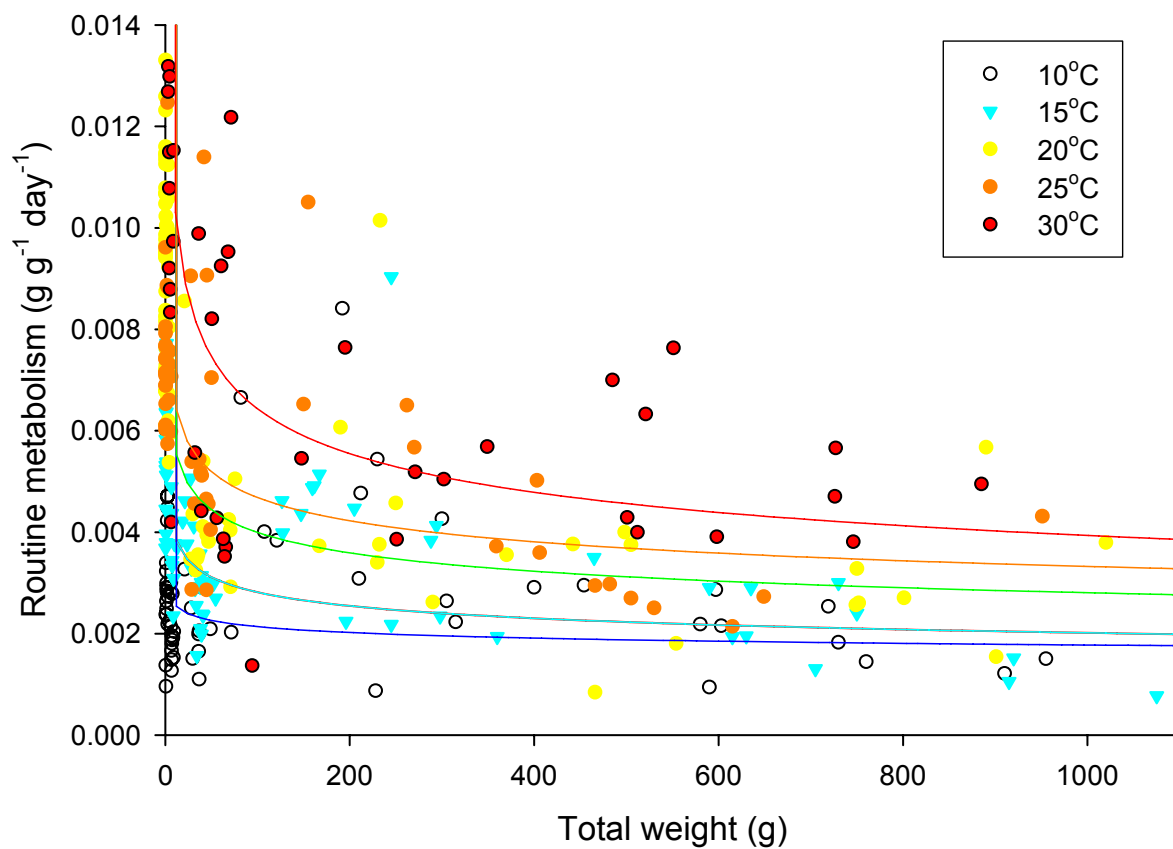
Figure 4.6: Routine metabolism as a function of temperature for three different size classes: a) <2.5g ($\circ$), 2.55-20g ($\bullet$) and b) >20g ($\blacktriangledown$).
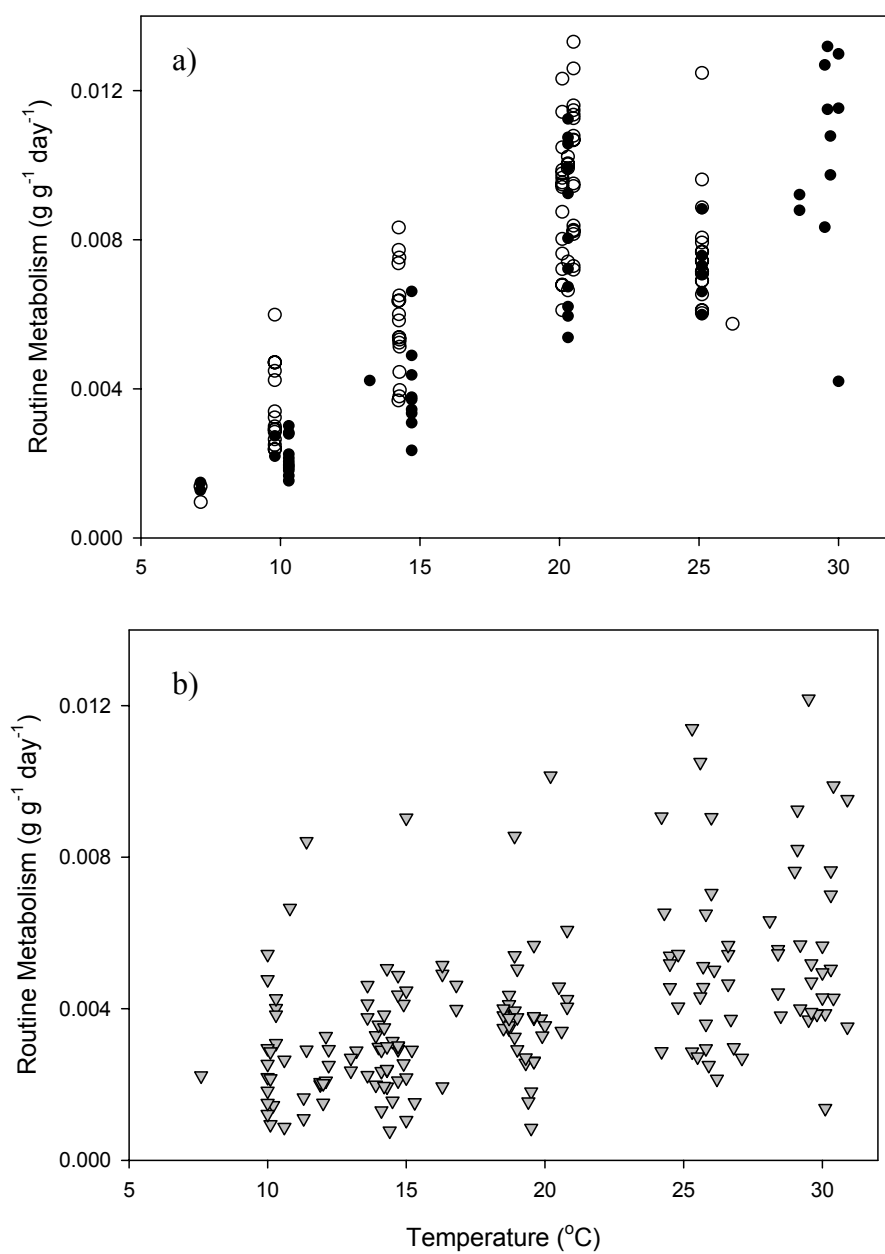
Figure 4.7: Observed oxygen consumption for fish a) 2.5-20g (●) and b) >20g (▽).
Curves represent the exponential models developed for the relationship between
temperature and metabolism.
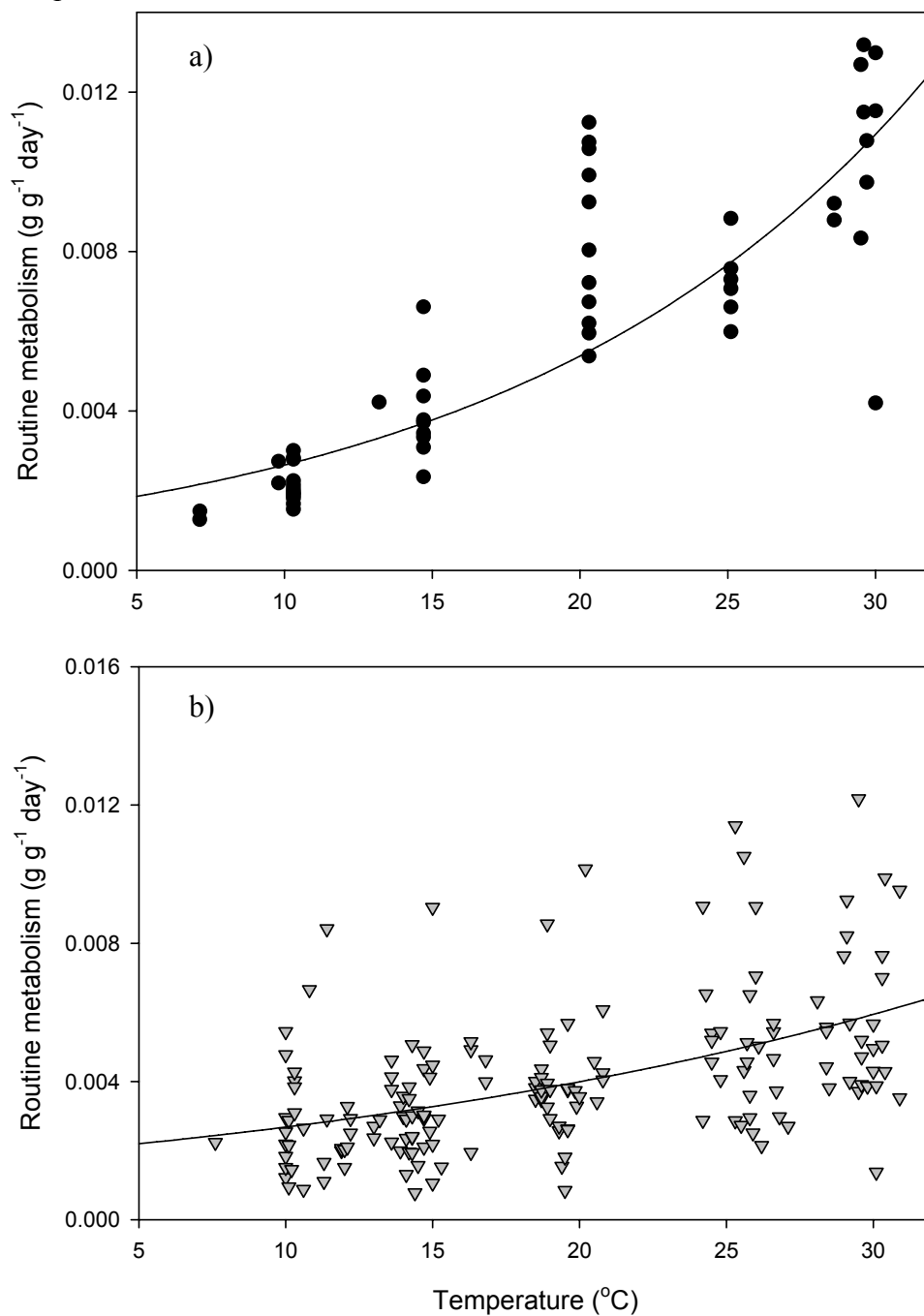
Figure 4.8: Observed and modeled (- - - -) oxygen consumption at temperature and for fish less than 2.5g.
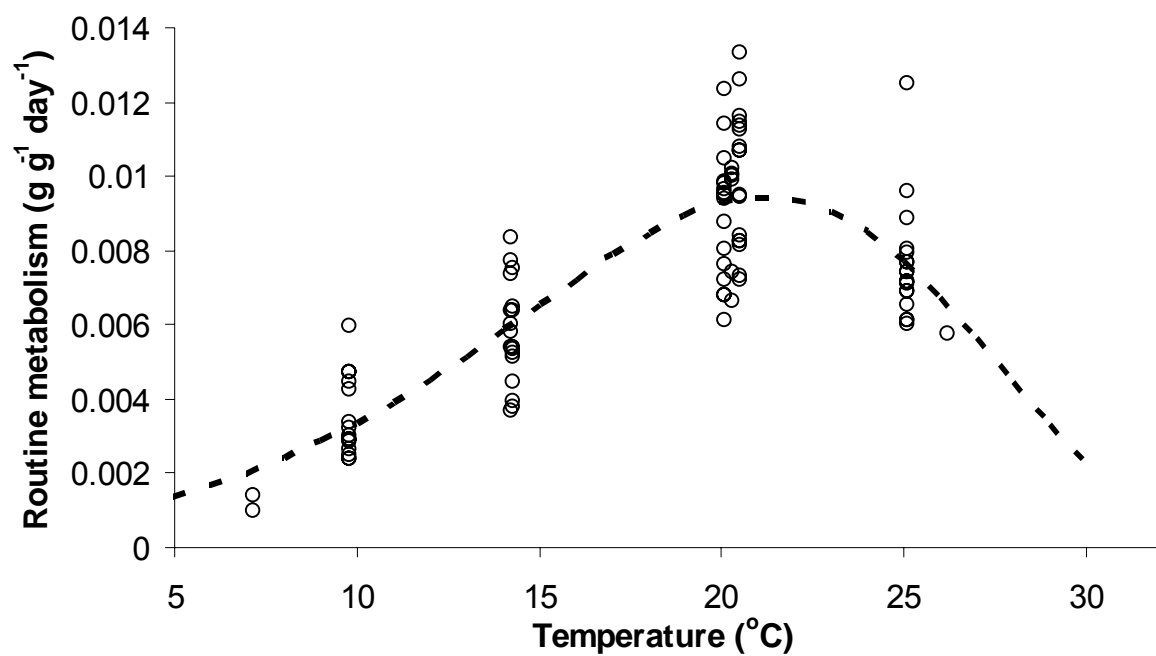
Figure 4.9: Residuals by temperature for respiration models developed for fish a) <2.5g (○), 2.55-20g (●) and b) >20g (▼).
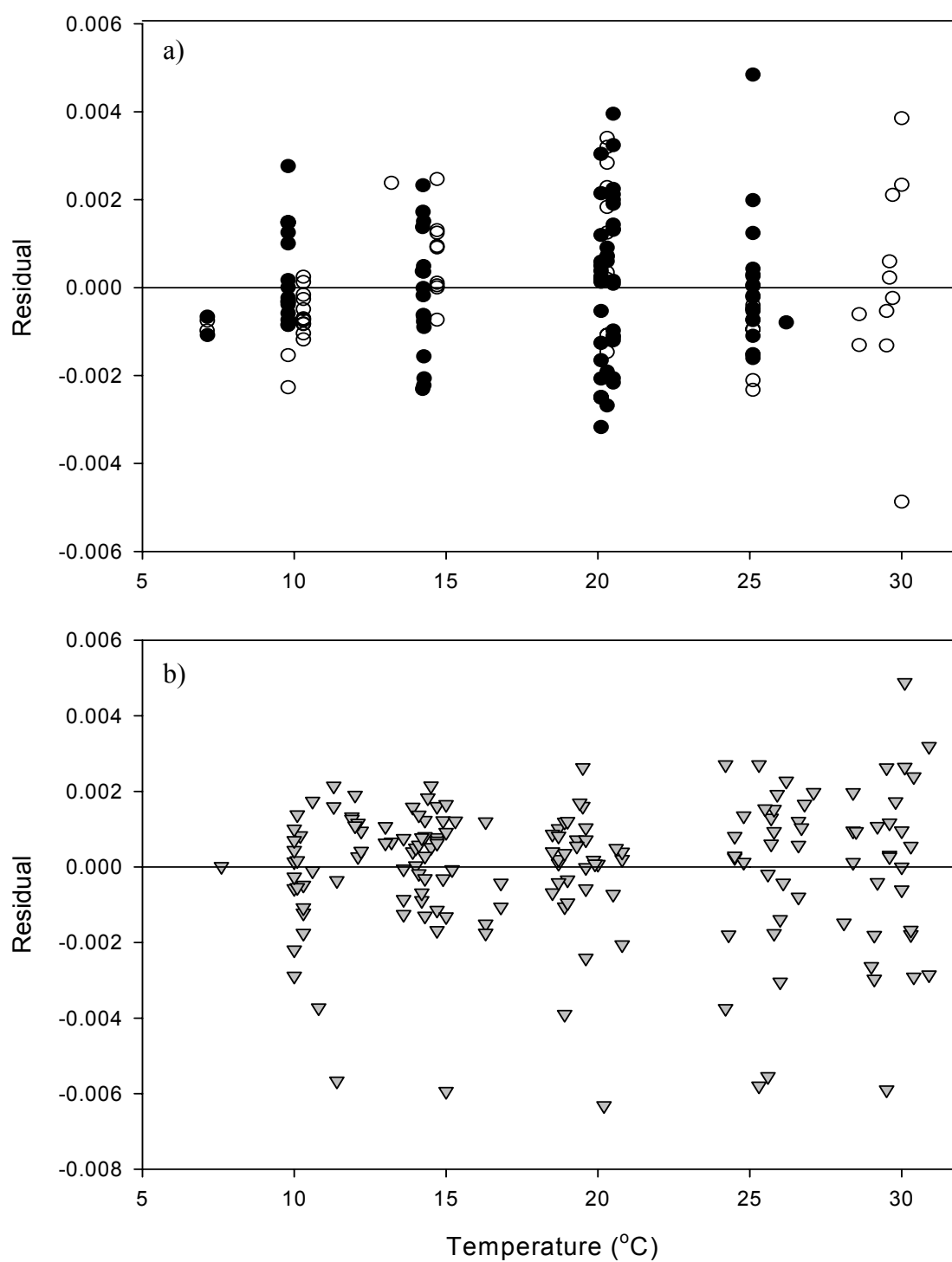
Figure 4.10:  Activity multiplier versus a) temperature and b) total weight for >20g
model and the <20g model.
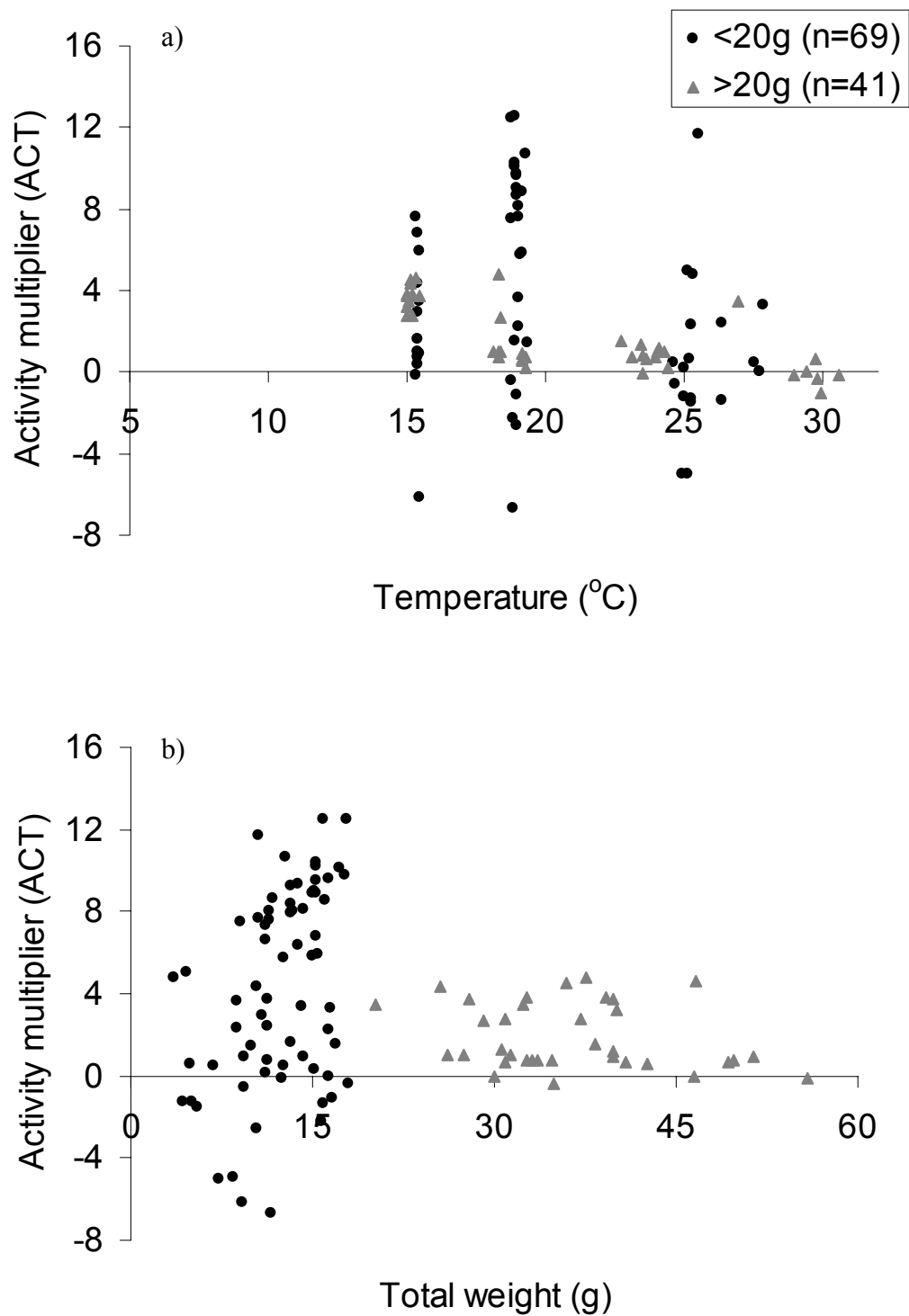
Figure 4.11: Scope for growth of fish standardized for a) 1 gram fish and b) 10g fish.
Metabolism=R+SDA+ACT and Waste=F+U.
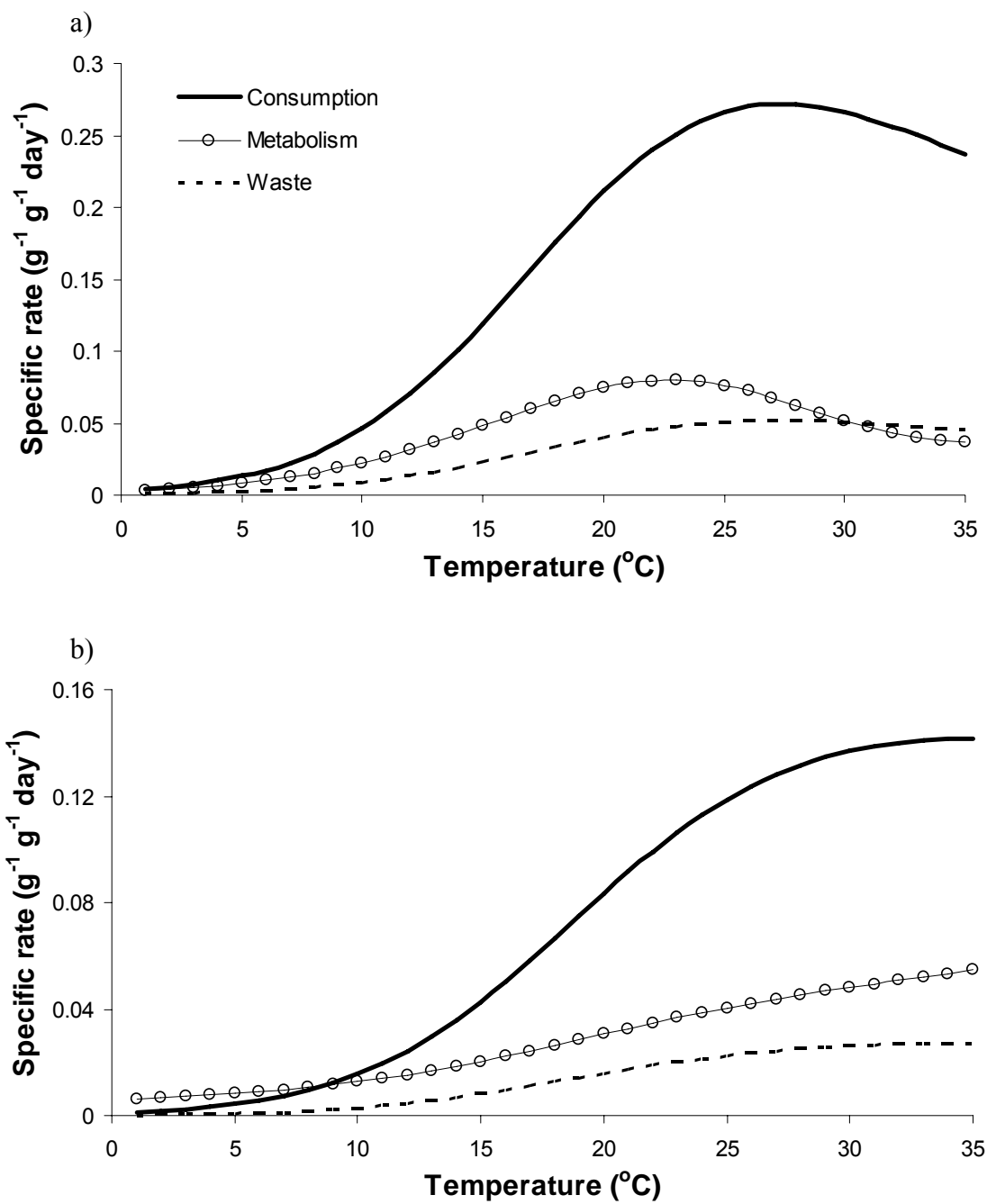
Figure 4.12: Scope for growth standardized for a) 30g fish and b) a 500g fish.
Metabolism=R+SDA+ACT and Waste=F+U.
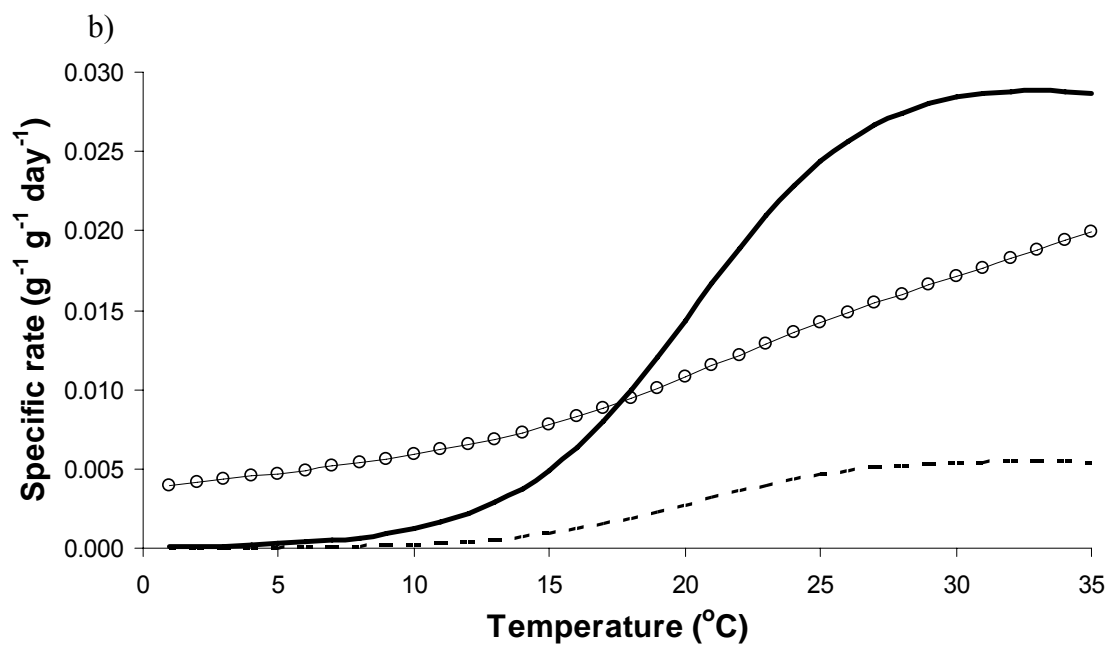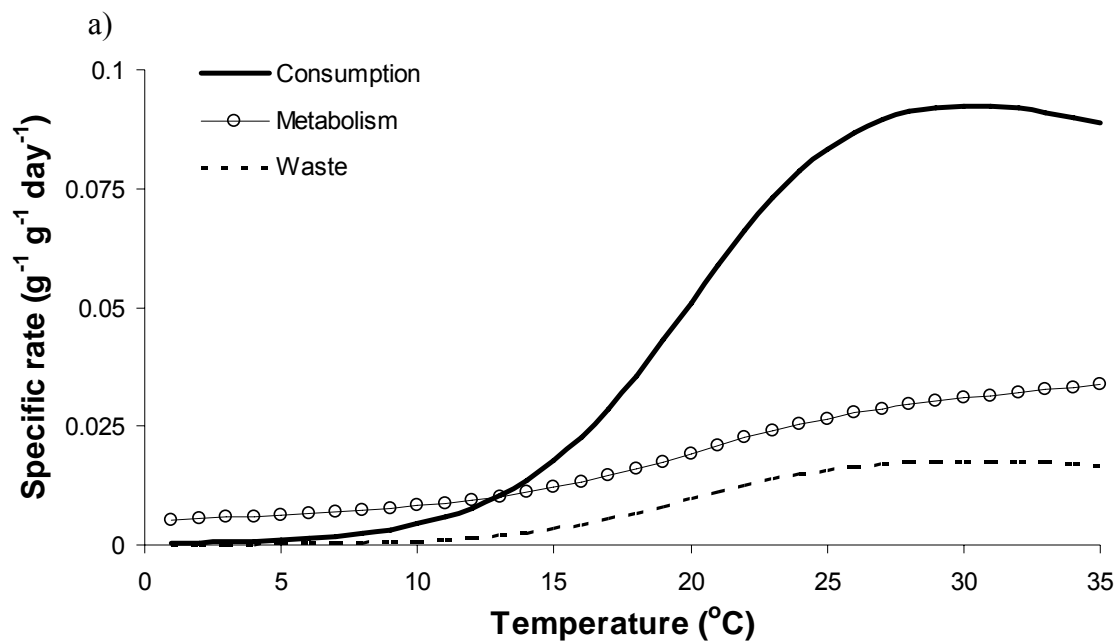
Figure 4.13: Daily specific growth rate (DSGR, % body weight per day) for food and ration treatment combinations in a) 12°C, b) 20°C, and c) 27°C growth experiments.
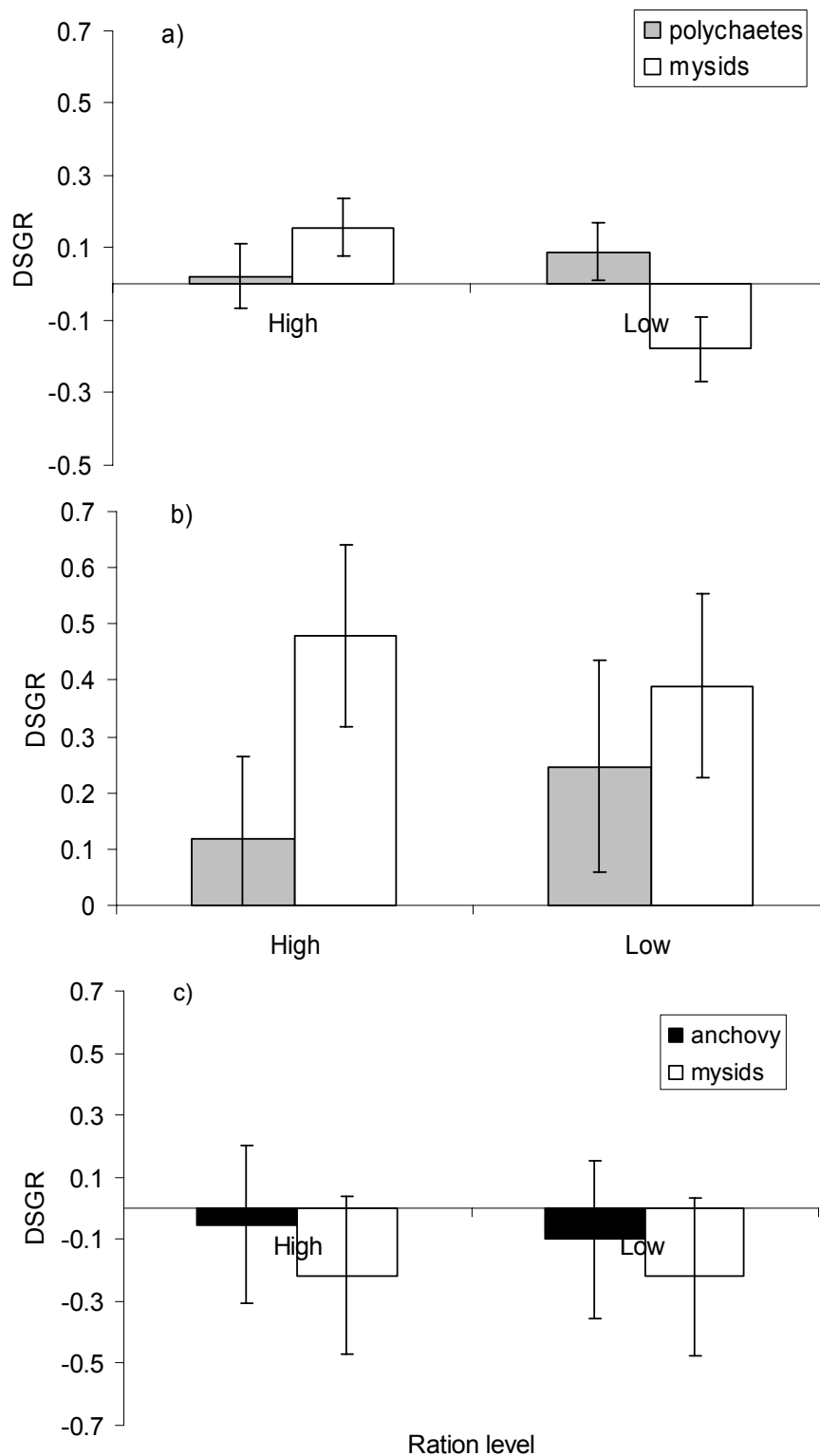
Figure 4.14:  Mean daily consumption (grams of food eaten per gram of fish per day) for food and ration treatment combinations in a) 12$^{o}$C, b) 20$^{o}$C, and c) 27$^{o}$C growth experiments.
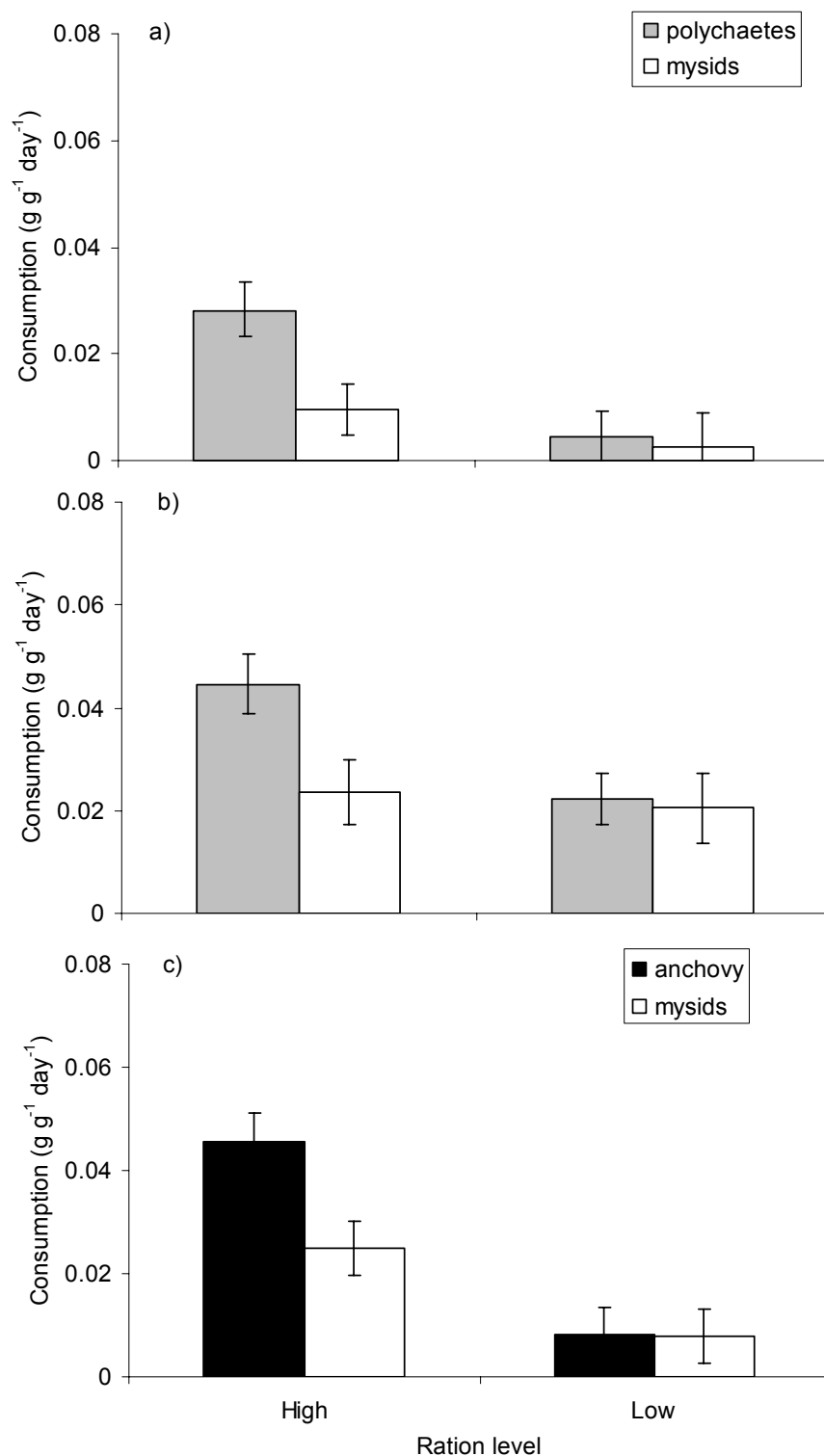
Figure 4.15: Absorption efficiency for Atlantic croaker at a) 10$^{o}$C and b) 20$^{o}$C at high and low rations and for two prey types. Capital letters above treatments indicate statistical differences.
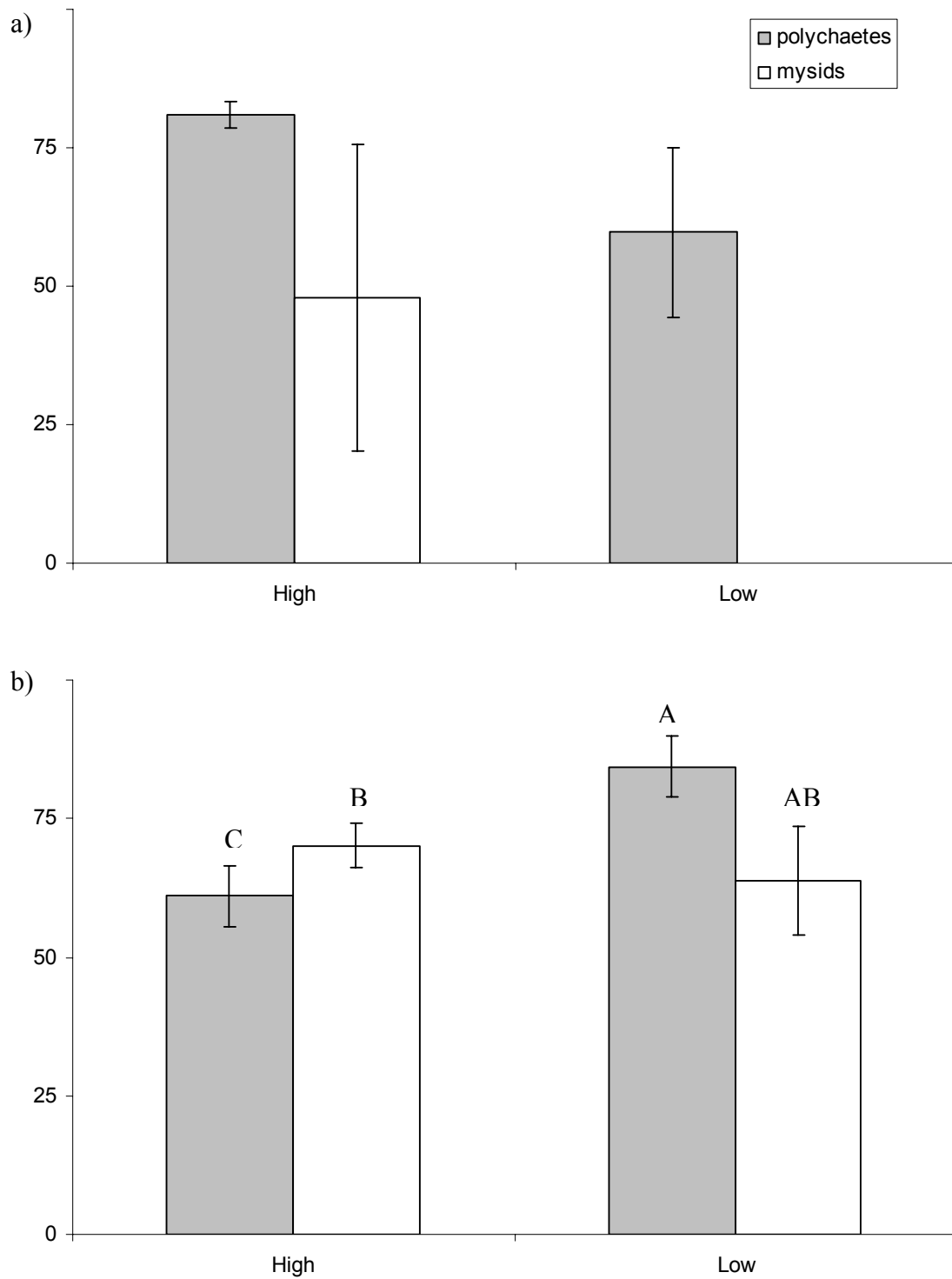
Figure 4.16:  Observed versus modeled total weights of fish at the end of growth experiments at 12 (●), 20 (○), and 27°C (▲) using the >20g model.   The 1:1 line added for reference.
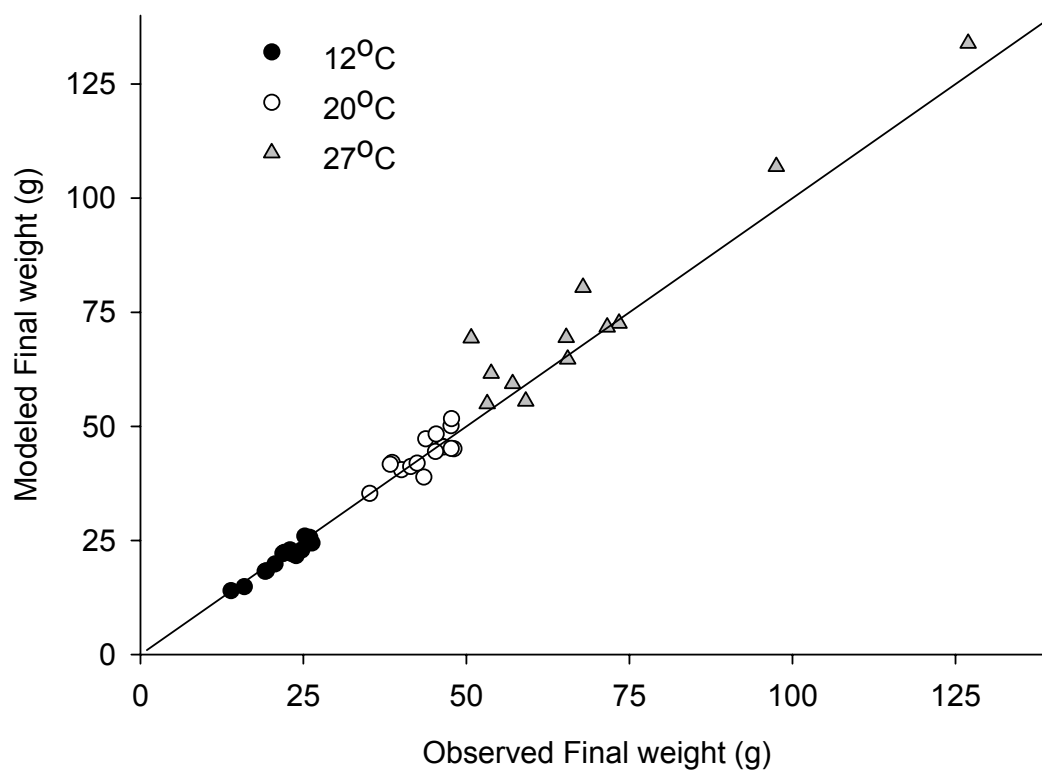
Figure 4.17: Observed versus modeled consumption over the 14-day growth experiments at 12 (●), 20 (○), and 27°C (▲) using the >20g model. The 1:1 line is shown for reference.
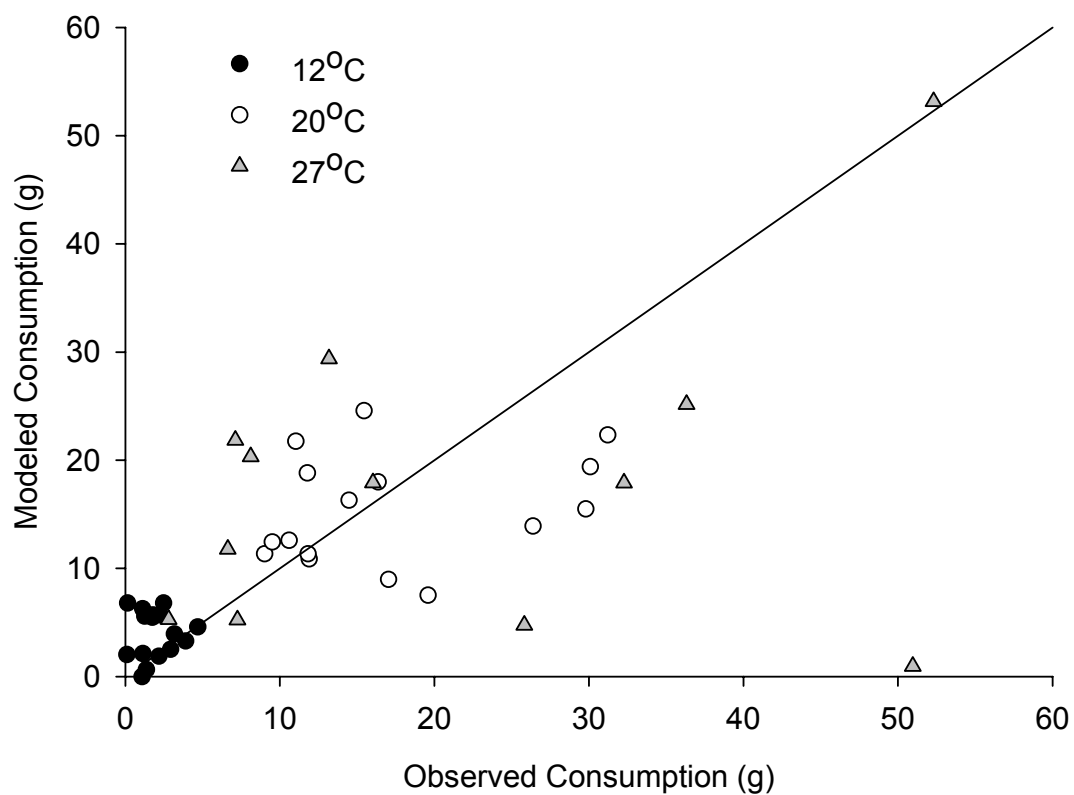
Figure 4.18: Observed and modeled final weight for three growth experiments at a) 12, b) 20, and c) 27°C using the >20g model.
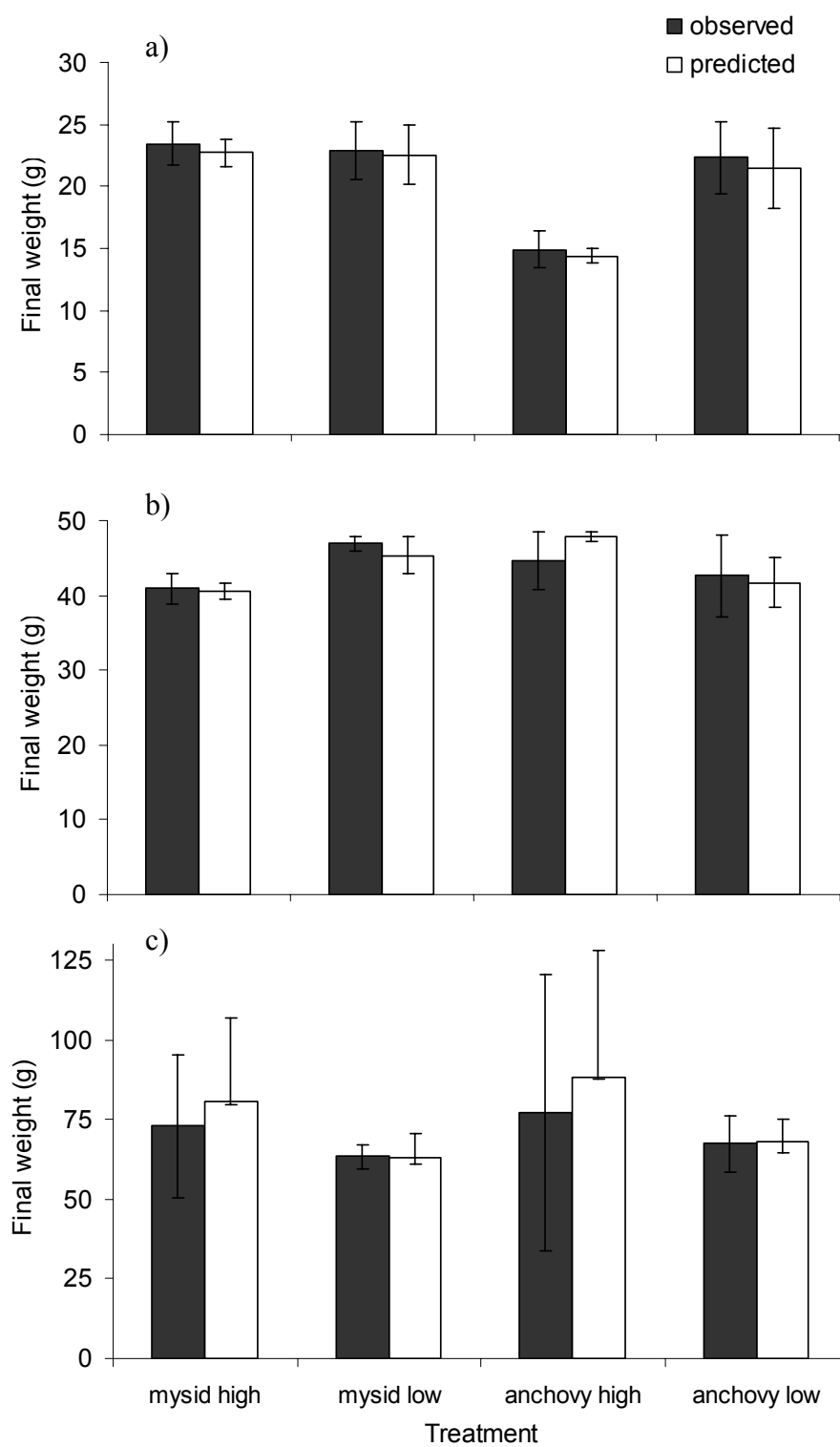
Figure 4.19: Comparison of observed and predicted consumption over the 14 day experiments using the >20g bioenergetic model for the a) 12, 20, and 27°C growth experiments.
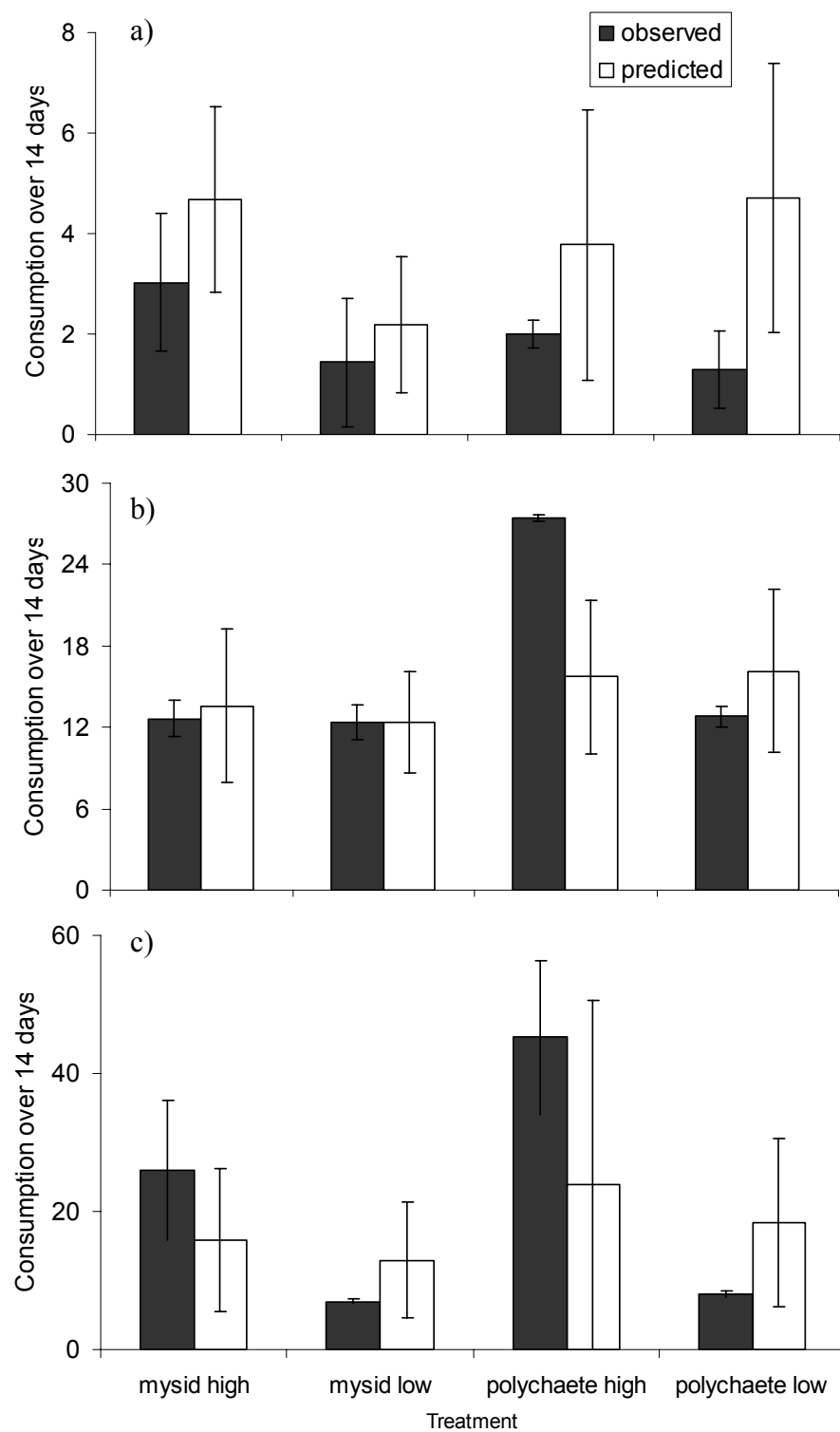
Figure 4.20:  Observed and modeled a) final weight and b) total consumption for small Atlantic croaker in growth experiments performed on fish from Delaware Bay (DE), North Carolina (NC), and Florida (FL) at $18^{o}C$.  Standard error bars were available for the observed values and numbers above the consumption and weight predicted by the <2.5g model indicate percent difference.
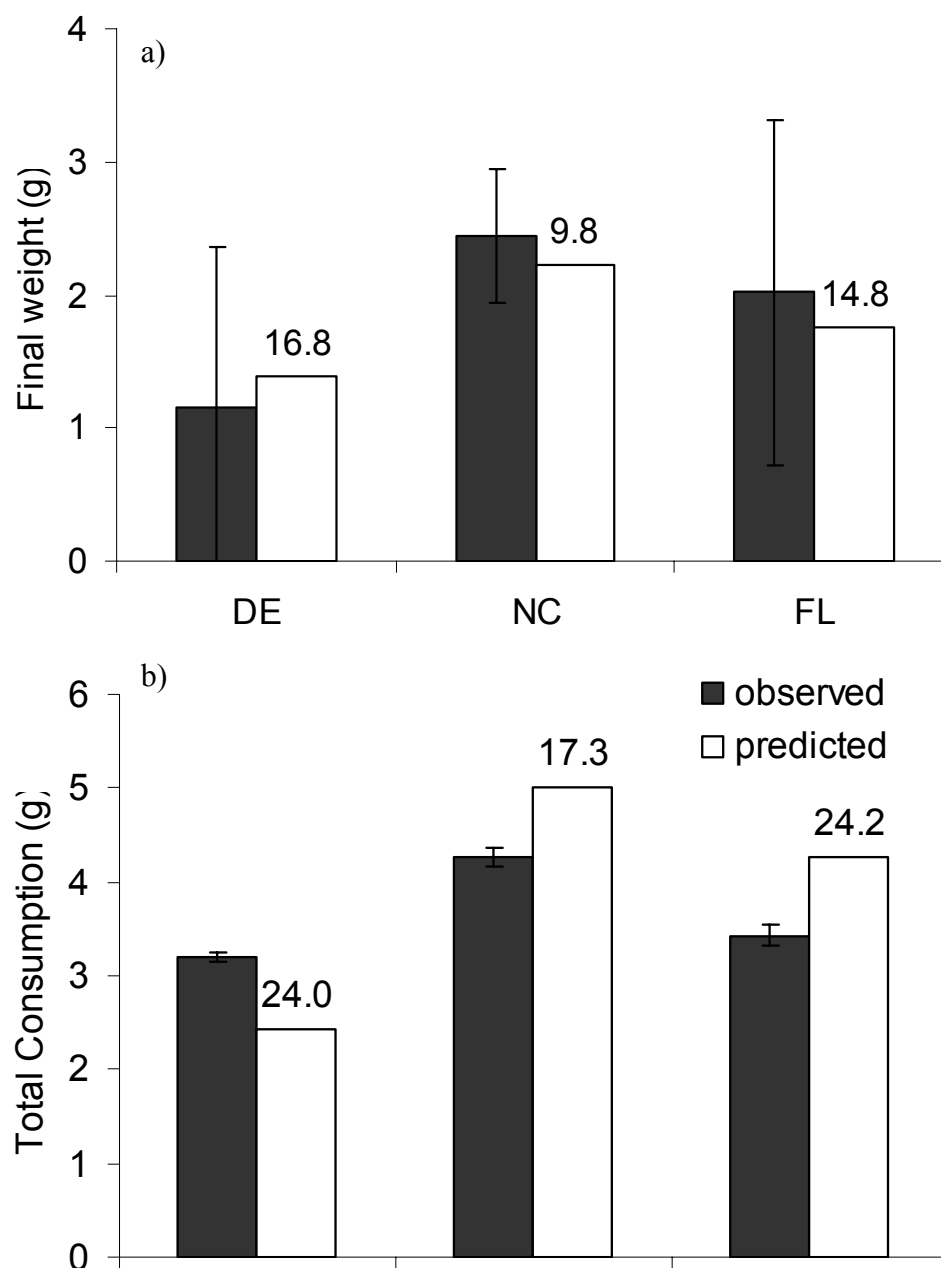
# CHAPTER 5: POPULATION CONSUMPTION OF ATLANTIC CROAKER *MICROPOGONIAS UNDULATUS* IN CHESAPEAKE BAY: IMPLICATIONS FOR THE CHESAPEAKE BAY ECOSYSTEM

## INTRODUCTION

There has been a recent interest in ecosystem-based approaches to fisheries management in many aquatic ecosystems including the Chesapeake Bay (Chesapeake Bay Fisheries Ecosystem Advisory Panel 2006, Link 2002, Miller et al. 1996). Like many estuarine ecosystems, the Chesapeake Bay has experienced considerable change in the recent past with the increase in nutrient loading being particular notable (Kemp et al. 2005). In addition to changes in nutrient dynamics, researchers have documented changes in both patterns of fish production (Jung and Houde 2005), and in fishery removals (Miller 2006). Miller et al. (1996) suggested that these changes likely have both direct and indirect effects on food web structure. In support of this hypothesis, Griffin and Margraf (2003) demonstrated shifts in the diet of striped bass between the 1950s and the 1990s from one dominated by large Atlantic menhaden *Brevoortia tyrannus* to one dominated by bay anchovy *Anchoa mitchilli*, a small pelagic species with higher rates of production than menhaden. Similarly demersal fishes including Atlantic croaker have changed diet in response to hypoxia (Pihl 1994, Pihl et al. 1992, Powers et al. 2005). Changes such as these exemplify why an understanding of the interactions among fish species and their predation on food resources in the ecosystem is needed.

Rather than ask if the ecosystem can support production of a single species of interest, the shift to an ecosystem approach to management prompts us to ask whether the ecosystem can support a diversity of healthy populations of fishes given the distribution of available food resources and suitable habitats (Pikitch et al. 2004). Additionally, ecosystem approaches to management challenge the traditional belief that there is surplus production available for harvest by a fishery. Instead, scientists and managers must consider what proportion of the "surplus" production is necessary to support predation by other members of the ecosystem and is therefore not available for harvest. Many studies suggest that piscivore production is limited by prey availability (Carpenter et al. 1985, Hartman 2003, Hartman and Margraf 1993). Thus, we might expect that ecosystem-based approaches will have their biggest impact when predatory species within the ecosystem are competing for their prey.

There are several quantitative approaches that can evaluate the importance of predation and biological interactions within an ecosystem-based framework (Latour et al. 2003, Whipple et al. 2000). The earliest examples used theoretical predator-prey models to examine the qualitative impact of harvest of one species on other species (Beddington and May 1982, May et al. 1979). Single species models can be modified to incorporate species interactions such as predation (Basson and Fogarty 1997), time-variable mortality (Fu and Quinn 2000) and density-dependent effects due to predation (Quinn and Deriso 1999). These simple models can b expanded to multispecies surplus production models (Sparre and Venema 1998) and to whole system models like ECOPATH with ECOSIM (Christensen and Walters 2004, Walters et al. 1997) which more fully integrate ecosystem based considerations. These models differ in the degree

of resolution with which they represent the complexity of the ecosystem and in the amount of data required to parameterize them (Plaganyi 2007). Increasingly these tools are being used to develop both multispecies reference points (Collie and Gislason 2001, Gislason 1999, Hightower 1990, Hollowed et al. 2000) and ecosystem-based reference points (Brodziak et al. 2002; Link 2005) to replace traditional single species reference points.

Bioenergetics models have been widely applied in studies of single species. But, because bioenergetic models are specific to individual species, their use in examining multispecies interactions may not be intuitive. However, unlike many of the models described above, bioenergetic models link basic fish physiology and behavior with environmental conditions. When combined with estimates of population abundance, bioenergetic models can be used to estimate production of the stock and population consumption (Yodzis and Innes 1992; Koen-Alonso and Yodzis 2005). Estimates of population level consumption are highly relevant to multispecies management efforts especially if these estimates can be made annually for key species within an ecosystem.

Hartman and Brandt (1995b) used bioenergetic models of striped bass *Morone saxatilis*, weakfish *Cynoscion regalis* and bluefish *Pomatomus saltatrix* to assess the potential for the Chesapeake Bay ecosystem to meet the trophic demands of each of these three piscivorous species. Hartman and Brandt reported that the ecosystem could routinely meet the trophic demand of bluefish. However, there was potential for the growth of weakfish and striped bass to be limited by prey resources (Hartman and Brandt 1995b, c). All three species consume bay anchovy as prey (Hartman and Brandt

1995c).  In Chapter 2, I demonstrated that Atlantic croaker has the potential to be an important additional consumer of bay anchovy production.  My diet studies indicated that in some seasons, bay anchovy represent up to 50% by weight of the diet of croaker (Chapter 1).  This fact, combined with the substantial increase in croaker abundance (ASMFC 2005) since Hartman and Brandt's assessment of predatory demand suggest that croaker might be an important but underappreciated predator on bay anchovy.  However, the additional impact of the trophic demand of Atlantic croaker on ecosystem dynamics is currently not quantified.

To estimate trophic demand of these piscivores within the Chesapeake Bay data on their growth while resident in the Bay are needed.  However, estimating what their growth is while resident in Chesapeake Bay is complicated by their seasonal use of the Bay.  For example, mature croaker spawn offshore and larvae enter the Bay in the fall and winter months (Norcross 1991).  Subsequently juvenile croaker feed and grow within the Chesapeake Bay during their first year of life (Nemerson 2002, Nixon and Jones 1997).  Adult croaker migrate into the Chesapeake Bay in the spring and remain there throughout the summer, likely to exploit the Bay's high production.  Croaker migrate out of the Bay in the summer to early fall.  Adult weakfish have a similar migration pattern to croaker in that they enter bays and estuaries in the spring (Thorrold et al. 2001).  Unlike croaker, weakfish spawn in the spring and summer months within bays and estuaries where juvenile weakfish utilize the productive nursery area of Chesapeake Bay (Lowerre-Barbieri et al. 1996).  Adult weakfish leave the estuary in the fall, followed later by juveniles.  Similarly, striped bass exhibit ontogenetic shifts in residence in the Chesapeake.  Eggs are spawned and larvae hatch in the vicinity of

density interfaces where fresh and salt water mix in late spring (North and Houde 2006). As larvae grow and metamorphose, they begin to utilize habitats of a wider range of salinities (Mansueti 1961, Massman and Pcheco 1961). A proportion of the population eventually joins the adult coastal stock in offshore waters returning as adults to spawn in estuarine waters (Secor and Piccoli 2007). However, a portion of the striped bass population is resident year-round in Chesapeake Bay. Given the seasonal movements that each species exhibit, it is important to correctly identify the growth that resulted specifically from the utilization of shared Chesapeake Bay resources during their period of residence. Although croaker, weakfish, and striped bass differ in the ways in which they exploit the Bay, there is considerable spatial and temporal overlap. Thus, it is important to understand the trophic ecology and total consumption of these fish when temporal and spatial overlap is highest in the spring and summer months because the potential for competitive interactions is greatest.

Predatory demand of striped bass, weakfish and bluefish has been estimated using bioenergetic models (Hartman and Brandt 1995b). Since that time, the abundance of all three species has changed dramatically (ASMFC 2005, Kahn et al. 2006, Striped Bass Technical Committee for the Atlantic Striped Bass Management Board 2005). However, knowledge of the abundance of bluefish remains controversial and recent assessments have been unable to produce reliable estimates of abundance. Accordingly, updating the assessment for this species is not possible at the moment. In Chapter 4, I developed parameter estimates required to implement a similar bioenergetic model for Atlantic croaker. Here I will use bioenergetic models for croaker, striped bass and weakfish, species for which reliable abundance estimates and

160

dietary patterns are available, to test the null hypothesis that there are sufficient prey resources to support current populations of these three historically abundant populations of fish in Chesapeake Bay,  To compare these three species, I must first quantify the trophic demand of Atlantic croaker while resident in Chesapeake Bay, which has not been done before.  I assessed trophic demand of croaker by using two methods to estimate seasonal growth.  First, I have estimated the growth of Atlantic croaker using season and year specific length frequency data to for 2002-2005.  This approach accounts for annual differences in growth rates.  Secondly, I estimated growth in croaker using average weight at age data pooled over many years to obtain an "average" value of consumption.  This is the same approach to estimating growth used in previous bioenergetic modeling studies.  Accordingly, I also estimated trophic demand of croaker, weakfish, and striped bass by interpolating average weight at age pooled over many years to compare trophic demand between species and to quantify their combined predation pressure.

**METHODS**

The bioenergetics models of Atlantic croaker, striped bass and weakfish were implemented in Fish Bioenergetics software (Hanson et al. 1997). In simple terms these models solve the daily energy balance equation

$$C = G + (R + U + F)$$  Eq 5.1

where C is consumption, G is growth, R is respiration, U is nitrogenous excretion and F is fecal loss.  Each term is size- and temperature- dependent.  For this application, I estimated the consumption (C) required to support the observed patterns of individual

growth (G) within each population given the known physiological energetics (R, U and F). The inputs needed to estimate annual consumption in each year from 2002-2005 for each species are growth (beginning and end weights), proportion of prey items in diet, energy content of each prey item, physiological energetics and temperature. Energy density of predators was assumed to be constant from 30 April to 1 October.

*Field Sampling*

Croaker data used in these analyses were obtained from the Chesapeake Bay Fisheries Independent Multispecies Survey (CHESFIMS) collections. Details of the CHESFIMS sampling are provided elsewhere (Chapter 1) and only summarized here. Briefly, CHESFIMS sampled the fish assemblage in the Chesapeake Bay using 20 min tows of an $18m^2$ midwater trawl during spring, summer and autumn cruises from 2001-2005. One supplementary cruise occurred in August to provide more temporal resolution in diet and growth data. On each cruise, 29-51 fixed transect and stratified random stations were sampled. For each species, the total catch was weighed and all fish were enumerated. The length of at least 100 fish of each species at each station were measured (TL, mm). A random subsample of croaker and weakfish were immediately frozen for subsequent dietary analysis (Chapter 1).

*Growth*

Growth of croaker during Chesapeake Bay residency was estimated using two methods. In the first method, growth was estimated using modal analysis of croaker size distributions derived from the croaker length frequencies for each cruise. Length frequency data were analyzed using a mixture model approach using the *mclust* library

162

in R (Fraley and Raftery 2007). MCLUST is a statistical library that utilizes iterative, maximum-likelihood estimation to fit the optimal mixture of Gaussian distributions to a single complex distribution. The iteration involves an estimation step which calculates the conditional probability that observation i belongs to group k given the current parameter estimates, followed by a maximization step which adjusts parameter estimates. Model fits are compared using the Bayesian Information Criterion (BIC) which penalizes the maximum likelihood according to the number of parameters estimated. The library uses

$$BIC = 2 \cdot \log lik(X|\theta) - (p) \cdot \log(n) \qquad \text{Eq 5.2}$$

where $\log lik(X|\theta)$ is the log likelihood of the parameters ($\Theta$) given the data (X), p is the number of parameters and n the number of observations. Up to three modes were identified for the length-frequency distribution from each cruise and the mean, standard deviation, relative contribution and BIC of each mode identified. The mean lengths of cohorts identified by the *mclust* algorithm were converted to weight using the species-specific weight-length relationship for all fish measured for CHESFIMS stomach processing. The relationship between total weight (TW, g) and total length (TL, mm) for croaker was TW=3.39x10$^{-6}$* TL $^{3.23}$.

I then linearly interpolated between the mean seasonal weights of each cohort to arrive upon start and end weights that were used in the bioenergetic modeling of croaker consumption. I used interpolated weights rather than observed weights for three reasons. First, cruises occurred on slightly different dates in each season from 2002-2005. By interpolating between the seasonal weights, I was able to estimate mean weight on the same day each year and keep growing periods consistent between

modeling years. By interpolating, I could use the linear growth rates to extrapolate to arrive upon hypothetical weights in both the fall in those years where some cohorts that were not detected in September and also on 1 October at which time no sampling was done. Lastly, by interpolating between the seasonal weights some uncertainty was removed in the assignment of cohorts and mean lengths in years where clear progression of cohorts was difficult to discern.

To corroborate the growth rates calculated by modal analysis, a random subsample (n=217) of croaker from 2001-2003 were aged by sectioning otoliths as described by Barbieri et al. (1994). Briefly, one sagitta from each fish was sectioned (0.75mm) and then mounted on a slide. Two independent readings were made for each otolith. If the readings did not agree, a third reading was made. If after a third reading, any otoliths did not have two identical readings, the sample was discarded from the analysis. The length frequency of all fish in 2002-2003 was compared to the length frequency of each age group to determine the age class of cohorts identified in length frequencies. Subsequently, I estimated growth of age class cohorts by linearly interpolating between mean weight in each season from 2002-2003. To calculate the average seasonal weights, I used the average weight age 1-2 and age 3+ croaker.

For the second method of calculating croaker growth, mean weight age data from otoliths was also used to calculate average weight at age of croaker in each season. I linearly interpolated between the mean weights of each age class to arrive upon daily weights that could be used as input into the bioenergetics software. I chose to interpolate between mean weight at age in the summer to do this because the full age structure of croaker was not well-represented in the spring or fall collections. Many

age-1 through age - 7 individuals were present in the summer CHESFIMS samples, but there was an obvious lack of age classes in the spring and fall due to migration. Fish as old as age 11 were present, but were rare. Consequently, only fish age-1 – age-7 were included in the population level estimates of consumption.

Because the full age structures of weakfish and striped bass are not captured on CHESFIMS cruises, growth of weakfish and striped bass in each season was derived by linearly interpolating between average weights at age. This approach was the same as the second method of growth estimation described for croaker. I interpolated between weights at age of weakfish in the spring reported in Lowerre-Barbieri et al. (1995). Growth of striped bass was estimated using weight at age following Hartman (2003). Hartman used fork length at age as reported by Setzler et al. (1980) and a relationship of wet weight to fork length as predicted by Jones et al. (1977). In the comparison of population consumption between croaker, weakfish, and striped bass growth was estimated using mean weight at age in order to maintain consistent methodology.

*Diet*

Diet data for croaker and weakfish was taken from a subsample of each species collected at each station of the CHESFIMS monitoring program. Details of the laboratory protocols and statistical analyses for dietary analyses are described in detail in Chapter 1 and are only summarized here. Briefly, frozen carcasses of both species were defrosted, their stomachs excised and preserved in ethanol. To quantify prey items, the full stomach was weighed, and the contents removed. The prey items in up to twenty stomachs per species per station were identified to the lowest taxonomic level possible and then weighed. The percent composition by weight (%W) was calculated

by a two-stage clustering scheme as described in Chapter 1 in Spring, Summer and Fall of each year (Tables 5.3, 5.4). Diet was assumed to be constant among years in striped bass using data from Hartman and Brandt (1995c).

*Energy content*

Energy content of prey items was measured for organisms collected opportunistically during the CHESFIMS sampling cruises when they were present in catches. Several individuals of each available species were pooled by station and dried in a drying oven until they reached a constant weight. Two subsamples for each prey item were measured for caloric content in a Parr 6200 bomb calorimeter (Parr Corporation, Moline, IL). The caloric content was measured in Joules/gram dry weight and then was converted to Joules gram$^{-1}$ wet weight using the ratio of wet weight to dry weight for input into the Fish Bioenergetics software (Table 5.1). The energy density of marine invertebrates observed in diets, but not sampled during CHESFIMS were obtained from literature values taken from Cummins and Wuycheck (1971) and those of marine macrophytes from Lamare and Wing (2001).

*Water temperature*

To drive the bioenergetic models, mean water temperatures were obtained for the polyhaline section of the Bay from the Chesapeake Bay Program Water Quality Monitoring Program (http://www.chesapeakebay.net/data/). The Chesapeake Bay Program defines the polyhaline area of the bay as that area from just south of the Potomac River to the mouth of the Bay. The Bay Program samples several depths and at multiple stations on two to four days per month. A polynomial equation was fit to

166

these data to calculate the mean daily temperature for April 1 to October 1 of 2002-2005 (Figure 5.1). The daily temperatures predicted by the polynomial equations were used as inputs into the bioenergetic model simulations.

*Population consumption*

To compare the annual population level consumption of croaker, weakfish, and striped bass in 2002-2005, I used mean weights at age as described earlier which assumes that species-specific growth was constant in each year. Growth rates are likely more variable than this method assumes. However, using mean weight at age allowed for a comparison of consumption with striped bass, weakfish, and croaker using consistent methodology among the three species. To estimate the consumption of each age class for each species, year-specific temperature, year-specific diets for weakfish and croaker, and mean energy density were input to the model were as described above.

Consumption by each age class was scaled up by using abundance estimates (number of fish) obtained from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), a fishery-independent survey conducted by the Virginia Institute of Marine Sciences that samples the entire mainstem of the Chesapeake Bay. ChesMMAP surveys estimate the minimum trawlable numbers in March, May, July, September, and November of several species (Bonzek et al. 2007). The May, July, and September time periods coincide with CHESFIMS sampling schemes where growth and diet data were obtained. Minimum trawlable numbers from the ChesMMAPP survey were used as estimates of population size and were calculated by:

$$N = \frac{C \cdot A}{a}$$

where C=the catch in numbers of fish, A=Total area surveyed, and a=area of the tow (http://www.fisheries.vims.edu/multispecies/chesmmap/chesmmap.htm). This estimate of abundance is relatively conservative because it represents the number of fish caught only for the total area surveyed rather than the entire area of the water body. Furthermore, N does not account for gear efficiency, which has been estimated to be between 31 and 84% for Atlantic croaker over hard and soft substrate respectively (Hoffman et al. 2006). To account for differences in how well the gear captures different species, N would be divided by gear efficiency (i.e. 0.84 for croaker over soft substrate) and abundance estimates would be higher. In this application, N, unadjusted for the size of the entire Chesapeake Bay and for gear efficiency represents a conservative estimate of croaker so that population consumption can be viewed as a lower bound of the amount of prey eaten by the population in Chesapeake Bay for each species. This approach also assumes that the gear efficiency is similar for each species.

The abundance of fish in each cohort was scaled to total abundance based on the proportion of fish in each age class. Proportion at age for croaker was estimated from otoliths processed from 2001-2003. Proportion at age for weakfish was taken from the Virtual Population Analysis (VPA) used in the weakfish stock assessments (Kahn et al. 2006). The 1999 proportion at age values were used because recent population estimates and proportions at age in VPA can be inaccurate. Proportion at age specific to the year for striped bass were taken from the recent VPA developed in the latest stock assessment (2005).

RESULTS

*Growth*

Mixture models successfully decomposed cruise-specific length frequencies
into a finite number of normal distributions (Table 5.5). In general, the mixture
modeling identified a minimum of two cohorts during each cruise, whose distributions
exhibited minimal overlap (Figure 5.2). These results indicate that the demographics of
Atlantic croaker varied seasonally and annually (Figure 5.2). In 2002, many adult fish
(>100mm) were present in the spring and remained abundant well into the fall so that
distinct cohorts were observed in all three seasons (Figure 5.2). In contrast, in 2003-
2005 few if any adult croaker were present in the fall (Figure 5.2). A supplementary
cruise in August 2005 indicated that adult fish were present in August 2005 (Figure
5.3), confirming that although adults migrate out by September, they were present in
the Bay for the majority of the April – September period.

Linear regressions described the growth rate of croaker well while in
Chesapeake Bay (Figure 5.3). Growth in the grams and growth rates (gram·day$^{-1}$)
varied annually and ranged from -0.321 to 2.10 gram·day$^{-1}$ (Table 5.6). The highest
growth rates for both Cohort 1 and Cohort 2 occurred in 2005. Because of additional
sampling in August in 2005, the growth of a third cohort of small Age 1 fish could be
estimated. The length distribution of known age croaker from 2002-2003 were used to
assign membership of the modal size classes (Figure 5.4). The smaller cohort (Cohort
2) corresponds to Age 1 and 2 fish whereas the larger cohort identified by modal
analysis (Cohort 1) in both years corresponds to Age-3 and older fish. Although
Cohort 1 and Cohort 2 corresponded to croaker Age 1-2 and Age 3+ in most years, the

growth of these cohorts as identified by age was lower than growth estimated by length-frequency analysis in all years except 2003 (Figure 5.5, Table 5.2).

Differences in growth and diet composition of Atlantic croaker are reflected in the predicted consumption estimates (Figure 5.6). The highest growth rates occurred in 2005 and this year also yielded the highest consumption estimates. Growth rates in 2002 and 2004 were also positive and consumption was higher than consumption in 2003 when growth rates were low to negative. The consumption estimated from the average growth rate calculated from average weight at age for the two dominant cohorts was in the middle of the range of annual consumption values predicted by the modal analysis. Croaker consumption consisted mostly of polychaetes followed by anchovy (Figure 5.7). The variability in the amount of each prey item eaten was low except for shrimp. Croaker consumed a much higher proportion of shrimp in 2004 compared to all other years.

Growth rates of weakfish (1.61 gram·day$^{-1}$) and striped bass (3.033 gram·day$^{-1}$) were generally higher than croaker and these two species reached much greater sizes (Tables 5.7, 5.8, 5.9). Thus, their total consumption was much higher than croaker before consumption was scaled up to the population level (Figure 5.8). There were annual and seasonal differences in minimum trawlable numbers as reported in the CHESMMAP survey in 2002-2006 (Figure 5.9). In 2002, abundance of croaker was similar across all seasons, but on average lower than all other years. The trend in croaker abundance was similar in 2003-2005 where abundance peaked in the summer, but the peak abundance was much lower in 2003 than in 2004 and 2005. In all years, weakfish abundance increased from March to November primarily as a result of

summer spawning of weakfish in Chesapeake Bay. Similar to croaker, the time at which adult weakfish entered the Bay varied annually. Adult weakfish (Age 1+) entered the Bay much later in 2003 than in other years. In contrast to croaker and weakfish, population trends of striped bass in the mainstem of the Bay showed the opposite trend where numbers were highest from fall to spring in the mainstem of the Bay. The low abundance of striped bass in the spring to summer months reflects their migration to spawning grounds in tributaries and elsewhere.

*Population consumption*

Total population-level consumption of Atlantic croaker was higher than the population-level consumption of both striped bass and weakfish in all four simulated years largely because of much higher population sizes (Figure 5.10). In addition to the effect of population size, consumption may also be higher in croaker because their diet includes a higher proportion of less energy-rich prey overall. Although, anchovy made up a smaller portion of the diet of individual croaker than in individuals of the two other species, at the level of population, croaker ate more anchovy than striped bass in all four simulated year. Croaker consumed more anchovy and fish combined than striped bass in 2002 and 2004. Weakfish consumed more anchovy than croaker and striped bass in all years. However, the predation of croaker on anchovy and fish was similar in magnitude to that of weakfish. The combined predation of croaker, weakfish, and striped bass on anchovy alone ranged from 3,328 MT in 2003 to 17,859 MT in 2004 (Table 5.9).

According to ChesMMAP relative abundance, croaker population was an order of magnitude higher than either weakfish or striped bass. These differences in

population size made the estimates of croaker total consumption much higher than the populations of either weakfish or striped bass. ChesMMAP relative abundance estimates agree with the coastwide estimates of abundance for croaker weakfish and striped bass where in recent years croaker abundance is at least 3 times higher than weakfish or striped bass (Figure 5.11). In addition to the magnitude of population size, migration also affected consumption estimates. For example, population size was highest in 2004 for croaker and weakfish (Figure 5.9), but early migration of weakfish into the estuary in 2003 effectively doubled its population consumption (Figure 5.10).

**DISCUSSION**

My results indicate that Atlantic croaker exerted considerable demand on prey resources within the Chesapeake Bay. Although anchovy and fish made up only a small portion of the diet of croaker, as a result of their current high abundance, croaker consumed much more anchovy on an annual basis than striped bass in all years examined. In some years, croaker consumed nearly as much anchovy on an annual basis as weakfish, a species for which at least 60% if its diet consists of anchovy and other fish according to diet data taken from CHESFIMS sampling. Previous studies have illustrated the importance of bottom-associated fish and crab predators on the abundance and size structure of the benthic infauna in Chesapeake Bay (Holland et al. 1987, Virnstein 1977). However, this is the first study to illustrate how a small component of the diet of an abundant demersal fish, the Atlantic croaker, can affect the pelagic components of the food web. This study not only highlights the importance of Atlantic croaker in the Chesapeake Bay ecosystem, but also the importance of small

components in the diet of abundant generalist consumer to ecosystem structure and function.

Bioenergetic estimates of consumption were sensitive to assumptions regarding growth, abundance and temperature. Differences in annual growth rates of croaker effectively doubled total consumption. The influence of temperature in estimates of consumption is multifaceted. The sensitivity of bioenergetic estimates of consumption to temperature is well known (Kitchell et al. 1977) and would affect estimates for all the species considered here. First, respiration and consumption are driven by temperature in the bioenergetic models of each species (Hanson et al. 1997). Thus, temperature affects growth rate. Although the seasonal differences in growth rate could not be incorporated into the multispecies population consumption comparison, variable growth was incorporated into croaker consumption estimates and was reflected in consumption estimates. In 2003, growth was extremely low and was negative for age1-2 croaker. This reduction in growth was reflected in the low consumption estimate. Thus, the consumption estimated for croaker, weakfish, and striped bass are likely a reduced because these fish likely experienced lower than average growth rates.

Secondly, biomass and seasonal migrations of all species considered are related to trends in temperature. The mean water temperature on 1 May was lower in 2003 than all other year. Population estimates, growth, and consumption estimates were also low in this year. This year was also characterized by a large hypoxic zone in the meso- to poly-haline areas of the bay as a result of high nutrient runoff (http://www.chesapeakebay.net/ lowdo2003.htm).

Differences in estimates of population size can dramatically change population consumption estimates and the way we understand the role of predators in the ecosystem. The population sizes of croaker were based on data from the CHESMMAP survey. The CHESMMAP survey uses a 45 foot 4-seam balloon otter trawl to derive estimates of abundance. The efficiency of this gear for Atlantic croaker has been estimated to range from 31% over hard surfaces and 84% over soft sediments (Hoffman et al. 2006). However, this variability seems to be equal both within and between surveys, suggesting limited potential for consistent temporal bias in my population-level consumption estimates resulting from gear efficiency. Similar concerns over abundance can be raised for the other species considered here. The efficiency of a bottom trawl to capture the more pelagic weakfish and striped bass might be lower than that of the more demersal Atlantic croaker. However, less information on patterns of variability of catchability for these species is available. Supporting the reliability of these estimates is that the relative abundance of croaker in the ChesMMAP data, expressed as minimum trawlable numbers, also reflect patterns in the coastwide estimates of croaker. Additionally, the relative ranking of survey catches of croaker, weakfish and striped bass in the ChesMMAP survey is corroborated by stock assessments of these species (Kahn et al. 2006, Striped Bass Technical Committee for the Atlantic Striped Bass Management Board 2005). Gear efficiency would have to be drastically different to compensate for the order of magnitude higher abundance of croaker in comparison to population sizes of weakfish and striped bass.

Even allowing for these uncertainties, it is likely that croaker likely exerts its strongest influence on the distribution and structure of population of benthic infauna.

The predominance of polychaetes and other infauna in croaker diets at both the individual and population level, translates to consumption of as much as 4,862-6,353 metric tons (MT) of polychaetes by croaker at the population level while they are resident in Chesapeake Bay from May to October. Estimates of polychaete standing stock biomass in the lower bay alone are 29,718 MT (Hagy 2002) meaning that croaker consume 15-22% of the standing stock of polychaetes from May to October. The standing stock biomass of bivalves is about 7,787 MT (Hagy 2002), which corresponds to croaker consumption of 3.6-16% of the standing stock biomass. These calculations suggest that baywide benthic resources are likely not limiting to croaker. However, on a smaller spatial scale croaker consumption could easily cause local depletion of prey resources. For example, the abundance of one species of terebellid polychaete, a family of worms found in croaker diets, was approximately 60 $g \cdot m^{-2}$ (Seitz and Schaffner 1995). The consumption of just one age 3+ croaker while resident in the Bay ranged from 600-1200g of polychaetes while resident in Chesapeake Bay. Therefore, it is easy to infer that croaker could easily cause local depletion of benthic prey resources.

Although anchovy was a small portion of croaker diets, calculations indicate that the croaker in Chesapeake Bay can consume 1,400 to 3,600 MT of anchovy in the Chesapeake Bay during their period of residence. Based on estimates of anchovy abundance in April to October (Jung and Houde (2004), I calculate that croaker consumption of anchovy is a small, but substantial proportion of mean anchovy biomass, up to 2-8% of the mean production of anchovy production. It seems unlikely that predation of croaker alone would limit anchovy production or recruitment. However, their piscivory in combination with weakfish and striped bass ranged from

about 3,300 to 17,900 MT, about 7-38% of the mean anchovy production during the spring and summer months.  Important to the comparison of predator consumption on their prey is that all estimates of consumption are conservative because estimates of population size were not scaled up to the entire area of the bay (only to the area of the survey) and because seasonal growth in Chesapeake Bay is likely higher than the estimates obtained by interpolating between weight at age.  Therefore, the levels of consumption reported here should be considered the lower bound of piscivory.  Jung and Houde (2004) estimated high anchovy production and that production contributed as much as 136,000 to 498,000 MT of biomass to predation from April to October.  The biomass and production of bay anchovy in Chesapeake Bay is high enough that prey limitation would seem unlikely for these three species.  However, this estimate of piscivory does not include piscivory of the many other fish that consume anchovies including bluefish and others such as white perch that eat anchovies (Nye, unpublished data).

Hartman (1995b) reported that a hypothetical population of bluefish consumes about 9,000 metric tons of anchovy while resident in Chesapeake Bay.  The consumption of anchovy by bluefish was double that of weakfish and striped bass populations of similar sizes.  Thus, I have suggested that the piscivory of croaker, weakfish, and striped bass could locally deplete anchovy abundance and their predation could affect recruitment of bay anchovy.  If bluefish consumption was added to these estimates of total piscivory, total consumption of anchovy would be much closer or exceed the contribution of biomass to predators estimated by Jung and Houde (2004).  Bluefish annual consumption was not estimated in this application because population

estimates are uncertain both coastwide and especially within Chesapeake Bay.  In addition, bluefish are much more migratory than the fish modeled herein.  Therefore, the number of bluefish that use the estuary and the duration of time spent in Chesapeake Bay would make population consumption estimates of this species highly questionable.  Bluefish catches in both the CHESFIMS and ChesMMAP surveys were rare and minimum trawlable numbers were an order of magnitude less than striped bass (Bonzek et al. 2007).

Although weakfish consumed more anchovy and fish than croaker in all years, weakfish consumption overall might be lower than I have estimated.  I used estimates of weakfish weight at age specific to Chesapeake Bay at a period when large weakfish were common coastwide (Lowerre-Barbieri et al. 1995).  Since the Lowerre-Barbieri (1995) study, recent stock assessments suggest that the age structure of the weakfish population is truncated and that weight at age has decreased (Kahn et al. 2006).  Furthermore, very few weakfish Age-4 and older were caught in CHESFIMS or ChesMMAP sampling (Bonzek et al. 2006), yet I modeled consumption of Age-5 and 6+ weakfish, assuming historic sizes.  Additionally, estimates of weakfish consumption on anchovy may be inflated because diet data used was for fish younger than Age 4, which were typically caught in CHESFIMS sampling.  Older weakfish consume more menhaden once they reach larger size (Hartman and Brandt 1995c).  Therefore, croaker may consume as much anchovy as weakfish.

Regardless of whether or not consumption by piscivores exceeds anchovy production, a reduction in the amount of anchovy by piscivory may effectively cause competition among fishes and reduce consumption and growth of predators.  This

possibility is interesting in the context of possible reductions in weight at age of weakfish and the poor condition observed in many striped bass. The predatory demand of striped bass, weakfish, and bluefish has been shown to be much higher than prey supply (Hartman and Brandt 1995b). This study suggests that prey resources may not be high enough to support growth of these piscivores at historical high population levels simultaneously. Similarly, it has been suggested that the population levels of menhaden and other alosids is not high enough to support historical levels of abundance of weakfish and striped bass (Hartman 2003, Uphoff Jr. 2003). In addition to the reduced capacity of menhaden production to provide forage for large piscivores, croaker play an interesting role by consuming bay anchovy and other alternative prey resources of weakfish and striped bass. Although croaker is not in direct competition with large piscivores for menhaden, they may limit anchovy production, which was once seen as a "limitless" alternate prey resource for weakfish and striped bass.

Competition for menhaden has been proposed as a mechanism for both poor condition in striped bass, reduced weight at age in weakfish, and the failure of the weakfish stock to recover (Uphoff 2006, Uphoff Jr. 2003). This work illustrates the high abundance of croaker may create a competitive interaction with weakfish. If this is true, the combined effect of croaker and striped bass consumption on multiple prey resources may explain low growth observed in weakfish and the failure of this fish stock to increase in abundance and biomass in recent years despite management restrictions.

This work illustrates the strengths of bioenergetic models in understanding ecosystem dynamics even though they are traditionally used to understand the growth

and consumption of a particular species.  Bioenergetic models have been used

increasingly in understanding ecosystem processes (Labar 1993, Megrey et al. 2007a,

Rand and Stewart 1998a) and even to evaluate management scenarios (Hartman 2003,

Yodzis 1994).  Through the use of bioenergetic models, I have shown that croaker has

important links to both the benthic and pelagic components of the Chesapeake Bay

foodweb.  Furthermore, management of striped bass and weakfish should include

consideration of unlikely competitors such as the demersal Atlantic croaker.

Considerable effort has been devoted to identifying keystone species (Paine

1966) – those species that have a large effect on the ecosystem even at relatively low

abundances (Libralato et al. 2006, Paine 1995, Power et al. 1996).  However, recent

work has shown that weak interactions, such as those demonstrated by croaker, are

actually more common in nature and are important in stabilizing ecosystems (McCann

2000, McCann et al. 1998).  In addition to having a stabilizing effect on the ecosystem,

"weak interactors" may increase spatiotemporal variability in community structure

(Berlow 1999).  In fact, species labeled as "weak interactors" exhibit much more

variation in interaction strength, making the understanding of their impact on the food

web difficult.  In this study, a small amount of dietary overlap between croaker and

weakfish and striped bass, resulted in a substantial potential for competition among

these species depending on patterns in their relative abundances and those of their prey.

Table 5.1: Prey categories and energy density (Joules/gram) values used in bioenergetic simulations of population consumption.

| Prey category | Description | Energy density | Source |
|---|---|---|---|
| Anchovy | Mostly bay anchovy, *Anchoa mitchilli*, but may include striped anchovy *Anchoa hepsetus* | 4984 | this study |
| Fish | Unidentified fish and fish remains, YOY weakfish *Cynoscion regalis,* YOY croaker Micropogonias undulatus, and some menhaden | 4664 | Hartman 1993 |
| Mysids | Mostly *Neomysis americanus*, but may include *Mysidopsis bigelowi* | 4815 | Cummins and Wuycheck 1971 |
| Polychaetes | Many unidentified species, but include trumpet worms *Pectinaria gouldi*, clam worms, *Neries spp.* and terebellid worms Terebellidae | 3552 | Cummins and Wuycheck 1971 |
| Other benthic | Hydroids, molluscs, gastropods, barnacles, cumaceans, isopods, *Cyathura spp.*, skeleton shrimp, other crustaceans, sea squirts, and ribbon worms | 3138 | Cummins and Wuycheck 1971 |
| Other pelagic | Squids, sea nettle, insects | 4681 | this study (squid) |
| Amphipods | Many species including *Gammarus spp*, *Leptocheirus plumulosus*, *Corophium lacustre*, *Monoculodes edwardsi* | 4127 | Cummins and Wuycheck 1971 |
| Shrimp | Unidentified shrimp remains, Caridean shrimps, *Pugeo spp.*, sand shrimp *Crangon septemspinosa*, and mantis shrimp *Squilla empusa* | 4361 | this study |
| Crabs | Unidentified crab remains and white fingered mud crab *Rhithropanopeus harrisii* | 4815 | Cummins and Wuycheck 1971 |
| Bivalves | Unidentified bivalves, clams and seedling mussels | 3138 | Cummins and Wuycheck 1971 |
| Detritus and macroalgae | Unidentified algae, inorganic matter, and plant matter | 2663 | Lamare and Wing 2001 |

Table 5.2: Seasonal change in diet of Atlantic croaker used to estimate population consumption for each year.  Values are percent composition by weight (%W).

| | Anchovy | Fish | Mysids | Polychaetes | Other benthic | Other pelagic | Amphipods | Shrimp | Crabs | Bivalves | Detritus |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **2002** | | | | | | | | | | | |
| **Spring** | 0.26 | 0 | 3.25 | 74.98 | 2.81 | 0 | 0.70 | 3.70 | 0.13 | 14.19 | 0 |
| **Summer** | 36.29 | 12.26 | 4.29 | 26.77 | 0.34 | 0 | 14.96 | 0 | 0 | 4.80 | 0.26 |
| **Fall** | 16.32 | 1.45 | 3.85 | 58.81 | 2.97 | 2.11 | 0.64 | 2.70 | 4.56 | 6.58 | 0 |
| | | | | | | | | | | | |
| **2003** | | | | | | | | | | | |
| **Spring** | 2.12 | 0 | 3.11 | 92.24 | 0.06 | 0 | 0.37 | 0.07 | 0.01 | 2.03 | 0 |
| **Summer** | 33.41 | 6.39 | 1.47 | 33.63 | 0.61 | 0.01 | 14.76 | 0.19 | 2.08 | 7.45 | 0 |
| **Fall** | 0 | 1.37 | 7.20 | 89.73 | 0.00 | 0 | 0 | 1.66 | 0 | 0.05 | 0 |
| | | | | | | | | | | | |
| **2004** | | | | | | | | | | | |
| **Spring** | 1.06 | 0.40 | 13.27 | 21.49 | 3.27 | 0 | 8.88 | 0.26 | 0.28 | 50.94 | 0.16 |
| **Summer** | 28.57 | 6.81 | 13.74 | 29.09 | 15.60 | 0 | 1.57 | 1.03 | 0 | 0.20 | 3.39 |
| **Fall** | 0.76 | 0.96 | 3.16 | 27.47 | 6.37 | 0 | 0.51 | 58.45 | 1.03 | 1.15 | 0.15 |
| | | | | | | | | | | | |
| **2005** | | | | | | | | | | | |
| **Spring** | 18.14 | 7.17 | 2.23 | 63.16 | 3.44 | 0 | 2.34 | 0.27 | 0.05 | 1.52 | 1.67 |
| **Summer** | 13.35 | 0 | 4.08 | 72.68 | 0.88 | 0 | 3.49 | 0.01 | 3.17 | 1.40 | 0.95 |
| **August** | 24.49 | 7.15 | 1.21 | 34.99 | 13.20 | 0 | 0.16 | 0.22 | 0.07 | 16.71 | 1.81 |
| **Fall** | 22.23 | 4.79 | 4.44 | 51.81 | 1.10 | 0.05 | 0.28 | 2.16 | 11.84 | 0.23 | 1.07 |
| | | | | | | | | | | | |
| **Average** | | | | | | | | | | | |
| **Spring** | 5.40 | 1.89 | 5.46 | 62.97 | 2.40 | 0 | 3.07 | 1.07 | 0.12 | 17.17 | 0.46 |
| **Summer** | 27.90 | 6.37 | 5.90 | 40.54 | 4.35 | 0 | 8.69 | 0.31 | 1.31 | 3.46 | 1.15 |
| **August** | 0.24 | 0.07 | 0.01 | 0.35 | 0.13 | 0 | 0 | 0 | 0 | 0.17 | 0.02 |
| **Fall** | 9.83 | 2.14 | 4.66 | 56.96 | 2.61 | 0.54 | 0.36 | 16.24 | 4.36 | 2.00 | 0.30 |

Table 5.3: Seasonal change in diet of weakfish used to estimate population consumption in each year. Values are percent composition by weight (%W).

| | Anchovy | Fish | Mysids | Polychaetes | Other Benthic | Other pelagic | Amphipods | Shrimp | Crabs |
|---|---|---|---|---|---|---|---|---|---|
| **2002** | | | | | | | | | |
| **Spring** | 30.61 | 0 | 17.80 | 2.58 | 2.10 | 0 | 0 | 46.91 | 0 |
| **Summer** | 50.15 | 33.58 | 13.06 | 0 | 0 | 0 | 0 | 3.21 | 0 |
| **Fall** | 61.92 | 18.87 | 13.14 | 1.74 | 0.060 | 0.82 | 0.18 | 2.64 | 0.63 |
| | | | | | | | | | |
| **2003** | | | | | 2003 | | | | |
| **Spring** | 46.15 | 29.25 | 16.43 | 0 | 2.23 | 0 | 4.67 | 1.27 | 0 |
| **Summer** | 26.59 | 55.43 | 16.15 | 0 | 1.82 | 0 | 0 | 0 | 0 |
| **Fall** | 47.09 | 7.54 | 39.39 | 0.023 | 0.038 | 0 | 5.84 | 0.088 | 0 |
| | | | | | | | | | |
| **2004** | | | | | 2004 | | | | |
| **Spring** | 12.90 | 24.12 | 12.96 | 0.023 | 0.65 | 0 | 1.63 | 47.73 | 0 |
| **Summer** | 0 | 0 | 99.62 | 0 | 0 | 0 | 0.38 | 0 | 0 |
| **Fall** | 88.55 | 0 | 10.19 | 0.35 | 0.00015 | 0 | 0.011 | 0.69 | 0.21 |
| | | | | | | | | | |
| **Average** | | | | | | | | | |
| **Spring** | 85.28 | 0 | 2.65 | 0.17 | 0 | 0 | 1.87 | 2.67 | 0 |
| **Summer** | 85.78 | 0 | 2.55 | 0.16 | 0 | 0 | 2.01 | 2.53 | 0 |
| **Fall** | 81.44 | 0 | 18 | 0.18 | 0 | 0 | 0.33 | 0 | 0.05 |

Table 5.4: Seasonal length at age (+/- standard deviation) of Atlantic croaker identified by modal analysis.

| Day of Year | Spring | Summer | August | Fall |
|---|---|---|---|---|
| | | 2002 | | |
| Cohort 1 | 272.6 (16.5) | 302.0 (17.4) | | 315.5 (17.8) |
| Cohort 2 | 45.2 (6.7) | 161.1 (12.7) | | 200.8 (14.2) |
| | | 2003 | | |
| Cohort 1 | 300.9 (17.3) | 294.4 (17.2) | | |
| Cohort 2 | 225.1 (15.0) | 225.4 (15.0) | | 232.5 (15.2) |
| | | 2004 | | |
| Cohort 1 | 302.2 (17.4) | 322.8 (18.0) | | |
| Cohort 2 | 251 (15.8) | 258 (16.1) | | |
| | | 2005 | | |
| Cohort 1 | 283.1 (16.8) | 294.4 (17.2) | | 353.9 (18.8) |
| Cohort 2 | | 215 (14.7) | 210.0 (14.5) | 240.0 (12.7) |
| Cohort 3 | | 160 (15.5) | | 206.0 (14.4) |
| | | Average | | |
| Ages 1-2 | 98.3 | 107.9 | | 116.7 |
| Ages 3+ | 314.8 | 324.4 | | 333.2 |

Table 5.5:  Growth (g) and linear growth rates (g day$^{-1}$) in Atlantic croaker as estimated from modal analysis.

| Day of Year | Spring (30 May-8 July) | Summer (8 July-8 Sept) | Fall (8 Sept -1 Oct) | Linear growth rate |
|---|---|---|---|---|
| | | 2002 | | |
| Cohort 1 | 79.1 | 72.2 | | 1.15 |
| Cohort 2 | 47.26 | 44.0 | 15.4 | 0.699 |
| | | 2003 | | |
| Cohort 1 | -6.9 | -5.8 | -2.0 | -0.321 |
| Cohort 2 | 8.6 | 7.2 | 2.6 | 0.118 |
| | | 2004 | | |
| Cohort 1 | 82.4 | 73 | 17.9 | 1.057 |
| Cohort 2 | 17.7 | 15.7 | 3.9 | 0.228 |
| | | 2005 | | |
| Cohort 1 | 37.9 | 96.5 | 25 | 2.097 |
| Cohort 2 | 58.8 | 49.4 | 1.7 | 0.701 |
| Cohort 3 | | 11.5 | 25.23 | 1.22 |
| | | Average | | |
| Age1-2 | 35.4 | 32.3 | 11.3 | 0.513 |
| Age 3+ | 37.4 | 34.2 | 11.9 | 0.542 |

Table 5.6: Seasonal weight at age (g) of Atlantic croaker derived by interpolating between weight at age in the summer averaged from 2002-2005. Mean values on each day were used as beginning and end weights to predict annual population level consumption of croaker.

| Day of Year | Age 1 | Age 2 | Age 3 | Age 4 | Age 5 | Age 6+ |
|---|---|---|---|---|---|---|
| 120 | 72.9 | 123.7 | 164.6 | 275.7 | 276.9 | 385.3 |
| 189 | 82.5 | 133.3 | 174.2 | 385.3 | 286.5 | 394.9 |
| 252 | 91.3 | 142.1 | 183.0 | 294.1 | 295.2 | 403.7 |
| 274 | 94.4 | 145.2 | 186.0 | 297.1 | 298.3 | 406.7 |

Table 5.7:  Seasonal weight at age of weakfish derived by interpolating between spring mean weight at age reported for Chesapeake Bay weakfish 1989-1992 (Lowerre-Barbieri et al. 1995b).  There values were used as beginning and end weights to predict annual consumption of weakfish.

| Day of Year | Age 1 | Age 2 | Age 3 | Age 4 | Age 5 | Age 6+ |
|---|---|---|---|---|---|---|
| 120 | 49 | 310 | 778 | 1494 | 2126 | 3268 |
| 189 | 98.3 | 398.5 | 913.5 | 1613.5 | 2341.9 | 3406.4 |
| 252 | 143.4 | 479.3 | 1036.9 | 1722.6 | 2539.0 | 3532.7 |
| 274 | 159.1 | 507.5 | 1080.1 | 1760.7 | 2607.8 | 3576.8 |

Table 5.8:  Seasonal weight at age of striped bass predicted using data from Setzler et al. (1980) and Jones et al. (1977).  These values were used as beginning and end weights to predict annual population level consumption of striped bass.

| Day of Year | Age 1 | Age 2 | Age 3 | Age 4 | Age 5 | Age 6 | Age 7 | Age 8 | Age 9+ |
|---|---|---|---|---|---|---|---|---|---|
| 120 | 138.5 | 524.6 | 1096.7 | 1833.3 | 2656.6 | 3629.7 | 6714.0 | 6714.0 | 9079.1 |
| 189 | 206.3 | 627.8 | 1244.0 | 1992.9 | 2845.4 | 3852.6 | 7274.4 | 7274.2 | 9411.5 |
| 252 | 257.9 | 706.2 | 1356.0 | 2114.3 | 2988.9 | 4022.1 | 7700.2 | 7700.2 | 9663.9 |
| 274 | 277.8 | 736.4 | 1399.2 | 2161.1 | 3044.3 | 4087.5 | 7864.6 | 7864.6 | 9761.4 |

Table 5.9: Total consumption (MT) of each prey category of Atlantic croaker, weakfish, and striped bass combined.

| Prey category | 2002 | 2003 | 2004 | 2005 |
|---|---|---|---|---|
| Amphipods | 835 | 818 | 753 | 144 |
| Anchovy | 6,140 | 3,328 | 17,859 | 6,272 |
| Bivalves | 728 | 271 | 2,512 | 1,134 |
| Crabs | 264 | 120 | 115 | 660 |
| Detritus | 14 | - | 442 | 174 |
| Fish | 3,586 | 2,498 | 1,912 | 5,413 |
| Mysids | 1,293 | 1,767 | 3,903 | 2,814 |
| Other benthic | 208 | 59 | 2,537 | 961 |
| Other pelagic | 110 | 0 | - | 2 |
| Polychaetes | 5,316 | 5,418 | 6,595 | 6,724 |
| Shrimp | 685 | 84 | 4,590 | 450 |
| Total consumption | 19,179 | 14,363 | 41,218 | 24,748 |

Figure 5.1:  Predicted temperatures from 1March-31December for 2002 (solid black), 2003 (dashed black), 2004 (solid grey), and 2004 (dashed grey).  Predicted temperatures at Day 120, 189, 252, and 272 of each year were used to model annual consumption from 1May-1October.
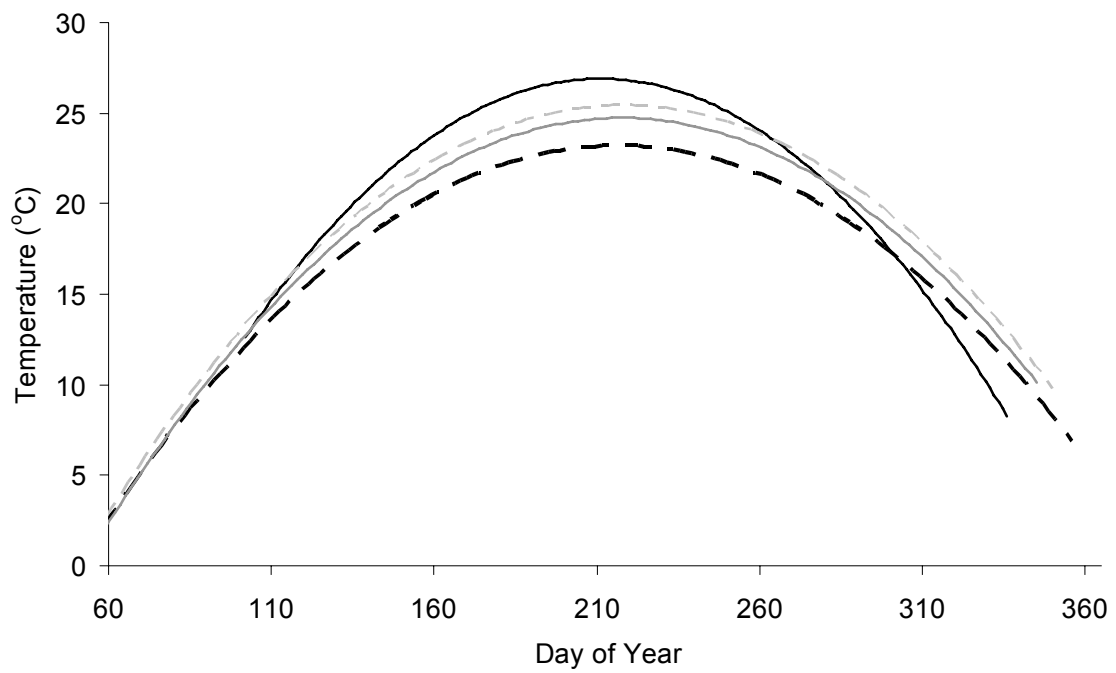
Figure 5.2: Modal analysis of lengths of Atlantic croaker caught on CHESFIMS cruises from 2002-2005 for spring (top panels), summer (middle panels) and fall (bottom panels). Panels are labeled with the year of the CHESFIMS cruise and season such that CF0201 is the 2002 Spring cruise, CF0202 is the 2002 Summer cruise, and CF0203 is the 2002 Fall cruise.
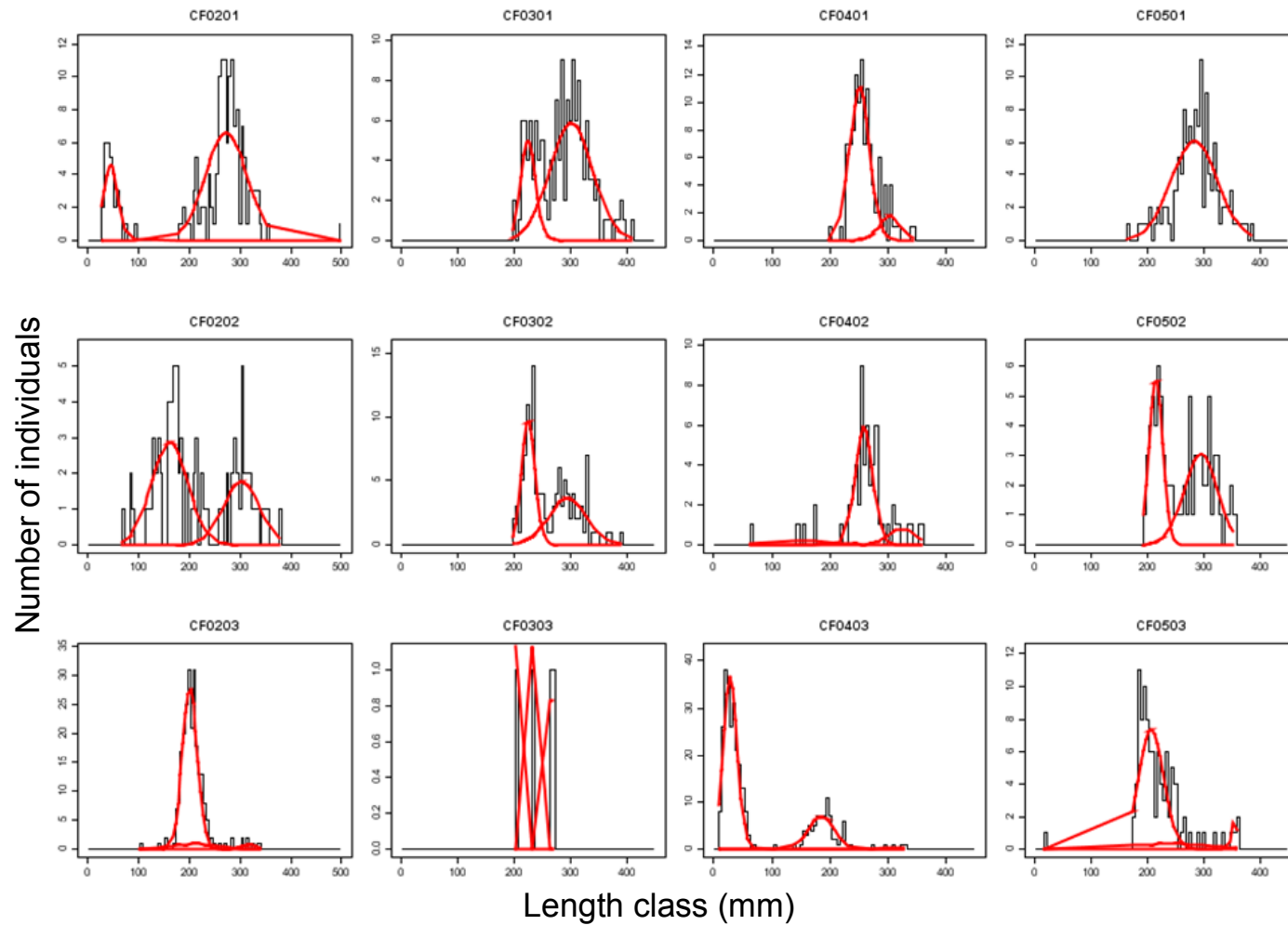
Figure 5.3:  Predicted growth in weight of Atlantic croaker in a) 2002, b) 2003, c) 2004, and d) 2005 derived from modal analysis and length-weight conversion.  Cohort 1 represents the largest cohort identified followed in size by Cohort 2 and Cohort 3.  Points are observed weights and lines are the linear regression to determine growth rates and estimate missing weight values.
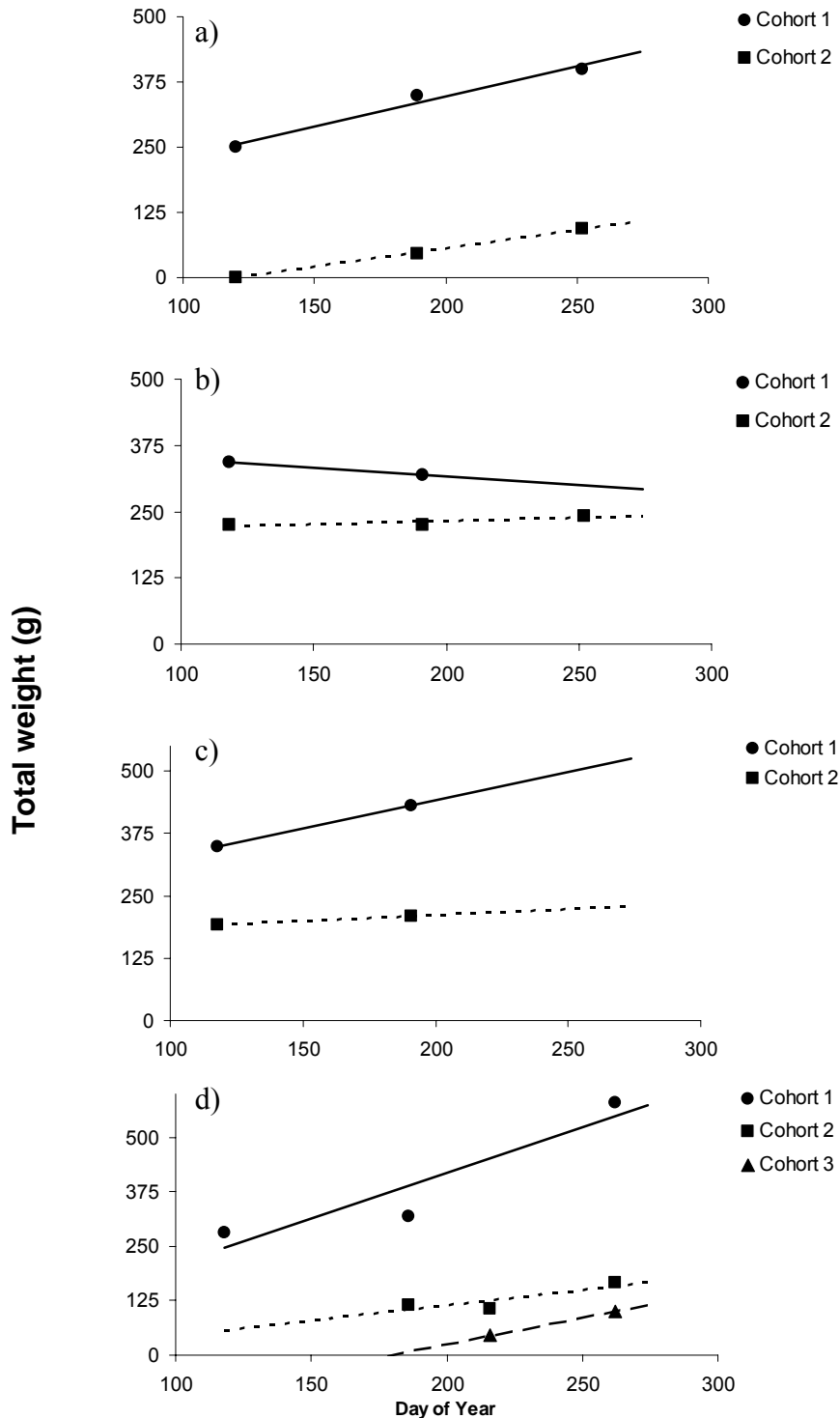
Figure 5.4:  Length-frequency distributions of Atlantic croaker a) pooled over 2001-2003 compared to length frequency distribution of Atlantic croaker b) by age for 2001-2003.
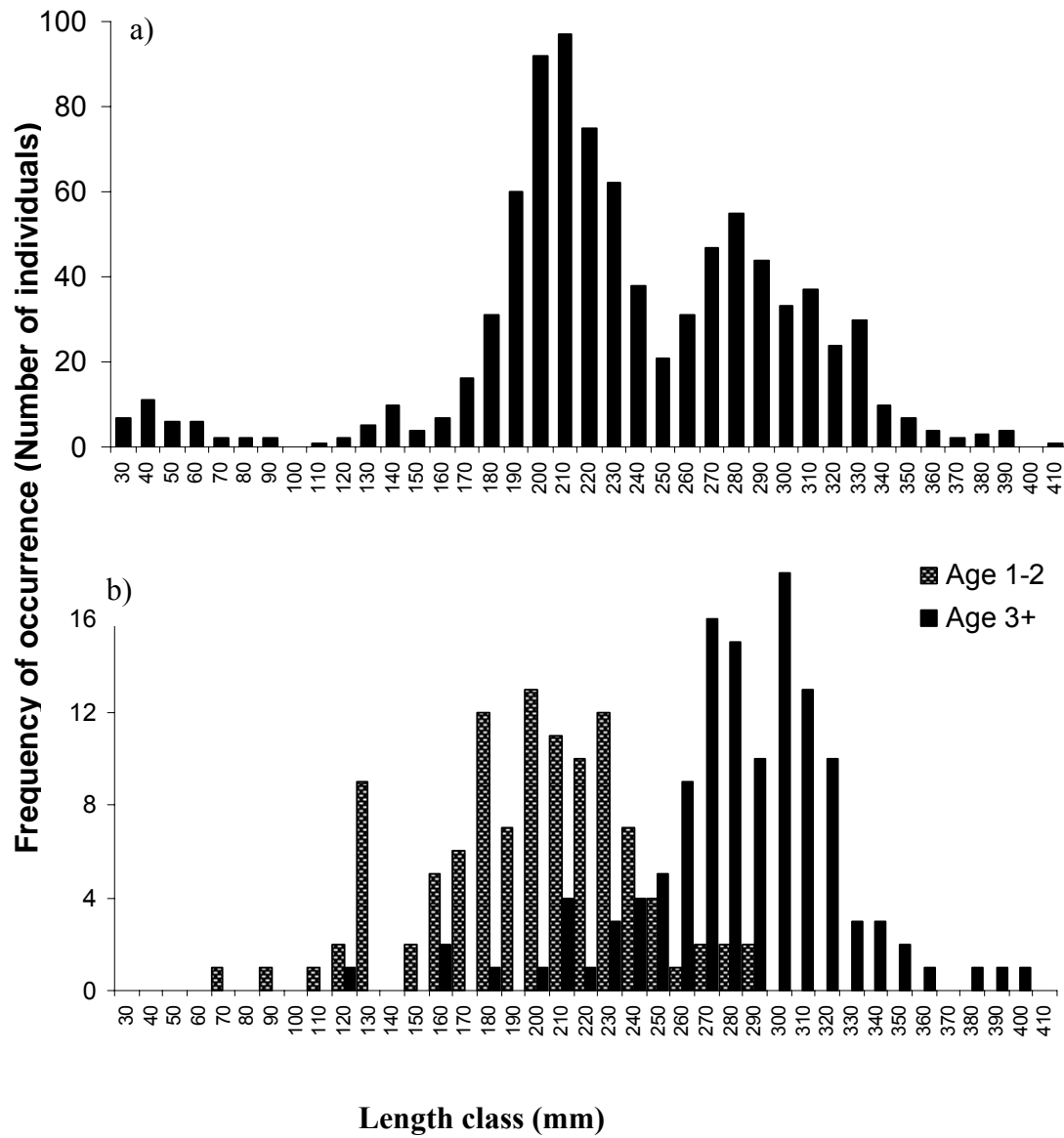
Figure 5.5: Growth of two cohorts identified by age. Points are the observed total weights and linear regressions represent the linear growth rate for each cohort.
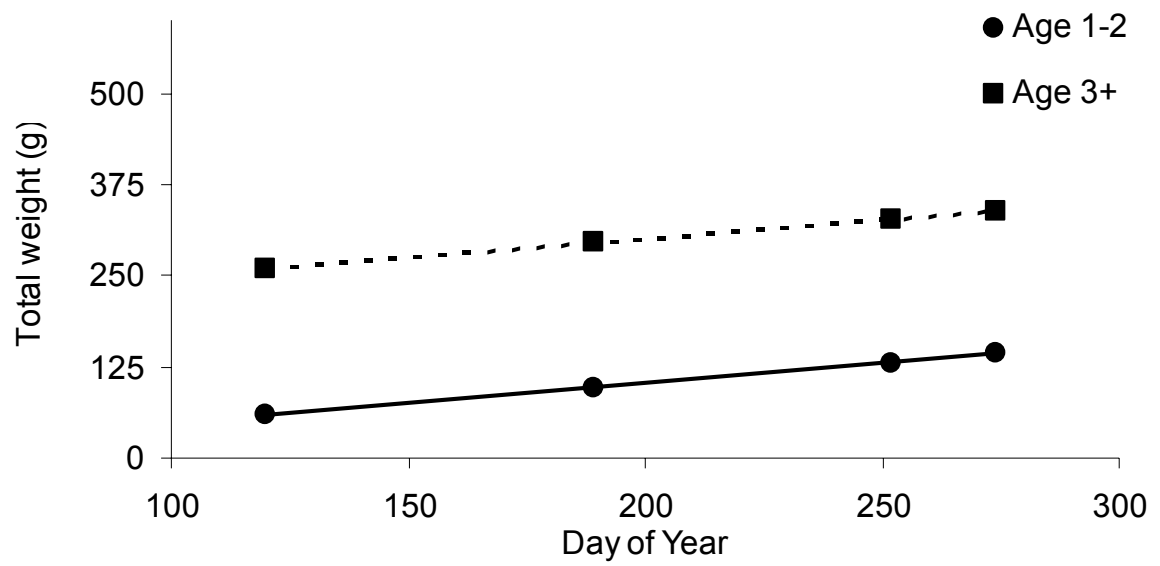
Figure 5.6: Consumption of Atlantic croaker (all cohorts combined, but unadjusted for population size) for each year from 2002-2005. Average growth of the two dominant cohorts are estimated from weight at age data.
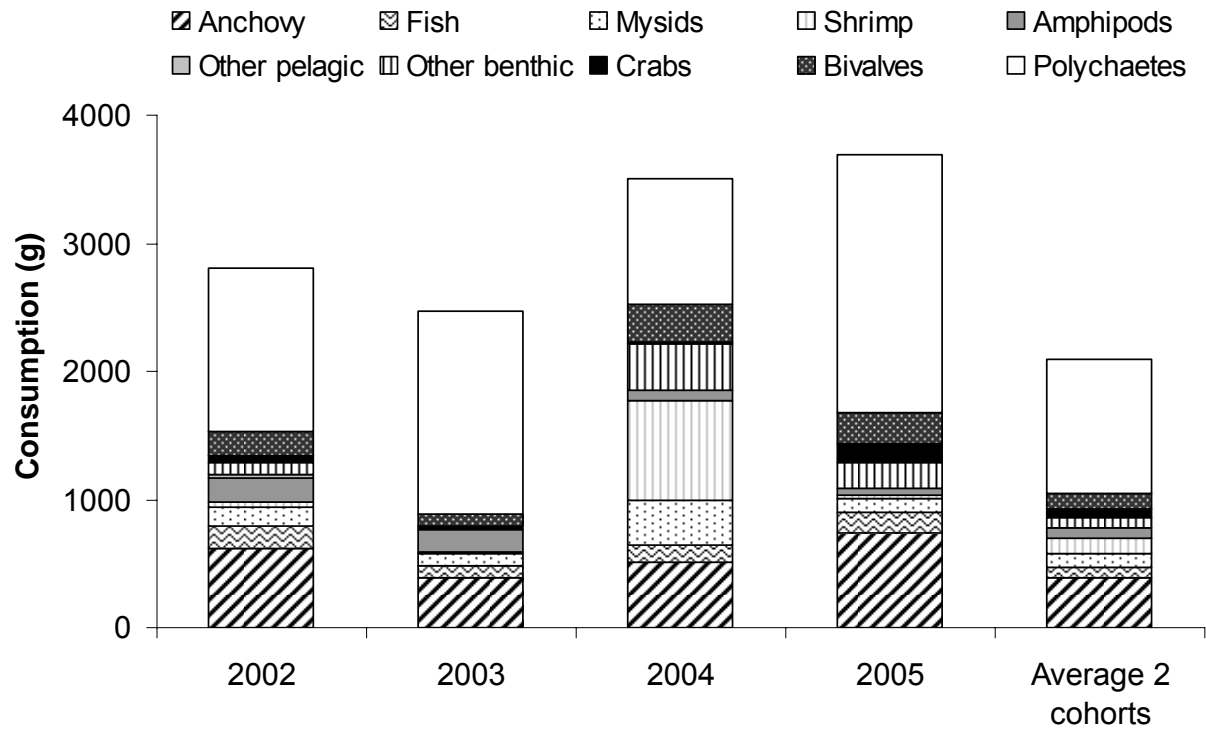
Figure 5.7: Mean consumption by prey category (+/- standard deviation) pooled for estimates from 2002-2005.
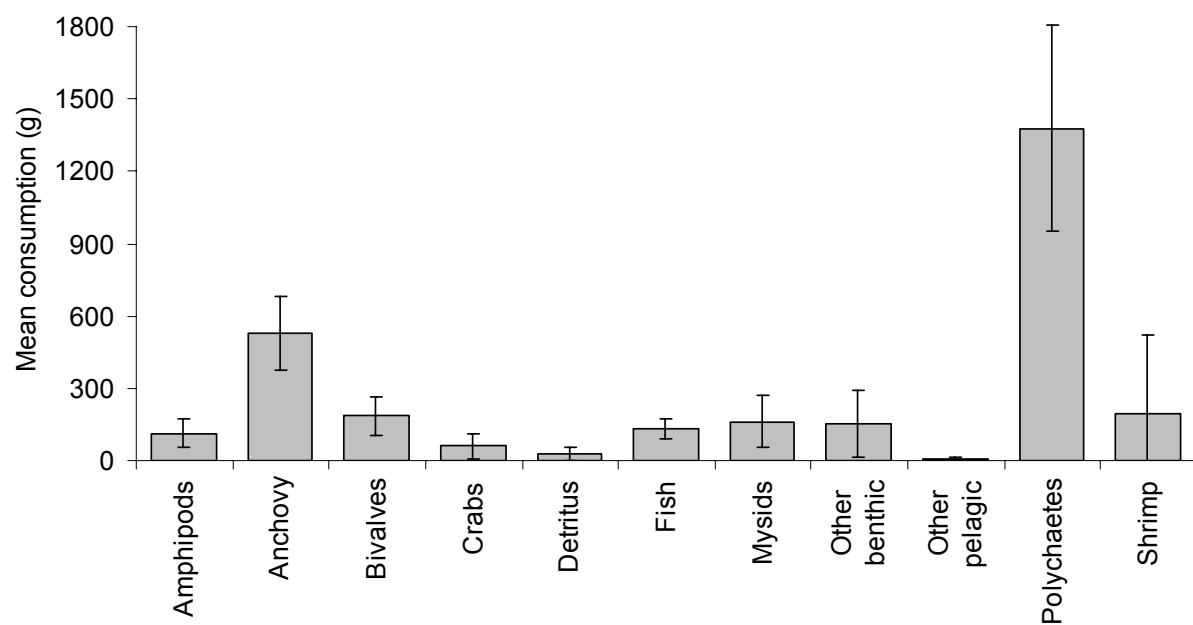
Figure 5.8: Annual consumption estimated by adding the consumption of one fish in each of several age classes by species in 2002, 2003, 2004, and 2005. Labels are the species followed by the last two digits of the year where CR=Croaker, WF=Weakfish, and SB=Striped Bass.
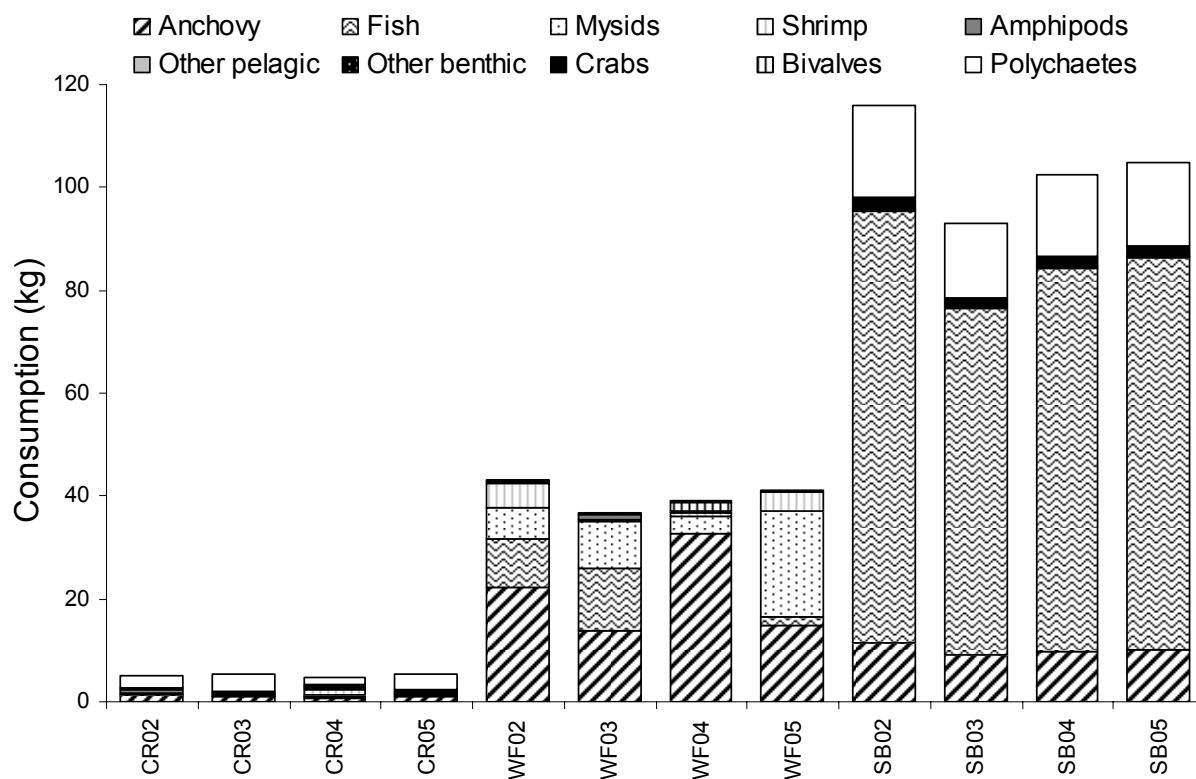
Figure 5.9: Population dynamics of croaker, weakfish, and striped bass in ChesMMAP survey.
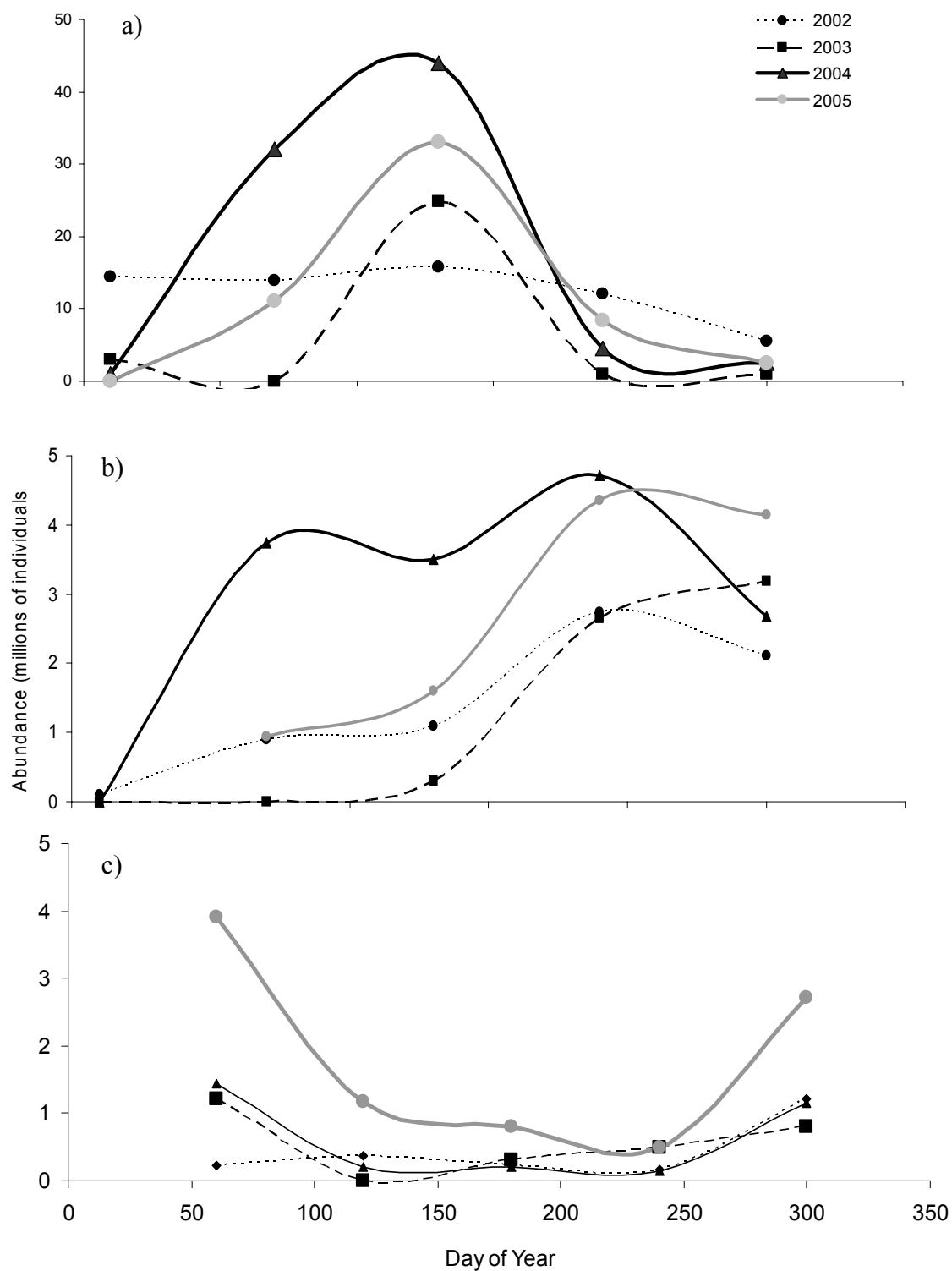
Figure 5.10: Population level consumption of Atlantic croaker, weakfish, and striped bass while resident in Chesapeake Bay for a) 2002, b) 2003, c) 2004 and d) 2005.
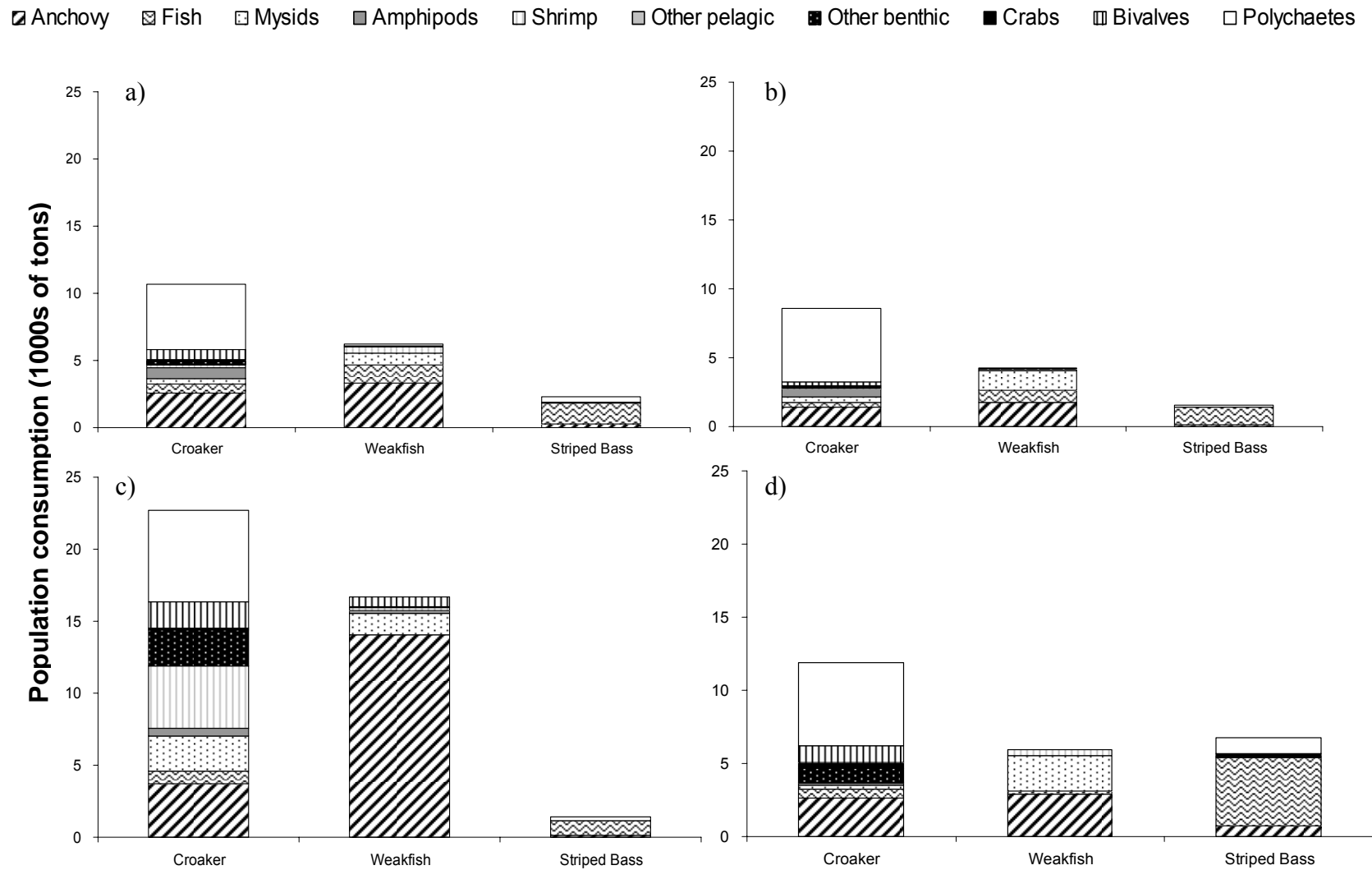
Figure 5.11: Coastwide abundance estimates of Atlantic croaker, striped bass, and weakfish as approximated by stock assessments.
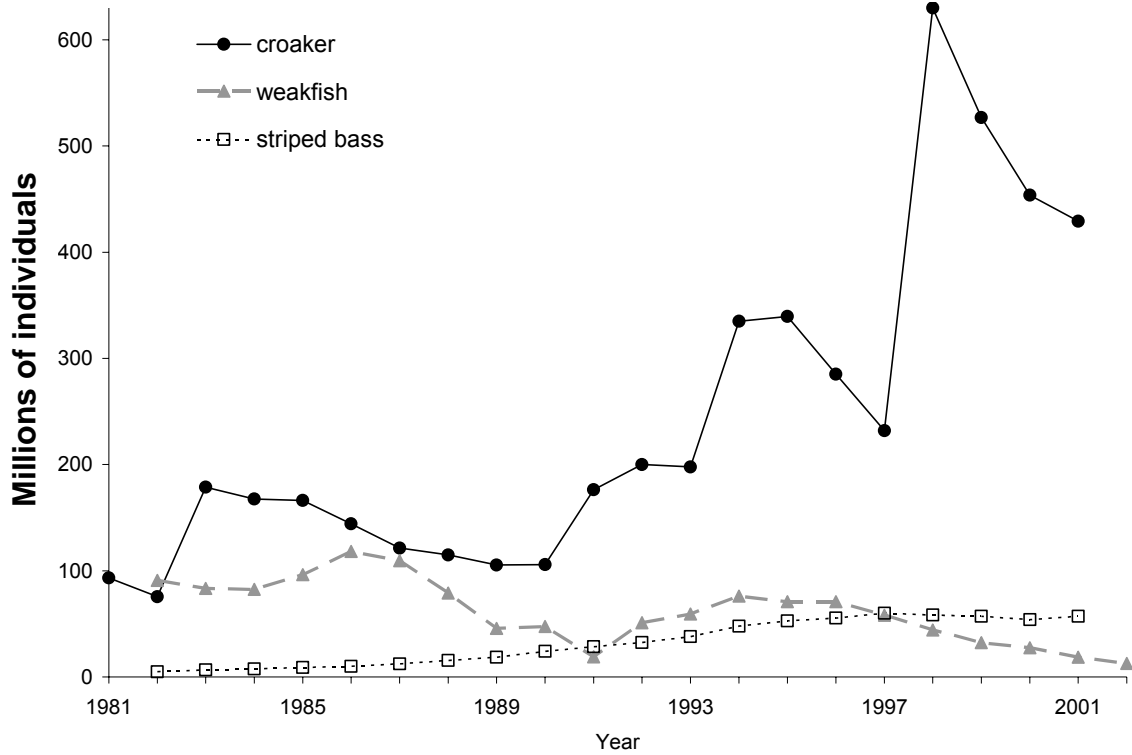
# CHAPTER 6: SUMMARY

The overall objective of this study was to test the hypothesis that seasonal and annual variation in croaker diet has bioenergetic consequences to individual croaker and to the Chesapeake Bay ecosystem.  In Chapter 2, I documented that the diet of croaker varies annually, seasonally, and spatially.  In particular, I found that about 20% of the croaker diet by weight consists of anchovy and some fish.  However, few studies have emphasized croaker feeding on these pelagic resources.  Croaker may feed on these resources because of changes in the Chesapeake Bay ecosystem, particularly eutrophication.  However, croaker consumption of anchovy is more likely a result of crepuscular feeding that has not been captured in previous studies that occurred during the day and with bottom trawls.  Additionally in chapter 2, I used generalized additive models (GAMs) to explore factors that affect croaker presence and abundance in Chesapeake Bay and found that it is important to account for seasonal effects when modeling croaker distribution.  Unique to this application of GAMs was the incorporation of not only abiotic factors, but also prey fields to predict croaker presence and abundance.  I hypothesized that abiotic factors would determine croaker presence and that biotic factors would determine their abundance.  However, I found that temperature, salinity and their interaction were consistently the most important factors determining croaker distribution even when presence and abundance were modeled separately by season.  Biotic variables were important factors in predicting presence, but not abundance.  The next step in this work would be to incorporate Chesapeake Bay benthic monitoring data into a two-stage GAM of

the summer croaker distribution. The benthic monitoring data includes abundance

and biomasses by species for the Maryland and Virginia portions of the Bay, but only

temporally overlaps with TIES and CHESFIMS summer cruises. Furthermore,

benthic monitoring occurs only at depths <12m while 40% of TIES and CHESFIMS

stations occur at depths >12m. In addition to these temporal and spatial

discrepancies, benthic monitoring data was not included in this analysis because it

required a substantial amount of data reorganizing and grain size was interpreted as

indicative of benthic resources. However, inclusion of more specific information on

benthic food resources might influence GAMs and change my conclusions.

In Chapter 3, I explored the consequences of a variable diet on the condition

of individual croaker. Several morphometric measures of condition predicted

condition well. I successfully used RNA:DNA ratios measured in the laboratory to

predict daily specific growth rate in large Atlantic croaker. RNA:DNA ratios have

typically been used to predict growth in larval and small juvenile fish, but based on

this work there is the potential for this technique to be used in larger fish. I

hypothesized that RNA:DNA ratios would be correlated with stomach contents

because these techniques measure growth and condition respectively on similar time

scales. RNA:DNA ratios were not correlated with the proportion of either anchovy or

polychaetes in croaker diets. However, energy density and K were both significantly

positively correlated with anchovy, but not with polychaetes in the diets of croaker.

Missing from this chapter is the stable isotope work that I initially proposed.

Preliminary analysis of laboratory experiments indicated that within 14 days, croaker

fed mysids could be distinguished from croaker fed polychaetes using carbon and

nitrogen stable isotope signatures.  However, the data to look at stable isotope values in field-caught fish was not available at the time of writing this dissertation.  Overall, no strong relationships were identified between measures of condition and diet, but more exact measures of diet such as stable isotopes and chemical biomarkers would likely elucidate this relationship.

In Chapter 4, I developed a laboratory based bioenergetic model of Atlantic croaker by defining the temperature and size dependent functions of respiration and metabolism.  I validated this bioenergetic model with independent growth experiments.  The bioenergetic model predicted growth from observed consumption values extremely well, but did not predict consumption from observed growth as well.  However, growth rates were very low in all validation experiments, preventing a full validation of the croaker bioenergetic model.  The model performed well, especially at temperatures above 12$^{\circ}$C, allowing this bioenergetic model to be used to estimate population consumption in croaker.  Given unlimited time and resources, a useful addition to this chapter would be additional laboratory validations and field validation of the bioenergetic model using growth and consumption estimates of fish in the field on a relatively small temporal and spatial scale.  Because the model is used to estimate consumption in the field, such a field-based validation of the model would lend support to the application of the model in Chapter 5.

In Chapter 5, I estimated the growth of Atlantic croaker and used the bioenergetic model to predict its consumption annually.  There were differences in annual consumption due to differences in growth rate, temperature, and diet composition.  When individual consumption of Atlantic croaker was compared to that

of weakfish and striped bass, striped bass, followed by weakfish, consumed more food and more fish than croaker. However, when consumption was scaled up to the population level, croaker consumed more anchovies than striped bass in all years and in some years consumed more anchovy and fish than striped bass. Weakfish consumed more anchovy than croaker and striped bass in every year. However, croaker consumption of anchovy was only slightly lower than weakfish in most years. These three fish species, in addition to other piscivores in Chesapeake Bay that were unaccounted for, exert considerable pressure on anchovy production. An interesting addition to this work would be to incorporate population consumption of bluefish into this multispecies comparison if reliable estimates of bluefish population size in Chesapeake Bay could be found. Estimates of consumption hinge on the growth rates of croaker, weakfish, and striped bass which were assumed to be constant in the multispecies comparison. Ideally, it would be better to use year-specific growth rates of each of these species and to explore the idea of growth-limitation induced by competition between these species.

In conclusion, this body of work illustrated the importance of small changes in the diet of an abundant demersal fish species at the population and ecosystem levels. This work has implications to ecosystem-based management in Chesapeake Bay, but also has broader implications on the role of weak interactions in an ecosystem. Although the anchovy is a small proportion of croaker diet, anchovy may be an important component of the diet of larger fish in improving their condition and reproductive output. More importantly, because of the current high abundance of croaker even a very small degree of dietary overlap with other species may cause

competitive interactions with unlikely species.  These results emphasize some of the strengths of ecosystem-based fisheries management approaches in that 1) trophic links must be better understood and quantified among all species, not just those that are most economically important and that 2) incorporation of these interactions into management decisions and possibly even assessment models may help avoid unexpected ecosystem change.

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224

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