Mechanistic links between climate and fisheries along the east coast of the United States: explaining population outbursts of Atlantic croaker (*Micropogonias undulatus*)

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ABSTRACT

Climate has been linked to variation in marine fish abundance and distribution, but often the mechanistic processes are unknown. Atlantic croaker (*Micropogonias undulatus*) is a common species in estuarine and coastal areas of the mid-Atlantic and southeast coasts of the U.S. Previous studies have identified a correlation between Atlantic croaker abundance and winter temperatures in Chesapeake Bay, and have determined thermal tolerances of juveniles. Here we re-examine the hypothesis that winter temperature variability controls Atlantic croaker population dynamics. Abundance indices were analyzed at four life history stages from three regions along the east coast of the U.S. Correlations suggest that year-class strength is decoupled from larval supply and is determined by temperature-linked, overwinter survival of juveniles. Using a relation between air and water temperatures, estuarine water temperature was estimated from 1930 to 2002. Periods of high adult catch corresponded with warm winter water temperatures. Prior studies indicate that winter temperature along the east coast is related to the North Atlantic Oscillation (NAO); variability in catch is also correlated with the NAO, thereby demonstrating a link between Atlantic croaker dynamics, thermal limited overwinter survival, and the larger climate system of the North Atlantic. We hypothesize that the environment drives the large-scale variability in Atlantic croaker abundance and distribution, but fishing and habitat loss decrease the resiliency of the population to periods of poor environmental conditions and subsequent weak year classes.

INTRODUCTION

Decadal-scale variability in fish populations has been documented in many of the world's oceans. The best examples come from the North Pacific and Bering Sea where regime shifts have resulted in ecosystem-wide changes in community structure, including fish population abundance and distribution (e.g. Anderson and Piatt, 1999; Hare and Mantua, 2000; Conners *et al.*, 2002; Duffy-Anderson *et al.*, 2005). In the North Atlantic, decadal-scale fluctuations in atmospheric pressure gradients and water temperatures are linked with an outburst of gadoids (Cushing, 1996; Sirabella *et al.*, 2001), assemblage-wide changes in estuarine fish ecology (Attrill and Power, 2002), and changes in the distributions of fish species in the North Sea (Perry *et al.*, 2005). Along the west coast of the Americas, shorter-scale climatic variability associated with El Niño is related to variability in fish population dynamics (Cowen, 1985; Lenarz *et al.*, 1995; Arcos *et al.*, 2001; Rebstock, 2003; Smith and Moser, 2003). These examples indicate that large-scale variability in fisheries can be driven by climatic processes.

Although a general coupling between climate and fisheries is indicated in many marine systems (see review by Roessig *et al.*, 2004), few studies have considered the link between ecosystem structure, fisheries production, and climatic forcing along the mid-Atlantic and southeast coast of the U.S. (Massachusetts to Florida). Murawski (1993) and Mountain (2002) documented links between interannual

variability in fish distributions and water temperature. Parker and Dixon (1998) found an increase in tropical fish abundance and diversity on reefs of the southeast U.S. shelf associated with warmer winter water temperatures. Oviatt (2004) indicated a decrease in boreal fish species in Narragansett Bay on the northeast U.S. shelf occurring over a time scale similar to the changes documented by Parker and Dixon (1998). In addition to changes in distribution, Sullivan *et al.* (2005) demonstrated a link between recruitment, shelf bottom temperature, and the North Atlantic Oscillation (NAO) for yellowtail flounder (*Limanda ferruginea*) in the mid-Atlantic region of the northeast U.S. shelf. Finally, in a study of Chesapeake Bay climate and fisheries, Austin (2002) argued that a regime shift occurred in 1977, and that this shift coincided with a change in the juvenile fish community. These studies indicate that climatic variation in temperature may have overarching effects on the fisheries of the east coast of the U.S.

Atlantic croaker (*Micropogonias undulatus*) is a common estuarine and coastal finfish along the east coast of the U.S. and in the northern Gulf of Mexico. Two large marine ecosystems are defined along the east coast of the U.S. with the boundary at Cape Hatteras, North Carolina (Fig. 1; Briggs, 1974; Boicourt *et al.*, 1998; Loder *et al.*, 1998; Grothues and Cowen, 1999); and aspects of Atlantic croaker life history differ between these two ecosystems (Fig. 2). On the northeast U.S. shelf, spawning occurs in late summer and early fall (Berrien and Sibunka, 1999), and larvae ingress into estuarine habitats in the fall (Norcross, 1991; Witting *et al.*, 1999). On the southeast U.S. shelf, spawning and larval ingress occur in the fall, winter, and spring (Warlen, 1982). Once in estuarine habitats, juveniles (age-0) move little until their fall migration out of estuaries and to the south (Miller and Able, 2002; Miller *et al.*, 2003; Able and Brown, 2005). Currently, the maximum lifespan is 8 yr (Ross, 1988; Barbieri *et al.*, 1994b), but historically it reached 12–15 yr (Hales and Reitz, 1992).

Atlantic croaker harvests have varied 50-fold from the 1890s through the 1970s, with periods of high catch interspersed with periods of low catch (Joseph, 1972; Norcross and Austin, 1981). Joseph (1972) hypothesized four potential causes for the observed declines in Atlantic croaker catch after 1945: (i) overfishing, (ii) habitat alteration by humans, (iii) multi-species interactions, and (iv) environmental forcing not directly related to human activities. Norcross and Austin (1981) focused on Atlantic croaker dynamics in Chesapeake Bay and linked an increase in

Figure 1. Map showing a portion of east coast of U.S. Location of larval ingress sampling platforms and other geographic places named in text are shown. The northeast U.S. continental shelf extends from Cape Hatteras to Scotian Shelf (not shown) and the southeast U.S. continental shelf extends from Cape Hatteras to Cape Canaveral. The mid-Atlantic Bight is the southern-most subregion of the northeast U.S. continental shelf and extends from Cape Hatteras to approximately the northern border of New Jersey.
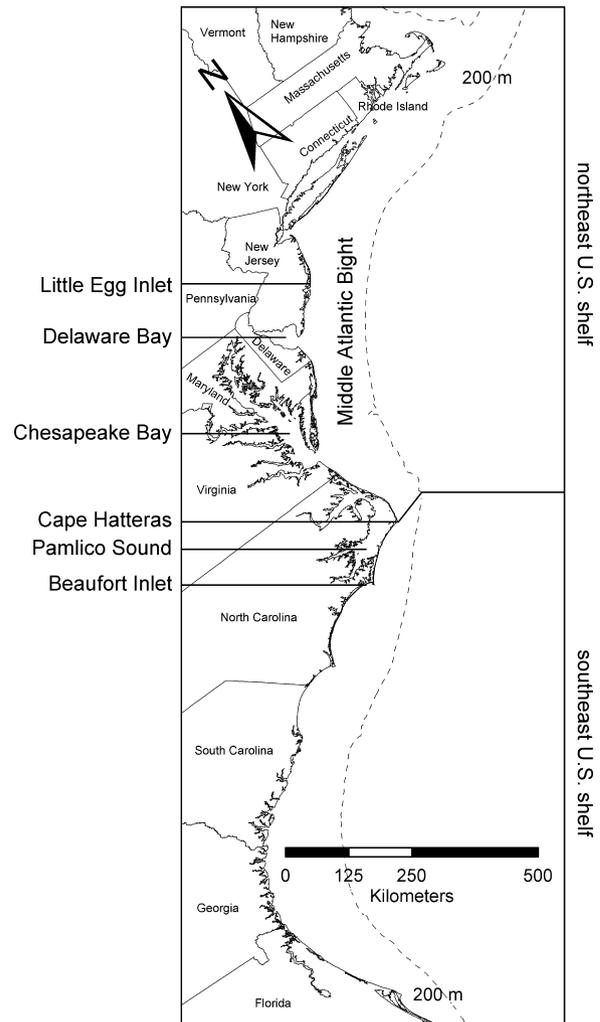
catch in the mid-1970s to warmer winter temperatures and a decrease in catch in the late 1970s to colder winter temperatures, thereby supporting Joseph's (1972) fourth hypothesis. Lankford and Targett (2001a) examined thermal tolerances of juveniles as the mechanism of lower survival during cold winters; in the laboratory, they found increases in mortality at 5°C, 100% mortality after 23 days at 3°C, and after 8 days at 1°C.

Figure 2. Summary of the timing of life history events of Atlantic croaker on the northeast and southeast U.S. continental shelf and adjacent estuaries. The first year and a half of life is shown in seasonal divisions (Su, summer; F, fall; W, winter; Sp, spring). Annuli formation in both otoliths and scales occurs in April and May (Ross, 1988; Barbieri *et al.*, 1994b); thus, the division between age-0 and age-1 is during the spring of the first year. Ingress occurs at sizes of 7–13 mm and ages of 20–70 days; size-at-ingress is nearly constant during the ingress season, whereas age-at-ingress increases through the season (Warlen, 1982). During the fall of the first year, juveniles are 150–250 mm and 10–12 months old in estuaries north of Cape Hatteras, and 80–210 mm and 6–10 months old in estuaries south of Cape Hatteras (Ross, 1988; Miller *et al.*, 2003). Atlantic croaker mature at age 1 and are serial spawners; batch size and spawning frequency are unknown (Barbieri *et al.*, 1994a).

Ecosystem	Life History Event	Age 0				Age 1	
		Su	F	W	Sp	Su	F
Northeast U.S. Continental Shelf	Spawned	—					
	Ingress	—					
	Estuarine residency		————————————————				
	Estuarine egress						—
Southeast U.S. Continental Shelf	Spawned	————————					
	Ingress	————————					
	Estuarine residency	————————————————————					
	Estuarine egress						—

The purpose of this study was to re-examine the relation between winter temperature and Atlantic croaker population dynamics, and to evaluate links to the larger North Atlantic climate system. Unlike previous studies, we examined Atlantic croaker abundance across late larval, juvenile, and adult stages. We also include data from a large portion of the east coast range: North Carolina, Virginia and New Jersey, an area of one unit stock based on genetics, fishery data, life history traits, and physiological traits (Barbieri *et al.*, 1994b; Lankford *et al.*, 1999; Lankford and Targett, 2001b). Our first specific objective was to evaluate whether patterns in larval and juvenile abundance are associated with patterns in subsequent adult abundance. Our second objective was to examine the relationship between winter temperatures and abundance during juvenile and adult stages. Our third objective was to evaluate the relationship between adult catch and long-term trends in winter temperature. Our fourth objective was to examine the dynamics of Atlantic croaker relative to the larger North Atlantic climate system, as indexed by the winter NAO (Hurrell, 1995). The ability to analyze abundance indices of a variety of life history stages was made possible by long-term monitoring programs conducted by various government agencies and academic researchers, and brought together here for the first time. The conceptual model that emerges has far-reaching implications for the population dynamics of many fishes along the east coast of the U.S.

MATERIALS AND METHODS

Atlantic croaker abundance data

Data were compiled to represent estimates of Atlantic croaker abundance at four life stages (Table 1). Late-larval abundance was derived from two ingress sampling programs: one near Beaufort Inlet, North Carolina and one near Little Egg Inlet, New Jersey (Fig. 1). Both programs sampled nighttime, flood tides weekly from bridges over channels (Table 1). Yearly Atlantic croaker abundance was calculated as a sum of larval concentrations from August to January at Little Egg Inlet, New Jersey and from November to May at Beaufort Inlet, North Carolina. Although weekly sampling may miss shorter-scale ingress events (e.g. sciaenid ingress events in the Gulf of Mexico, Brown *et al.*, 2004), Hettler *et al.* (1997) sampled daily ingress at Beaufort Inlet and showed that weekly sampling accurately reflects annual ingress magnitude of Atlantic croaker.

Fall and spring juvenile abundance indices from Pamlico Sound, Chesapeake Bay, and coastal New Jersey were included in the analyses (Table 1; Fig. 1). The North Carolina Division of Marine Fisheries conducts the Pamlico Sound Survey (Program 195; West and Wilson, 1994) in June and September. Data collected in June were used here as a spring juvenile abundance index, and an average Atlantic croaker CPUE was calculated for each year. The Virginia Institute of Marine Science (VIMS) conducts a monthly trawl survey of the lower Chesapeake Bay and major rivers. Two Atlantic croaker indices have been

Table 1. Summary of Atlantic croaker abundance data from the east coast of the U.S. used in this study. Data attributes and sources are also provided.

Location	Stage	Size	Gear	Time period	Frequency	Years	Source
North Carolina — Beaufort Inlet	Larvae	7–13 mm	2 m² surface net with 1 mm mesh	November to April	Weekly	1985–2000	1
Pamlico Sound	Spring juveniles	No specific size limit	9.1 m mongoose trawl with 2.2 cm mesh and 1.9 cm mesh liner	June	Once per year	1987–2002	2
Virginia — Chesapeake Bay	Fall juveniles	<80 mm October, <100 mm in November, <100 mm in December	9.1 m otter trawl with 3.8 cm stretch mesh and 0.64 cm mesh liner	October to December	Monthly	1979–2002	3
Chesapeake Bay	Spring juveniles	<135 mm in May, <160 mm in June, <180 mm in July, <220 mm in August	9.1 m otter trawl with 3.8 cm stretch mesh and 0.64 cm mesh liner	May to August	Monthly	1979–2002	4
New Jersey — Little Egg Inlet	Larvae	7–13 mm	1 m diameter plankton net with 1 mm mesh	Year-round	Weekly	1988–2002	5
Coastal New Jersey	Fall juveniles	<100 mm	25 m three-in-one trawl with 7.6 cm stretch mesh and 0.6 cm mesh liner	October	Once per year	1988–2002	6
Coastal New Jersey	Spring juveniles	<160 mm	25 m three-in-one trawl with 7.6 cm stretch mesh and 0.6 cm mesh liner	June	Once per year	1988–2002	6
All states — East coast of US	Age-2	NA	Various indices	Estimated for January 1 of given year	NA	1977–2000	7
All states — East coast of Florida to Rhode Island by state	Adults	No size restrictions	Various commercial	Year-round	Year-round	1930–2002	8

Source: 1, see Warlen (1994) for description of monitoring program; 2, see West and Wilson (1994) for description of monitoring program; 3, data from Virginia Institute of Marine Science, Juvenile Fish and Blue Crab Trawl Survey (2005); 4, data from Virginia Institute of Marine Science, (2005); 5, see Witting *et al.* (1999) for description of monitoring program; 6, see Byrne (1994) for description of monitoring program; 7, data from Atlantic States Marine Fisheries Commission (ASMFC) (2005); 8, data from 1950 to 2002 from National Marine Fisheries Service (NMFS) (2003); data prior to 1950 reported in Mercer (1987). NA indicates that category is not applicable.

developed: a fall index and a spring index (Table 1). The indices are geometric means of fish of appropriate size collected at river stations only. The New Jersey Division of Fish and Wildlife conducts a trawl survey of coastal waters (6–15 m depth, Byrne, 1994). The average number of Atlantic croaker young-of-the-year per tow in October and June were used as estimates of juvenile abundance in fall and spring, respectively.

Adult abundance was derived from a recent Atlantic croaker stock assessment [Atlantic States Marine Fisheries Commission (ASMFC), 2005; E. Williams, pers. comm.]. Abundance at age-2 was used to represent adult fish in the fishery. A number of fishery-independent and fishery-dependent data were used in the stock assessment to derive abundance-at-age. One of the fishery-independent data sources was the VIMS spring river index (see above). A special model run was made that excluded the Virginia Institute of Marine Sciences spring river index and the NOAA NMFS Northeast Fisheries Science Center Fall Trawl Survey Index from the calculation of abundance-at-age (E. Williams, NMFS, Beaufort, North Carolina, unpublished data). The two estimates of abundance at age-2 (those with and without the Virginia Institute of Marine Sciences spring trawl survey) were highly correlated (Spearman rank correlation 0.921, $P < 0.001$); however, abundance at age-2 calculated without the VIMS spring river index was used here to preserve the statistical independence of spring juvenile and age-2 abundance.

Year class in this study was defined by the fall when spawning was initiated. For example, larvae spawned in the fall and winter of 1989 and the winter and spring of 1990 were assigned to the 1989 yr-class (Fig. 2). Juveniles collected in the fall of 1989 and spring of 1990 were assigned to the 1989 yr-class. The abundance-at-age estimates from the stock assessment are for age-2 on January 1 (ASMFC, in press); thus, age-2 fish in 1990 were assigned to the 1987 yr class.

Commercial catch data were used as a proxy of Atlantic croaker abundance for periods preceding estimates from the stock assessment (before 1973). Data were obtained from 1950 to 2000 for each state from NOAA Fisheries [National Marine Fisheries Service (NMFS), 2003]. These data were supplemented with commercial catch data from Virginia from 1930 to 1949 (Mercer, 1987). Although catch is potentially a biased estimate of fish population abundance, this bias is relatively small for Atlantic croaker compared with other fishery species. The methods to capture Atlantic croaker have remained largely similar since 1950 (haul seines, pound nets, gill nets, and otter trawl, but there has been a shift from haul seines to pound nets and trawling; Mercer, 1987; ASMFC, 2005). In addition, through much of the period considered, there were no commercial size restrictions or catch limits (Mercer, 1987; ASMFC, 2005); recently, size limits have been implemented in Maryland and Georgia and efforts to reduce by-catch have been implemented in North Carolina (ASMFC, 2005). Also, the value of the fishery has remained fairly constant (Mercer, 1987) indicating that market conditions have been stable. Comparison of trends in catch with trends in age-2 abundance from the stock assessment further support the use of catch as a measure of abundance prior to the early 1970s; both catch and abundance exhibit peaks in the 1970s, 1980s and 1990s.

Comparison of larval, juvenile, and adult abundances

Our first objective was to evaluate whether patterns in larval and juvenile abundance are associated with patterns in subsequent adult abundance, as measured by numbers at age-2. The abundance data were grouped by region and life stage. Three regions were used: North Carolina including the Beaufort Inlet ingress sampling and the Pamlico Sound spring juvenile trawl survey, Virginia including the Virginia Institute of Marine Sciences fall and spring juvenile trawl surveys, and New Jersey including the Little Egg Inlet ingress sampling and the fall and spring New Jersey trawl survey. Adult (age-2) abundance from the stock assessment was not segregated by region and was used for comparison in every region. Within each region, the abundance indices represent sequential measures of Atlantic croaker year-class strength. Spearman rank correlation coefficients (r_s) were calculated between indices within a region to determine at what point in the life history year-class strength is determined.

Water temperature and juvenile and adult abundance

Our second objective was to examine the relationship between winter temperatures and abundance indices during spring juvenile and adult life stages. Prior studies have indicated a correlation between winter water temperatures and spring juvenile abundance (Norcross and Austin, 1981), and defined increasing mortality as temperatures decreased below 5°C (Lankford and Targett, 2001a,b). Estuarine water temperature data were obtained from the larval ingress monitoring programs at Little Egg Inlet and Beaufort Inlet and from the Virginia Institute of Marine Science Dock temperature data series from the York River, Virginia. The minimum monthly mean from December to March was used as the minimum winter water temperature. Minimum winter water temperature observed during December 1989 and January to March 1990

corresponds with the conditions experienced by the 1989 yr class. The point samples are not representative of the actual temperatures throughout the three estuarine systems. However, temperature variability in these systems is spatially coherent (Cronin *et al.*, 2003; J. A. Hare, unpublished data) and thus, point samples are representative of relative interannual variability.

Spearman rank correlation coefficients (r_s) were calculated between minimum winter water temperature and spring juvenile abundance in New Jersey, Virginia, and North Carolina. Spearman rank correlation coefficients also were calculated between age-2 abundance and minimum winter water temperature in North Carolina, Virginia, and New Jersey.

Winter temperature and adult catch

Our third objective was to evaluate the relationship between adult catch and long-term trends in winter temperature. Adult catch records extend back to 1930 for Virginia and to 1950 for all Atlantic states, but estuarine water temperature data extend back to 1975, 1957, and 1977 for Beaufort Inlet, North Carolina, York River, Virginia, and Little Egg Inlet, New Jersey. A longer temperature data source is required for a complete comparison with the adult catch records.

Estuarine water temperatures are closely linked to air temperature (Roelofs and Bumpus, 1953; Hettler and Chester, 1982), owing to efficient air-water heat exchange in shallow water (Smith and Kierspe, 1981). Thus, the relation between minimum winter air temperature (independent variable) and minimum winter water temperature (dependent variable) was described to predict minimum winter water temperature for years preceding collection of water temperature data. Monthly New Jersey air temperatures were obtained from the Office of New Jersey State Climatologist (2004). Virginia and North Carolina monthly air temperatures were obtained from the Southeast Regional Climate Center (2004). The minimum monthly mean air temperature from December to March was used. Linear regressions were calculated for the period of overlap between air (T_A) and water (T_W) temperature observations ($T_W = a + b \cdot T_A$), where a and b are the regression parameters. These regressions were then used to estimate minimum winter water temperatures from minimum winter air temperatures from 1930 to 2003.

Adult catch is composed of multiple year classes, so to compare the estimated minimum winter water temperatures to adult catch, a composite temperature was calculated of the estimated minimum water temperatures experienced by the combination of age classes represented in the adult catch. A static age structure was assumed based on Barbieri *et al.* (1994a).

For example, the estimated minimum winter water temperature experienced by the adult catch in 1990 was calculated as $p_{age1} \cdot T_{1989} + p_{age2} \cdot T_{1988} + p_{age3} \cdot T_{1987} + p_{age4} \cdot T_{1986} + p_{age5} \cdot T_{1985} + p_{age6} \cdot T_{1984} + p_{age7} \cdot T_{1983} + p_{age8} \cdot T_{1982}$, where p_{agex} is the proportion of age x fish in the fishery and T_y is the estimated minimum winter water temperature in year y. The proportions of age x fish in the fishery were $p_{age1} = 0.1194$, $p_{age2} = 0.3064$, $p_{age3} = 0.2485$, $p_{age4} = 0.1693$, $p_{age5} = 0.0745$, $p_{age6} = 0.0637$, $p_{age7} = 0.0171$, and $p_{age8} = 0.0011$ (Barbieri *et al.*, 1994b). A Spearman rank correlation coefficient (r_s) was then calculated between catch and age-class-adjusted minimum winter temperature.

*North Atlantic Oscillation, winter temperature, and adult catch*

Our fourth objective was to evaluate the relationship between adult catch, winter temperature, and the larger North Atlantic climate system. The NAO represents a dominant interannual- to decadal-scale climate signal over the North Atlantic (Hurrell *et al.*, 2003). The NAO index is the sea-level pressure difference between Portugal and Iceland (Hurrell, 1995). Atmospheric variability related to NAO (e.g. wind speed, direction, air temperature, Hurrell *et al.*, 2003) forces variability in water temperature, salinity, and circulation (Visbeck *et al.*, 2003). Specifically, the winter NAO index (December through March) is related to the severity of winter over the eastern U.S. (Joyce, 2002; Hurrell *et al.*, 2003). NAO has been linked to a number of biological patterns in the North Atlantic, but typically the mechanistic causes of the correlations remain undescribed (Drinkwater *et al.*, 2003). The relation between adult Atlantic croaker catch and NAO was examined here. The winter NAO index was obtained from the National Center for Atmospheric Research (2004). As adult catch is composed of multiple year classes, a composite winter NAO index was calculated for comparison with adult catch using the method described above for temperature. Spearman rank correlation coefficients (r_s) were then calculated between the composite NAO and adult catch coastwide from 1950 to 2002 and adult catch in Virginia from 1930 to 2002.

RESULTS

General patterns of commercial catch

Adult Atlantic croaker catch from commercial landing data shows decadal variability and periods of coastwide coherence (Fig. 3). From 1930 to 2000, four

Figure 3. Commercial catch of Atlantic croaker in all states along the U.S. east coast (top panel) and by each state individually (remaining panels).
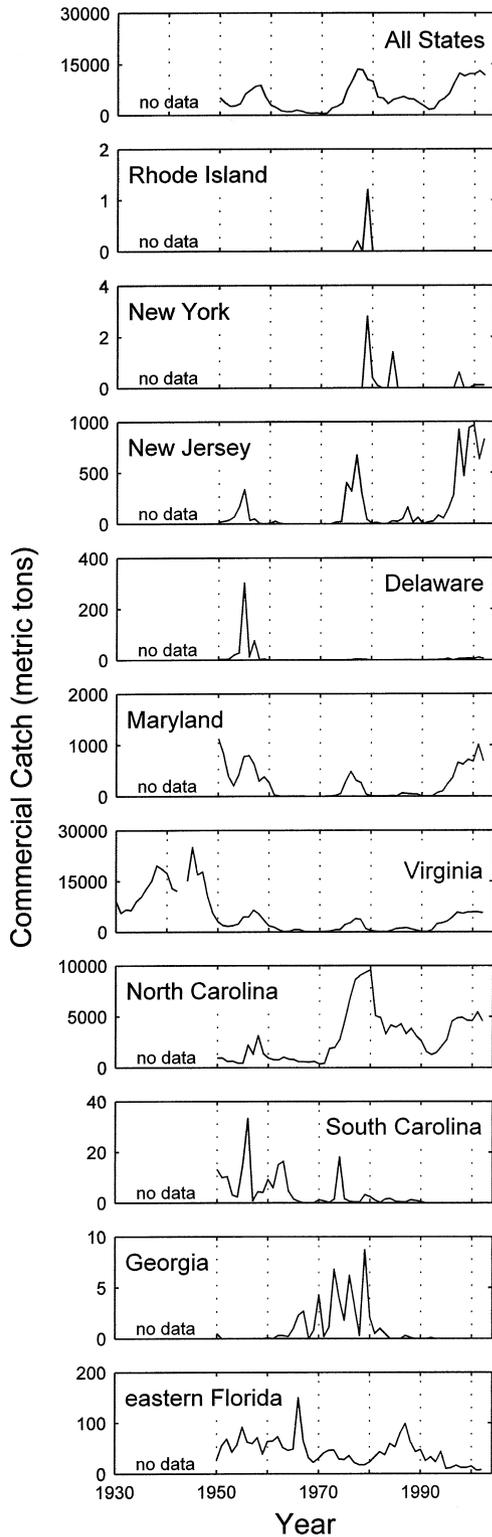
periods of high catch occurred in Virginia (mid-1930s to 1940s, late 1950s, late 1970s, and mid-1990s to 2002). The latter three periods of high catch also occurred in all states combined, with moderately high catches also occurring in the mid-1980s. In examining the data by state, some periods of high catch were observed along the entire coast, for example late 1970s to 1980s. In contrast, other periods of high catch (late 1950s) were observed in the central portion of the coast (Virginia and North Carolina) but not in the northern (New York and Rhode Island) or southern extremes (Georgia and eastern Florida). Temporal patterns in catch from North Carolina to Rhode Island were significantly coherent (Kendall's coefficient of concordance = 0.400, $P < 0.001$).

Comparison of larval, juvenile, and adult abundances

Abundances during adjacent life stages exhibited the highest correlations, and spring juveniles abundances were more highly correlated to adult (age-2) abundance than larval and fall juvenile abundances (Table 2; Fig. 4). In New Jersey, larval ingress was positively correlated with fall juvenile abundance, but

Table 2. Spearman rank correlation coefficients between abundance estimates of Atlantic croaker at four life stages (larvae, fall juveniles, spring juveniles, and age-2 adults) in three geographic regions (New Jersey, Virginia, and North Carolina).

Location	Life stages		
	Larvae	Fall juvenile	Spring juvenile
New Jersey			
Larvae	–		
Fall juvenile	0.824***	–	
Spring juvenile	0.479	0.516	–
Adults (age-2)	0.098	−0.202	0.413
Virginia			
Larvae	–		
Fall juvenile	ND	–	
Spring juvenile	ND	0.362	–
Adults (age-2)	ND	0.340	0.747***
North Carolina			
Larvae	–		
Fall juvenile	ND	–	
Spring juvenile	−0.361	ND	–
Adults (age-2)	−0.058	ND	0.674**

Significance of correlations are indicated as *<0.05, **<0.01, and ***<0.001.
ND indicates abundance estimates of a particular life stage are not available.

Figure 4. Time series of larval ingress, fall juvenile, spring juvenile, and adult (age-2) abundance in each of three regions of the east coast of the U.S. Data are lagged to show year classes and are standardized by removing the mean and dividing by the standard deviation.
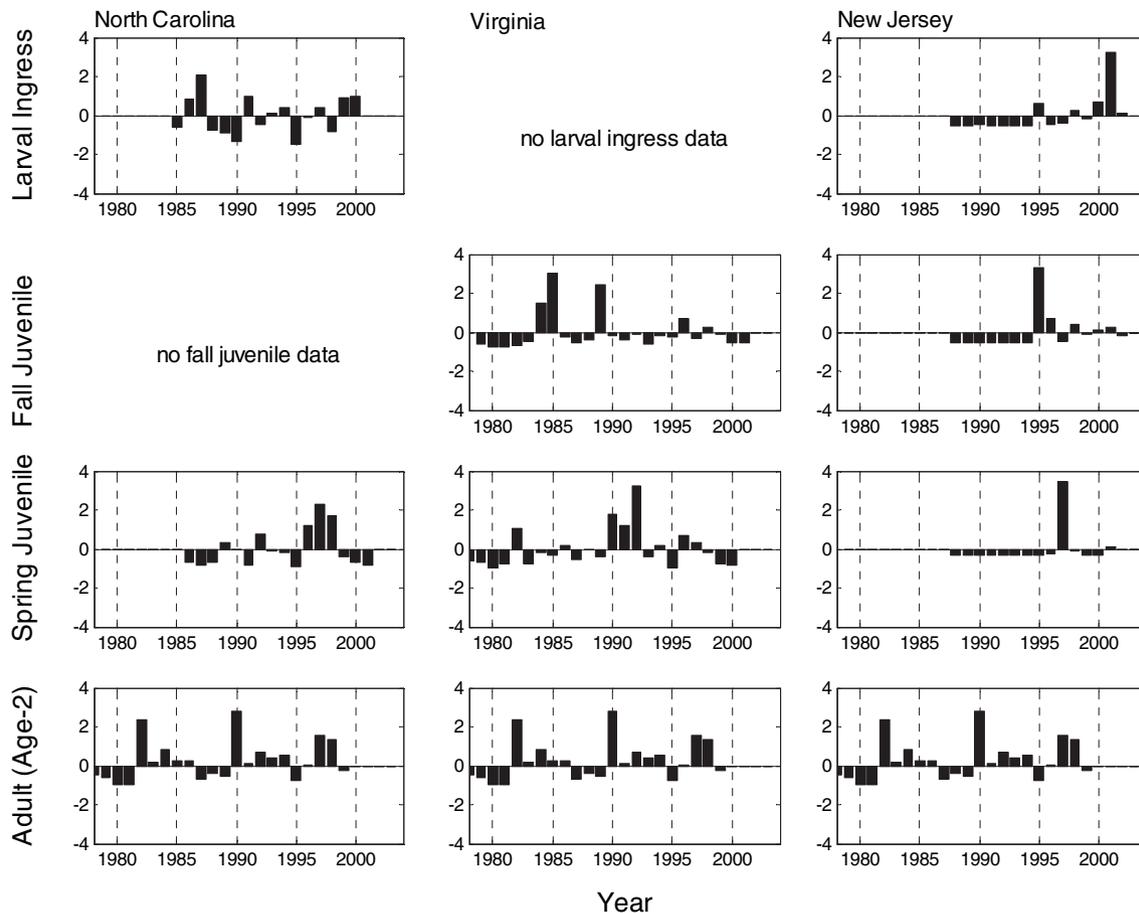
larval and fall juvenile abundance were not significantly correlated with spring juvenile or adult (age-2) abundance. Similarly in Virginia, fall juvenile abundance was not significantly correlated with spring juvenile or age-2 abundance, but spring juvenile abundance was correlated with adult (age-2) abundance. Patterns in North Carolina mirrored those in Virginia; larval abundance was not significantly correlated with spring juvenile or adult (age-2) abundance, but spring juvenile abundance was significantly correlated with adult (age-2) abundance. These results indicate that abundance patterns are significantly modified during the winter and that year-class strength is largely set by the spring of the first year.

*Water temperature and juvenile and adult abundance*

Winter water temperatures were positively correlated with spring juvenile and adult (age-2) abundance (Fig. 5). In North Carolina and New Jersey, winter

water temperature and spring juvenile abundance were positively related but correlations were not significant ($r_s = 0.365$, $P > 0.05$; 0.073, $P > 0.05$, respectively); however, above average spring juvenile abundances only occurred in years with above average minimum winter temperatures. In Virginia, spring juvenile abundance was significantly correlated with minimum winter water temperature ($r_s = 0.638$, $P < 0.01$). Adult (age-2) abundance was significantly correlated with minimum winter temperatures in New Jersey ($r_s = 0.601$, $P < 0.01$), Virginia ($r_s = 0.638$, $P < 0.01$), and North Carolina ($r_s = 0.608$, $P < 0.01$). These data indicate a link between winter water temperature, spring juvenile abundance, and subsequent recruitment to the fishery.

Water temperatures, air temperatures, and adult catch

The time series of estuarine water temperature and coastal air temperature showed clear correspondence,

Figure 5. Time series of spring juvenile abundance, adult (age-2) abundance, and estuarine water temperature for New Jersey, North Carolina, and Virginia. Data are lagged to show year classes and are standardized by removing the mean and dividing by the standard deviation. Temperature values are shown relative to 3°C because 100% mortality occurred in juvenile Atlantic croaker held at 3°C for 23 days (Lankford and Targett, 2001a).
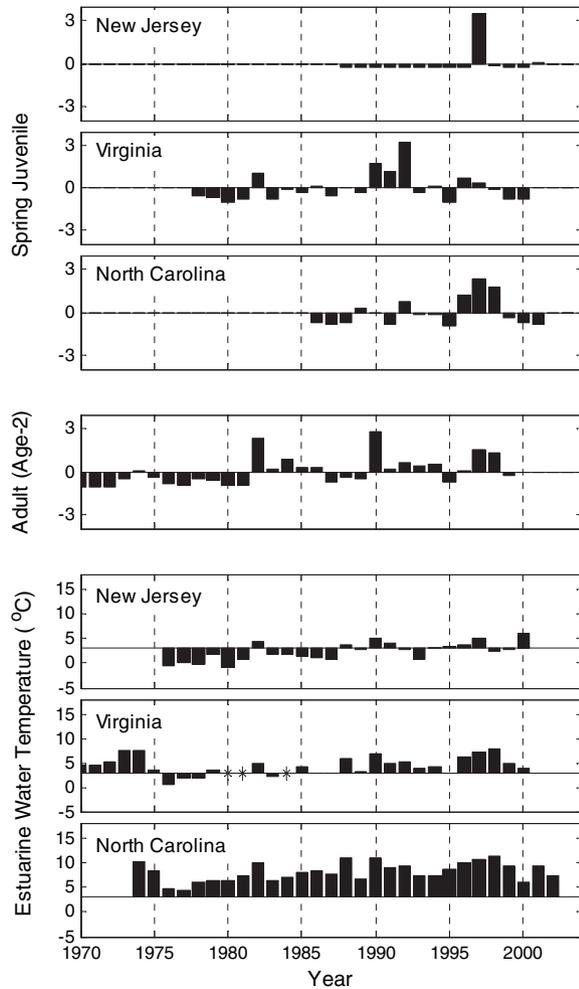
and minimum winter air temperature was significantly correlated with minimum winter water temperatures (Fig. 6). Linear regression coefficients (r^2) ranged from 0.712 to 0.788. These high regression coefficients mean that minimum winter water temperatures can be predicted from minimum winter air temperatures. Further, interannual variability in air temperatures was similar among the three regions (Kendall's coefficient of concordance = 0.897, $P < 0.001$), indicating that minimum winter air and water temperatures are coherent over much of the range of Atlantic croaker along the east coast of the U.S.

Periods of high adult catches coincided with periods of high minimum estimated winter water temperatures (Fig. 7). Since the 1950s, there were three periods of high adult catches and warm minimum estimated winter water temperatures (1950s, 1970s, and 1990s). An additional period of high catches in late 1930s and 1940s corresponds with warm winter water temperatures through the 1930s. Estimated minimum winter water temperature in Virginia was significantly correlated with coastwide adult catch for the period 1950–2000 ($r_s = 0.378$, $P < 0.01$) and with Virginia adult catch for the period 1930–2000 ($r_s = 0.628$, $P < 0.001$).

North Atlantic Oscillation and adult catch

Adult catch was significantly correlated with the composite winter NAO index (Fig. 7). The three periods of high catch in the 1950s, 1970s, and 1990s coincided with positive composite NAO values, and the correlation between the two was significant ($r_s = 0.646$, $P < 0.001$). The relation between the composite winter NAO index and Virginia adult catch from 1930 to 2000 was also significant ($r_s = 0.307$, $P < 0.01$), but with low explanatory power.

DISCUSSION

Conceptual model for Atlantic croaker population dynamics

The results of this study allow the development of a conceptual model of Atlantic croaker population dynamics along the east coast of the U.S. The 'outbursts' of Atlantic croaker are caused by relatively warm winters that result in high juvenile survival in mid-Atlantic estuaries. This 'thermal opening' of estuaries provides approximately 165% more juvenile habitat [National Oceanic and Atmospheric Administration (NOAA), 1985], which allows for the formation of large year classes. These large year classes then carry the population for 3–5 yr (based on the age structure of the commercial catch; Ross, 1988; Barbieri et al., 1994b). Sequential warm winters lead to sequential large year classes that extend the duration of the outburst. As the outburst develops, Atlantic croaker range extends farther north and as a result, spawning extends farther north. Larvae then are supplied to estuaries farther north (e.g. along the New Jersey coast), and if sequential warm winters occur, the outburst continues as a result of additional juvenile habitat opening to the population. The outburst ends when relatively cold winters create a 'thermal closure' of estuarine nursery habitats north of Cape Hatteras,
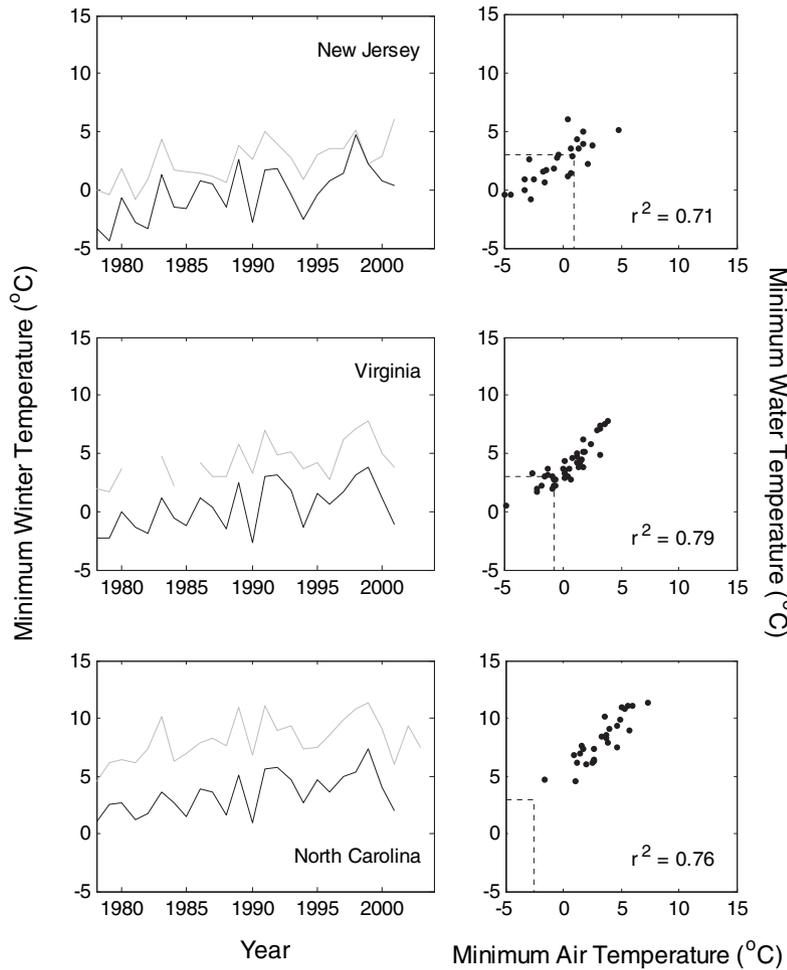
Figure 6. Relation between minimum estuarine water temperatures (gray line) and minimum monthly air temperature (black line) in December, January, February, and March for New Jersey, North Carolina, and Virginia. Data are shown as time series (left column) and as scatterplots (right column). Water temperatures of 3°C and their corresponding air temperatures are shown for reference because 100% mortality occurred in juvenile Atlantic croaker held at 3°C for 23 days (Lankford and Targett, 2001a).

thereby causing the formation of weak year classes. The strong year classes then pass from the population owing to natural mortality and fishing. When fishing mortality was lower, the maximum age of Atlantic croaker was greater (Hales and Reitz, 1992). As a result, the population was able to sustain these outbursts for longer of periods of time (e.g. 1930s and 1940s), owing to increased resiliency of the population to bridge the periods between the formation of strong year classes.

In this conceptual model, the role of larval supply is minimal. Examination of the outburst that occurred in the early 1990s reveals that the increases in ingress in New Jersey followed the initiation of the outburst. Based on the conceptual model above, the increase of larvae in New Jersey was caused by a northward expansion of the spawning range during the outburst, and was thus a consequence, not a cause. However, larval supply may be important in regulating abundance within the outburst and non-outburst phases of the population.

Fishing and by-catch have been proposed as important factors influencing the dynamics of Atlantic croaker along the east coast of the U.S. (Diamond et al., 1999, 2000), but we hypothesize that their role is secondary. The conceptual model proposes that the dominant scale of variability in abundance is linked to long-term trends in winter temperature. After successive cold winters have closed juvenile nurseries in northeast U.S. estuaries, a switch from outburst to non-outburst phase would occur eventually through natural mortality, but could be facilitated by fishing and by-catch.

Problems with analyses/improvements

The conceptual model presented above is based upon a synthesis of data presented here, the laboratory results of Lankford and Targett (2001a,b), and the initial work by Norcross and Austin (1981). Our analyses are correlative and do not address causation. However, temperature as a causative agent of juvenile croaker mortality has been demonstrated experimentally

Figure 7. Commercial catch of Atlantic croaker in Virginia (black line) and in North Carolina to Rhode Island combined (gray line). Time series of estimated minimum winter water temperature in Virginia adjusted for year-class composition of adult catch relative to 3°C because 100% mortality occurred in juvenile Atlantic croaker held at 3°C for 23 days (Lankford and Targett, 2001a). Time series of winter NAO index adjusted for year-class composition of adult catch.
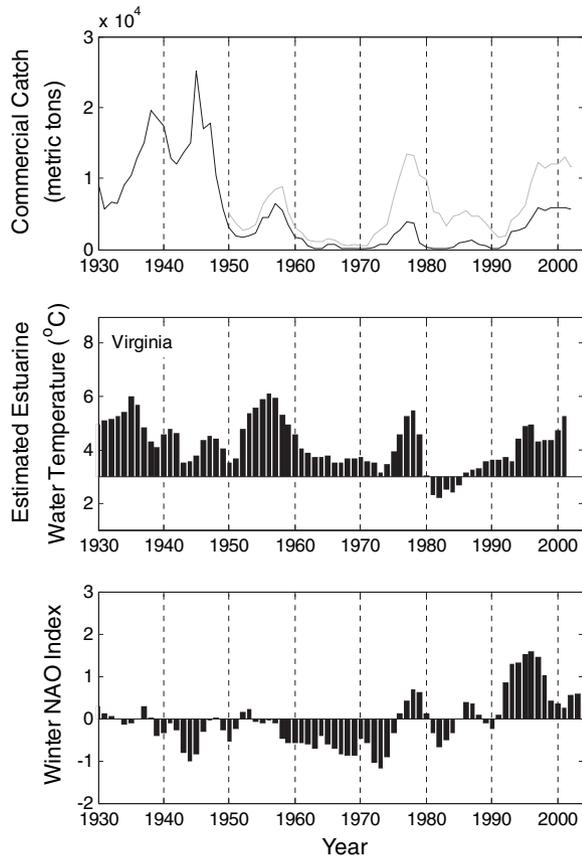
(Lankford and Targett, 2001a,b). Also, the 1990s represent, in essence, a test of the initial hypothesis of Norcross and Austin (1981); based on their correlative analysis using data from 1955 to 1977, increases in Atlantic croaker abundance would have been predicted during the 1990s owing to warmer winter estuarine water temperatures. Thus, although our analyses are correlative, they are supported by a demonstrated mechanism and continuation of the relation between abundance and winter water temperatures through several cycles. It is important to note, however, that other hypotheses can be developed to explain the correlations found here; we hope that our conceptual model will encourage further testing and investigation of these ideas, as well as alternative explanations.

Juvenile ecology (apart from temperature-related overwinter mortality) is not emphasized in the conceptual model, largely owing to a lack of specific data. Even in cold winters, there are likely areas of warmer water in estuarine systems north of Cape Hatteras (e.g. in deep channels, in the vicinity of power plant discharges, Marcy, 2004); such thermal refuges could provide habitat for overwinter survival. Although there are relatively few predators in estuaries north of Cape Hatteras in the winter (Murdy *et al.*, 1997; Able and Brown, 2005), variability in predation pressure and consumption rates of potential predators during winter need to be quantified. Information on feeding is also needed for a more detailed understanding of population variability (e.g. Kimmerer *et al.*, 2000). Finally, the interaction between appropriate habitat and distribution and abundance of predators and prey may play a role in population variability of Atlantic croaker (e.g. Hartman and Brandt, 1995a,b). Thus, the conceptual model proposed here could be improved by a more specific treatment of juvenile ecology during winter.

The lack of larval ingress data from Chesapeake Bay is another weakness of our study. Barbieri *et al.* (1994b) concluded their examination of Atlantic croaker life history traits with a call for sampling programs over time describing size and age compositions of Atlantic croaker throughout their range. Similar comprehensive data sets have been called for to improve the understanding of bluefish population dynamics (Hare and Cowen, 1993; Able *et al.*, 2003). One method to achieve such comprehensive data sets is for the federal government and fishery management councils to support the inception, development, and implementation of comprehensive data collection. Another method is to incorporate ingress and juvenile abundance monitoring into coastal ocean observing systems. The return is a better understanding of the processes affecting the dynamics of commercially and recreationally important species and the possibility to forecast future population abundance and thus, more effectively manage these resources.

Ecological forecasting and stock assessments

The analyses presented here provide several mechanisms to forecast future Atlantic croaker catch (see Williams and Quinn, 2000; Clark *et al.*, 2001). Abundance data from New Jersey may provide measures of the phase of the outburst. As such, adult catch could be forecast 2 yr following ingress and juvenile sampling. Additionally, monitoring of estuarine temperatures along the east coast of the U.S. would provide the ability to forecast year-class strength and by

extension, the initiation, continuation, or end of population outbursts. Based on the cold winters of 2002/2003, 2003/2004, and 2004/2005, we predict the formation of weak year classes and possibly an end to the recent outburst, yet the mild winter of 2005/2006 may allow the outburst to continue. Making such predictions is risky, but represents a test of our hypothesis based on the conceptual model of Atlantic croaker population dynamics.

The conceptual model also has implications for the stock assessment process. The hypothesized determinant role of winter temperature on the status of the population provides an excellent opportunity to develop an environmentally explicit stock assessment (Maunder and Watters, 2003). This stock assessment model could produce improved hindcasts of population status and formally couple forecasts, such as those proposed above, with harvest policies. The conceptual model, however, leads to some problems with current stock assessment practices. How is virgin biomass and virgin recruitment defined in a species where environmental variability causes two population phases? Further, the frequency and duration of outbursts will vary under different climate scenarios. These issues are likely common to many fisheries, and need to be considered in the stock assessment process.

Decadal-scale variability in fish populations along east coast of U.S.

In the conceptual model of Atlantic croaker population dynamics, winter temperature controls recruitment to the fishery and the oscillation between outburst and non-outburst population phases. Winter temperature along the east coast of the U.S. is related to the NAO (Joyce, 2002; Hurrell et al., 2003), and thus the dynamics of Atlantic croaker are linked to NAO through winter air temperature, winter estuarine water temperature, and overwinter survival of Atlantic croaker juveniles. The relation between NAO and fisheries has recently been reviewed by Drinkwater et al. (2003), yet our conceptual model specifies the mechanism through which climate affects population dynamics.

Although only one species was examined here, there may very well be multi-species patterns in recruitment and population dynamics that are linked to climatic forcing along the east coast of the U.S. Long-term trends in abundance are known for many of the regions fisheries: for example, Spanish mackerel (Chittenden et al., 1993) and yellowtail flounder (Sullivan et al., 2005). These long-term patterns are usually explained by changes in fishing mortality (Chittenden et al., 1993), but the contributing effect of climate variability is now being investigated (Sullivan et al., 2005). Further, the conceptual model for Atlantic croaker suggests that increased fishing mortality may make populations more susceptible to variability in abundance caused by climatic-scale variability in the environment by reducing the capacity of the population to sustain abundance between strong year classes. Thus, the large-scale patterns in climate described along the east coast (Joyce, 2002; Hurrell et al., 2003) may have broad impacts on fisheries similar to those described on the west coast of the U.S. for groundfish species (Hollowed et al., 2001). These impacts need to be quantified and incorporated into the stock assessment process for successful long-term management of marine fish species.

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