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ARTICLE

Environmental Influences on Juvenile Fish Abundances in a River-Dominated Coastal System

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Abstract

We investigated the influence of climatic and environmental factors on interannual variations in juvenile abundances of marine fishes in a river-dominated coastal system of the north-central Gulf of Mexico, where an elevated primary productivity sustains fisheries of high economic importance. Fish were collected monthly with an otter trawl at three stations near Mobile Bay from 1982 to 2007. Fish sizes were used to isolate juvenile stages within the data set, and monthly patterns in juvenile fish abundance and size were then used to identify seasonal peaks for each species. The average numbers of juvenile fish collected during these seasonal peaks in each year were used as indices of annual juvenile abundances and were related to corresponding seasonal averages of selected environmental factors via a combination of principal components analysis and co-inertia analysis. Factors contributing the most to explain interannual variations in juvenile fish abundances were river discharge and water temperature during early spring–early summer, wind speed and North Atlantic Oscillation index during late fall–winter, and atmospheric pressure and wind speed during summer–fall. For example, juvenile abundances of southern kingfish *Menticirrhus americanus* during summer–fall were positively associated with atmospheric pressure and negatively associated with wind speed during this period. Southern kingfish juvenile abundances during late fall–winter were also negatively associated with wind speed during the same period and were positively associated with river discharge during early spring–early summer. Juvenile abundances of the Atlantic croaker *Micropogonias undulatus* during early spring–early summer were negatively associated with river discharge and North Atlantic Oscillation during late fall–winter. Overall, the importance of river discharge for many of the species examined emphasizes the major role of watershed processes for marine fisheries production in coastal waters of the north-central Gulf of Mexico.

Long-term monitoring of many marine fish populations has revealed the importance of temporal variability at interannual and decadal scales (Hollowed et al. 2001; Lehodey et al. 2006). Interannual variations in adult fish abundances are mainly dependent on processes occurring during the early life stages (Cushing 1996; Fuiman and Werner 2002). In turn, survival rates of juvenile fish are a principal driver of variable year-class strength in the resulting adult population (Houde 1997; Miller and Kendall 2009). Identifying the factors that affect the interannual variability in juvenile fish abundances is thus critical for

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a better understanding of variability in adult fish abundances and fisheries landings, and of fish population responses to a changing environment (Myers 1998; Brunel and Boucher 2007).

Among the factors affecting interannual patterns in juvenile fish abundances, climatic and local environmental variability plays an important role (Cushing 1996; Brunel and Boucher 2007). Juvenile abundances of a variety of fish species throughout the world have been related to indices of large-scale climate patterns, such as the Pacific Decadal Oscillation, the North Atlantic Oscillation (NAO), or El Niño–Southern Oscillation Index (SOI; Hollowed et al. 2001; Lehodey et al. 2006). These general climatic indices are synthetic representations of climate patterns at ocean basin scales, which affect local environmental conditions influencing juvenile fish abundances at the local habitat level. For example, minimum winter air temperature along the East Coast of the United States was shown to track larger-scale variations in NAO and was identified as a potential mechanism explaining juvenile abundances of the Atlantic croaker *Micropogonias undulatus* (Hare and Able 2007). Variability in sea surface temperatures (Ciannelli et al. 2005; Brunel and Boucher 2007), river discharge (Crecco et al. 1986; Martino and Houde 2010), and wind patterns (Daskalov 2003; Lloret et al. 2004) also participate in shaping variable estuarine–coastal hydrodynamic conditions that influence juvenile fish abundances.

The extent to which earlier studies can be generalized, however, remains uncertain because the intensity of climatic and environmental controls on juvenile fish abundances varies as a function of space and time (Myers 1998; Planque and Buffaz 2008). For example, correlations between environmental factors and juvenile fish abundances are generally more obvious and robust at the edges of the biogeographical ranges of fish species (Myers 1998) or during specific seasons or climatic phases (Ottersen et al. 2006; Planque and Buffaz 2008). Moreover, different components of environmental variability influence fish production at high versus low latitudes (Brander 2007). Biological factors, such as spawning stock biomass, have also been shown to affect the strength and significance of environmental controls on juvenile fish abundance patterns (Ottersen et al. 2006; Brander 2007). These spatial, temporal, and population-specific variations emphasize a need for addressing the influence of environmental factors on juvenile fish abundances for multiple fish species in diverse ecosystems. This may provide crucial information on the consistency or variability of environment–juvenile abundance linkages for specific species and help in developing local tools for forecasting fish population responses to environmental changes.

Whereas many studies have addressed the effect of climatic and environmental factors on juvenile fish abundance dynamics along the U.S. East Coast (e.g., Lankford and Targett 2001; Hare and Able 2007) and West Coast (e.g., Kimmerer et al. 2001; Clark and Hare 2002), this question has rarely been examined in the northern Gulf of Mexico despite the economic importance of fisheries from this region (Browder 1993). The northern Gulf of Mexico is characterized by several coastal river systems that are known to enhance coastal primary productivity and support large finfish and penaeid shrimp fisheries (Browder 1993). Much of the research conducted in the region has focused on the Mississippi–Atchafalaya River system, which contributes 90% of the freshwater input to the Gulf of Mexico (Rabalais et al. 1996) and has been linked to fisheries production (Govoni 1997; Grimes 2001). However, relatively little research has focused on other Gulf river systems and their relationships to fisheries production. The Mobile Bay River system, in particular, which is formed at the confluence of the Tombigbee and Alabama rivers, drains an area of 115,000 km^2 and represents the fourth-largest discharge in the USA and the second largest in the Gulf of Mexico (Schroeder 1978).

In the Mobile Bay area, published studies dealing with the ecology of fish early life stages had so far been limited to analyses of ichthyoplankton seasonality (Hernandez et al. 2010a, 2010b). Information about juvenile fish dynamics and responses to environmental factors is thus essential for a better understanding of interannual variability in fisheries production in this area. The objectives of the present study are thus to (1) describe interannual patterns in juvenile abundance displayed by common coastal marine fish species over a 26-year time series in coastal waters off Mobile Bay, Alabama, and (2) explore the relationships between these abundance patterns and a variety of climatic and local environmental factors.

METHODS

Data sources.—Fish abundance data were provided by a fisheries-independent survey, the Fisheries Assessment and Monitoring Program (FAMP), conducted by the Alabama Department of Conservation and Natural Resources (ADCNR), Marine Resources Division (MRD). Sampling consisted of monthly otter trawl collections at a variety of sites along the Alabama coast from 1982 to 2007. The otter trawl had a 4.9-m opening and was made of 35-mm stretched mesh with a 4.5-mm cod end fitted with a 4.7-mm liner. For the present study, data obtained at three coastal stations near Mobile Bay were compiled: Petit Bois Pass, Mobile Pass, and Perdido Pass (Figure 1). At each station and month (i.e., each sample), fish collected were identified and a maximum of 50 individuals were measured for each species (standard length, to the nearest 1 mm). Due to some modifications in the sampling design over the course of this long-term survey, 12 out of the 312 months of sampling were missing (no sample in October, November, or December 1998; January, June, July, August, or October 1999; January, March, or May 2000; or August 2005). In these instances, fish abundance values were replaced by the corresponding monthly averages over the 26-year period (i.e., 1982–2007).

Two general climate indices and seven local environmental factors (listed in Table 1) were obtained from National Oceanic and Atmospheric Administration (NOAA) National Weather Service (NWS) Climate Prediction Center (NOAA 2010a), NOAA National Data Buoy Center (NDBC; NOAA 2010b),

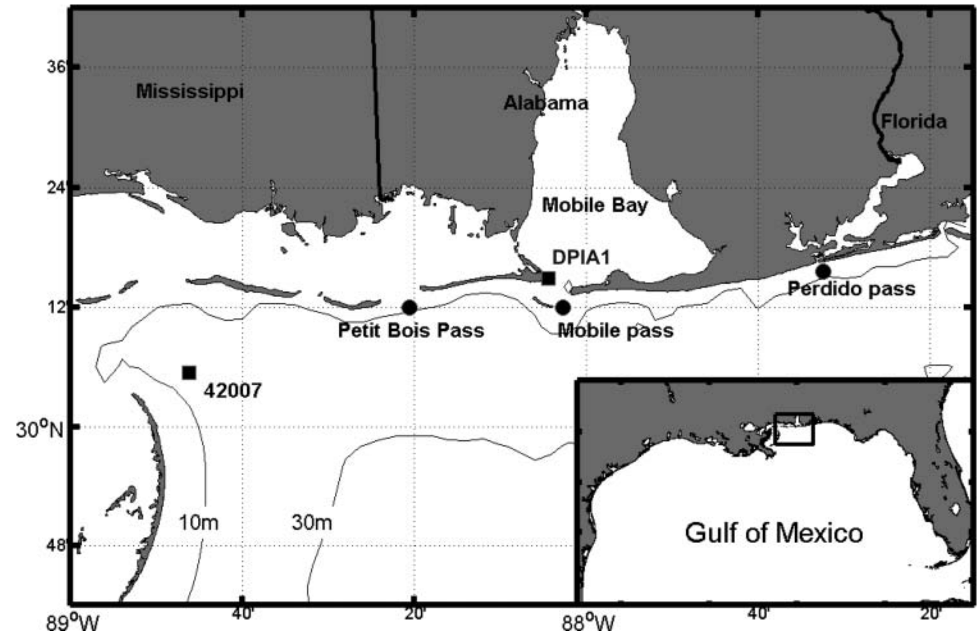


FIGURE 1. Locations of otter trawl stations (circles) of the Fisheries Assessment and Monitoring Program conducted by the Alabama Department of Conservation and Natural Resources' Marine Resources Division, and locations of environmental stations (squares) of the National Oceanic and Atmospheric Administration's National Data Buoy Center (stations DPIA1 and 42007). Locations of the two U.S. Geological Survey gaging stations (Alabama and Tombigbee rivers; USGS 2010a, 2010b) are not shown because they are situated farther north on land.

and U.S. Geological Survey (USGS) websites (USGS 2010a, 2010b). Data from NOAA–NWS were provided at monthly intervals. Data from NOAA–NDBC were collected at hourly intervals. Daily river discharge data were collected from two USGS gaging stations in the Alabama River (Clairborne Lock and Dam; USGS 2010a) and in the Tombigbee River (Coffeeville Lock and Dam; USGS 2010b). Their sum was used as a total freshwater discharge into Mobile Bay (Park et al. 2007).

Fish data analysis.—Due to the scarcity of information regarding relationships between juvenile fish abundances and environmental conditions in the study area, a multispecies approach was favored. We removed very rare species since their highly variable abundance and occurrence may confound multispecies patterns of interest (Wood and Austin 2009). Only the species contributing to at least 0.5% of the total fish abundance observed over the 26-year period were thus retained. Furthermore, fish age estimations are not available in the FAMP data set used in this study and published size-at-age relationships are not available for the retained species in the study region. We thus used size data to sort out juvenile stages in the data set.

TABLE 1. Climatic and environmental factors examined, with their respective units, sources, and codes. Measurement stations are depicted in Figure 1.

Variable	Units	Source	Code
General climatic factors			
El Niño–Southern Oscillation Index		NOAA 2010a	soi
North Atlantic Oscillation index		NOAA 2010a	nao
Local environmental factors			
Air temperature	°C	NOAA 2010b (stations 42007 and DPIA1)	AT
Water temperature	°C	NOAA 2010b (stations 42007 and DPIA1)	WT
Wind speed	m/s	NOAA 2010b (stations 42007 and DPIA1)	WS
u-wind component (alongshore)	m/s	NOAA 2010b (stations 42007 and DPIA1)	uW
v-wind component (cross-shore)	m/s	NOAA 2010b (stations 42007 and DPIA1)	vW
Atmospheric pressure	bar	NOAA 2010b (stations 42007 and DPIA1)	AP
River discharge	m^3/s	USGS 2010a (Clairborne Lock and Dam, Alabama River); USGS 2010b (Coffeeville Lock and Dam, Tombigbee River)	RD

TABLE 2. Fish species commonly collected as juveniles in otter trawl samples at three stations in the Mobile Bay area from 1982 to 2007, the respective juvenile size boundaries (standard length, mm), total number of juveniles (estimated *N*), 3-month peaks in juvenile abundance (2-month peaks for pinfish; see Figure 3), and corresponding seasonal groups and codes. Species are ordered alphabetically. Monthly patterns in juvenile abundance and mean size are depicted in Figure 3. See Methods for details on juvenile fish abundance estimations and on the determination of juvenile size boundaries and seasonal groups. Juvenile fish size distribution plots are provided in Figure 2.

Species	Juvenile size boundaries (mm)	Estimated *N*	Peak months	Seasonal group	Code
Bay anchovy *Anchoa mitchilli*	25–36	943	May–Jul	Early spring–early summer	anmit(I)
Hardhead catfish *Ariopsis felis* (formerly *Arius felis*)	60–125	2,172	Nov–Jan	Late fall and winter	arfel(II)
Atlantic bumper *Chloroscombrus chrysurus*	30–97	1,591	Sep–Nov	Summer and fall	chchr(III)
Sand seatrout *Cynoscion arenarius*	30–128	245	Apr–Jun	Early spring–early summer	cyare(I)
			Nov–Jan	Late fall and winter	cyare(II)
Silver seatrout *Cynoscion nothus*	30–159	278	Sep–Nov	Summer and fall	cynot(III)
Fringed flounder *Etropus crossotus*	20–84	565	Dec–Feb	Late fall and winter	etcro(II)
			Jul–Sep	Summer and fall	etcro(III)
Pinfish *Lagodon rhomboides*	30–105	161	Dec, Jan	Late fall and winter	larho(II)
			Aug, Sep	Summer and fall	larho(III)
Spot *Leiostomus xanthurus*	30–122	719	Dec–Feb	Late fall and winter	lexan(II)
			Jun–Aug	Summer and fall	lexan(III)
Southern kingfish *Menticirrhus americanus*	30–136	279	Nov–Jan	Late fall and winter	meame(II)
			Jun–Aug	Summer and fall	meame(III)
Atlantic croaker *Micropogonias undulatus*	30–139	1,936	May–Jul	Early spring–early summer	miund(I)
Atlantic thread herring *Opisthonema oglinum*	30–109	2,851	Apr–Jun	Early spring–early summer	opogl(I)
Gulf butterfish *Peprilus burti*	16–99	618	Feb–Apr	Early spring–early summer	pebur(I)
Atlantic moonfish *Selene setapinnis*	20–236	294	Aug–Oct	Summer and fall	seset(III)
Blackcheek tonguefish *Symphurus plagiusa*	20–90	772	May–Jul	Early spring–early summer	sypla(I)
			Nov–Jan	Late fall and winter	sypla(II)
Hogchoker *Trinectes maculatus*	20–99	247	Jul–Sep	Summer and fall	trmac(III)

We followed Miller and Kendall's (2009) definition of the juvenile stage: only fish larger than the size at metamorphosis, size at which squamation begins, size at which fin rays development is completed (depending on data availability in the literature), or a combination thereof, and smaller than the size at maturity, were considered as juveniles. Consequently, only species for which the latter parameters were available in the literature were finally retained (Table 2).

Species-specific sizes at maturity (S_{mat}) were obtained from FishBase (Froese and Pauly 2010) and Pattillo et al. (1997). When S_{mat} estimates differed between the two references, the lower value was retained because using a lower S_{mat} value reduces the likelihood that any mature individuals are included in the analysis (i.e., most conservative approach). Size at metamorphosis, size at which squamation begins, or size at which fin ray development is completed were obtained from Gallaway and Strawn (1974), Richards (2006), Fahay (2007), and Able and Fahay (2010) for hardhead catfish; Martin and Drewry (1978), Ditty and Truesdale (1983), and Rotunno and Cowen (1997) for Gulf butterfish; and Switzer (2003) for blackcheek tonguefish. When these latter estimates differed between different references for a given species, the larger value (i.e., most conservative) was retained. Juvenile size boundaries were then refined for each species by visualizing length frequency plots of all measured fish for each species (data not shown). Final juvenile size boundaries are shown in Table 2, and length frequency plots of measured juvenile fish for each species are shown in Figure 2. For each sample, the proportion of measured individuals comprised within the juvenile size boundaries was then calculated and applied to the total number of fish collected for each species, providing an estimate of the abundance of juveniles for each species in each sample (Table 2).

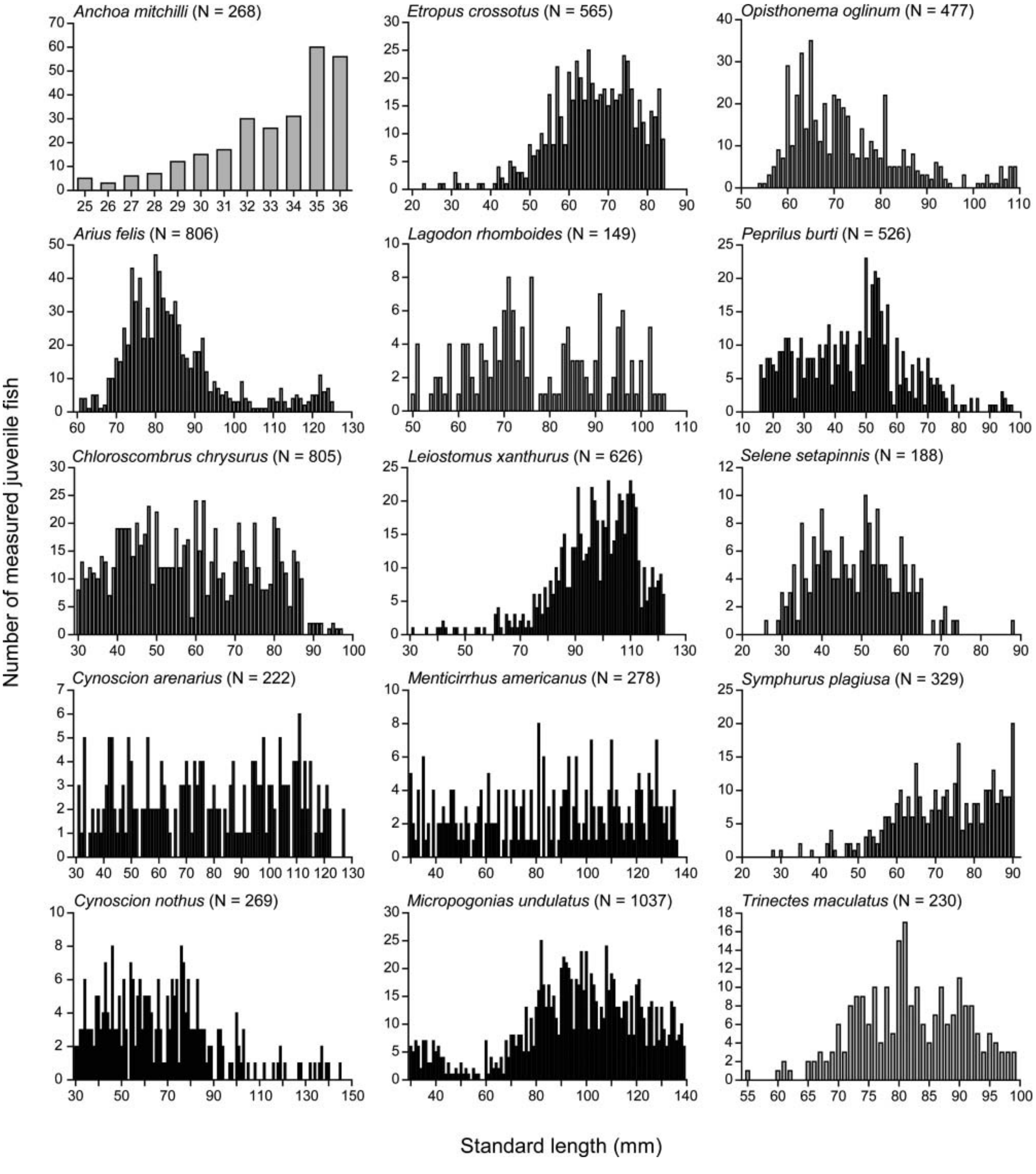


FIGURE 2. Size distribution of measured juvenile fish from 15 species collected between 1982 and 2007 with an otter trawl at three stations from the Mobile Bay area, Alabama. Common names of species are provided in Table 2.

Monthly patterns in juvenile fish abundances over the 26-year study period were examined in order to identify seasonal peaks for each species (Figure 3). Depending on species, one to two seasonal peaks were selected, a seasonal peak corresponding to the three consecutive months (two months in the case of pinfish) during which juvenile abundances were the highest (Figure 3). Based on these seasonal peaks, three groups of species were identified: (1) species for which juvenile

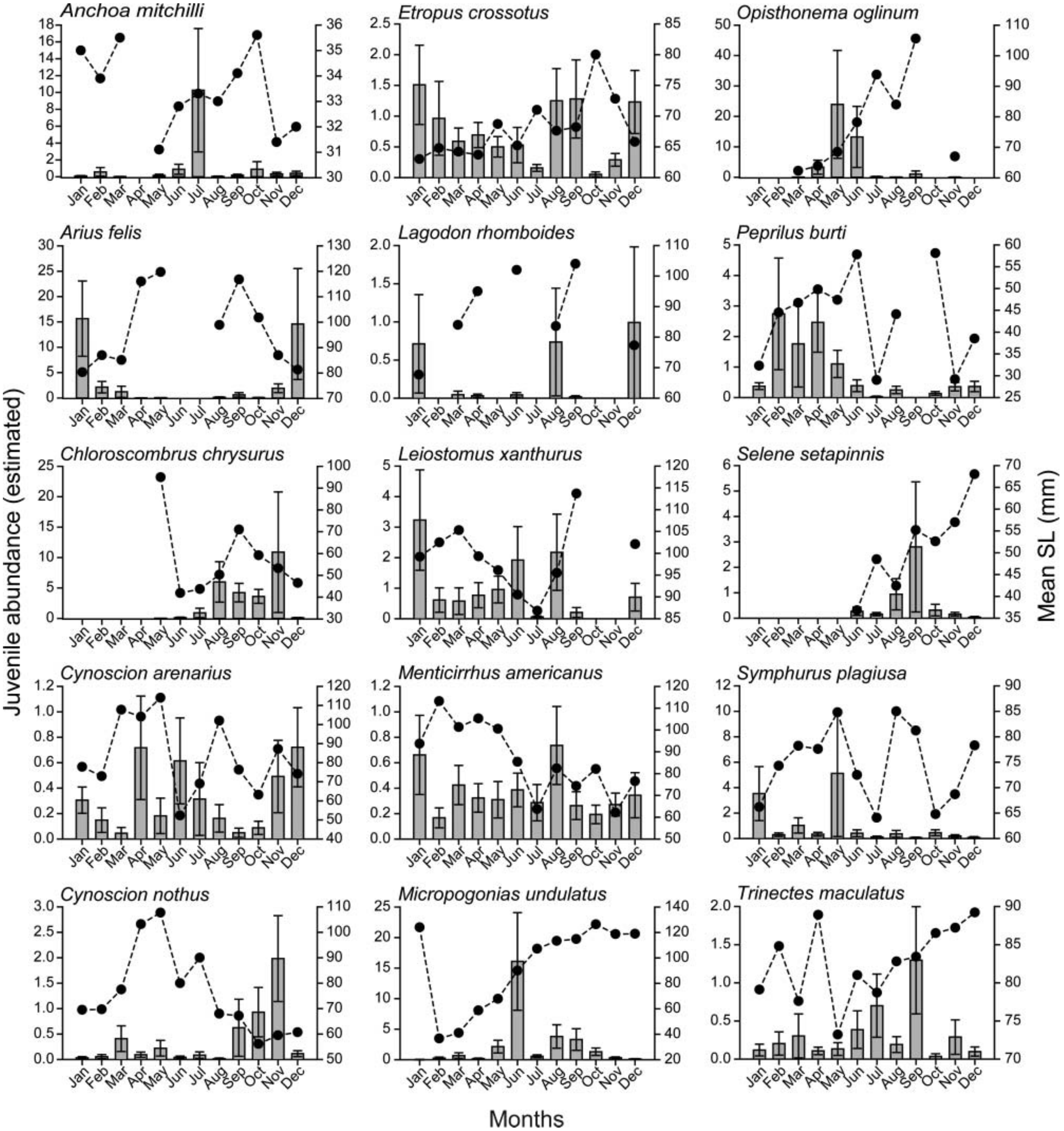


FIGURE 3. Monthly patterns in juvenile abundance and mean size for 15 fish species collected in 1982–2007 at three sites (Figure 1). Average (±SE) juvenile abundances are shown with column charts and are associated with the left *y*-axes. Mean sizes (standard length [SL], mm) are represented by black shaded circles and are associated with the right *y*-axes. Species are presented in alphabetical order. Months selected for the calculation of annual juvenile abundance indices and corresponding seasonal groups for each species are shown in Table 2; common names of species are also provided in Table 2.

abundances peaked from early spring through early summer (i.e., group I, six species), (2) species for which juvenile abundances peaked in late fall and winter (group II, seven species), and (3) species for which juvenile abundances peaked during summer and fall (group III, eight species; Figure 3; Table 2). For each group, the average number of juvenile fish collected during the seasonal peak was used as the annual juvenile fish abundance index (JAI) for each species (JAIs were thus based on average numbers of juveniles collected in the two to three seasonal peak months × three stations = six to nine samples per year).

The JAIs were processed to obtain standardized annual anomalies by removing the mean and dividing with the SD over the 26-year period. Multispecies patterns in JAIs were then analyzed using centered principal components analysis (PCA), which is adapted to the treatment of variables expressed in similar units, and relies on the computation of covariances between variables (Legendre and Legendre 1998). The JAIs were $\log_{10}(x + 1)$ transformed in order to clarify the projection of highly variable observations (years) and descriptors (species) on the factorial axes (principal components [PCs]), as recommended by Legendre and Legendre (1998) for Poisson distributed data. Three centered PCAs were conducted, one for each fish species group (I, II, III). The visualization of covariances between species (columns) and years (lines) on the two first PCs (PC1–PC2) provided a graphical synthetic representation of interannual patterns in juvenile abundances for each group of species. The absolute contributions (i.e., loadings) of each species on PC1 and PC2 were finally examined to isolate species that had a minor contribution (i.e., $<5\%$) in driving interannual patterns in juvenile abundances for each group. This resulted in a total of three species from group III that were ignored in analyses of environment–juvenile abundance relationships.

Environmental data analysis.—Data for all climatic and environmental factors were processed to obtain monthly averages for each variable. These monthly averages were obtained from higher resolution data for environmental factors (minimum of 20 d of data for each monthly average) or directly provided for climatic factors (Table 1). Short gaps in the NOAA–NDBC data (less than 13 h) were replaced with an estimated value determined by linear interpolation between the two closest data points. Due to large gaps in temperature and wind data, two NDBC stations (42007 and DPIA1 in Figure 1) were merged into a single time series. Gaps in the DPIA1 time series were filled using data from station 42007 that was adjusted using a linear fit to account for the minor magnitude differences for each parameter at the individual sites.

Monthly averages were then used to calculate seasonal averages for each factor. These seasonal averages were computed in accordance with the seasonal groups identified in fish data: (1) average of months included in JAI calculations for fish species of group I, February–July (i.e., early spring–early summer); (2) average of months included in JAI calculations for fish species of group II, November–February (i.e., late fall–winter); and (3) average of months included in JAI calculations for fish species of group III, June–November (i.e., summer–fall). Seasonal averages of environmental factors were then analyzed using normed PCA (Legendre and Legendre 1998), which is adapted to the treatment of variables expressed with different units and relies on the computation of correlations between variables (Legendre and Legendre 1998). Three normed PCAs were conducted, one for each seasonal group (I, II, III). The visualization of correlations between environmental factors (columns) and years (lines) on the two first PCs (PC1–PC2) provided a graphical synthetic representation of interannual patterns in environmental conditions for each seasonal group. Moreover, correlations between variables on PC1–PC2 and absolute contributions (i.e., loadings) of variables were used to isolate a small number of independent factors that drove interannual patterns in environmental conditions at each season. Only variables with a contribution greater than 20% were retained, and when two variables were found highly correlated, only the one showing the highest contribution on PC1–PC2 was selected. This resulted in a total of 12 variables (four per seasonal group) that were retained for analyses of environment–juvenile fish abundance relationships.

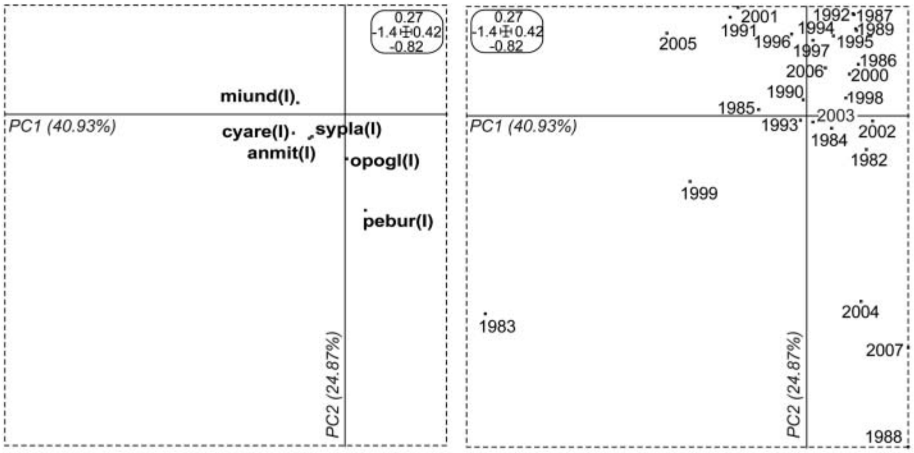
Analysis of relationships between environmental and fish data.—The influence of environmental variables on interannual patterns in juvenile fish abundances was studied using a co-inertia analysis (COIA). Co-inertia analysis is a two-table symmetric coupling method that provides great flexibility in identifying the common structure in a pair of data tables (Dolédec and Chessel 1994; Dray et al. 2003). Co-inertia analysis is based on the statistic of co-inertia, which provides a measure of concordance between two data sets (Dray et al. 2003). The principle of COIA is to search for a vector in the environmental space and a vector in the faunistic space that maximizes the co-inertia between them (Thioulouse et al. 2004). These two vectors are used to define a new ordination plan on which environmental and faunistic variables are compared. Graphical results are then interpreted as in other multivariate methods: the distance of variables to the origin is indicative of their contribution on the ordination plan, and the angle between them measures their relationship (Legendre and Legendre 1998). In the present study, COIA was based on the matching between the coordinates of selected environmental factors on a new normed PCA and of selected fish variables on a new centered PCA (PCA–PCA–COIA; Dray et al. 2003). The normed PCA on environmental factors was based on a matrix composed of 26 lines (years) and 12 columns (four variables per seasonal group). The centered PCA on fish data was based on a matrix composed of 26 lines (years) and 18 columns (six species from group I, seven species from group II, and five species from group III). A Monte-Carlo test with 1,000 permutations of the observations was used to confirm the significance of the co-inertia results (fixed-D test; Dray et al. 2003). All multivariate analyses were performed with the ADE-4 software (Thioulouse et al. 2001).

RESULTS

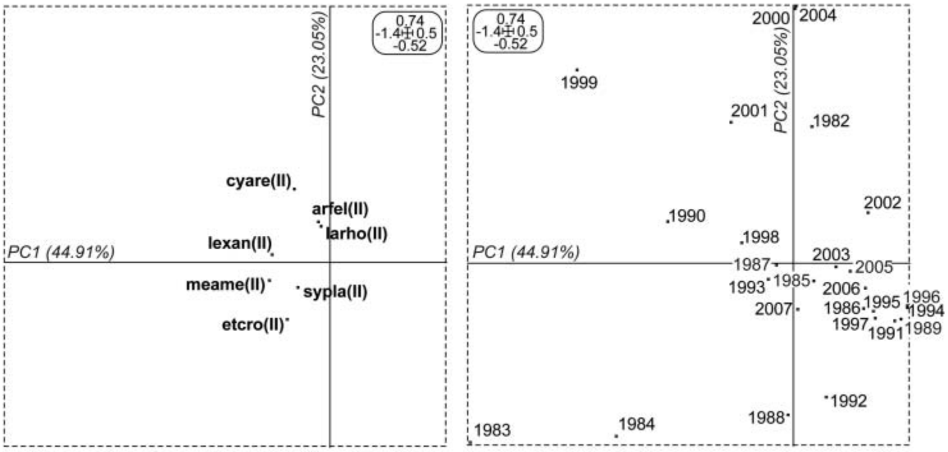
Interannual Variations in Juvenile Fish Abundances

The two first PCs of the PCA conducted on fish group I (species for which juvenile abundances peaked in early spring through early summer; Figure 4a) explained 65.8% of interannual variability in juvenile abundances. Relatively high JAIs

a) Early spring through early summer



b) Late fall and winter



c) Summer and fall

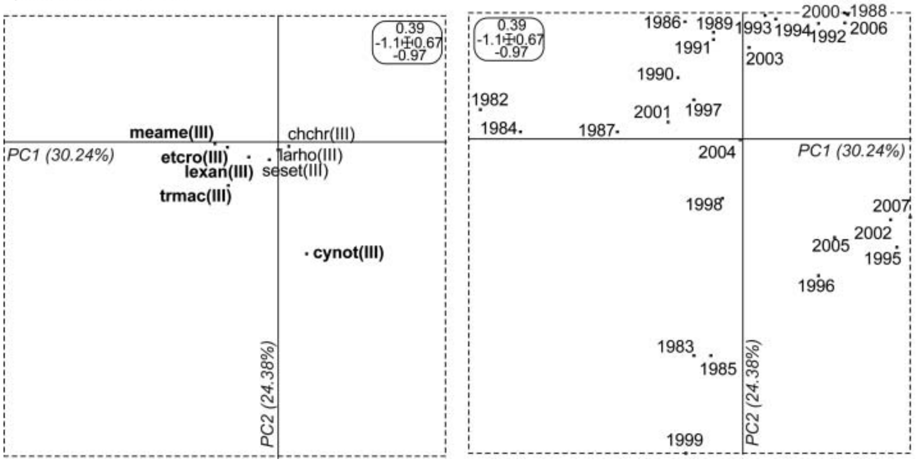


FIGURE 4. Principal components analyses conducted on $\log_{10}(x + 1)$ transformed standardized annual juvenile abundance indices of **(a)** six fish species characterized by juvenile seasonal peaks in early spring through early summer (seasonal group I), **(b)** seven fish species characterized by juvenile seasonal peaks in late fall and winter (seasonal group II), and **(c)** eight fish species characterized by juvenile seasonal peaks in summer and fall (seasonal group III). Covariances between species and projections of years on the principal components 1 and 2 (PC1–PC2) are represented in the left and right columns, respectively. Bold labels indicate species that were retained for co-inertia analysis of environment–juvenile abundance relationships (i.e., species with total contributions $> 5\%$ on PC1–PC2; Table 3). Scales are given in the rounded boxes. Fish species codes and seasonal groups are defined in Table 2. Six species were represented in more than one seasonal group as a result of large juvenile abundances throughout several seasons (Figure 3; Table 2): sand seatrout and blackcheek tonguefish in groups I and II; and fringed flounder, pinfish, spot, and southern kingfish in groups II and III.

TABLE 3. Absolute contributions (%) of environmental variables and fish species on the two first principal components (PC1, PC2, and sum of PC1–PC2) of the normed and centered principal components analyses (PCAs), respectively. For each data set, three PCAs were conducted: one on early spring–early summer values (group I), one on late fall–winter values (group II), and one on summer–fall values (group III). Projections of variables–species and years on the PC1–PC2 plane are depicted in Figures 4 and 5. Codes of environmental variables are defined in Table 1. Fish species codes and groups are defined in Table 2. See Methods for details on the selection of variables and species retained for the co-inertia analysis.

	PCA group I			PCA group II			PCA group III		
Variable or species	PC1	PC2	Sum	PC1	PC2	Sum	PC1	PC2	Sum
Environmental Variables									
soi	22.91	3.85	26.76	13.46	15.33	28.79	3.93	0.54	4.47
nao	8.34	0.34	8.68	1.80	19.63	21.43	9.98	0.64	10.62
AT	16.58	19.77	36.35	25.27	12.56	37.83	14.92	27.54	42.46
WT	8.65	35.04	43.69	24.52	9.96	34.48	25.63	5.48	31.11
WS	3.78	20.09	23.87	6.78	6.79	13.57	11.03	27.68	38.71
uW	0.10	3.24	3.34	0.50	11.68	12.18	4.68	0.32	5.00
vW	9.43	0.02	9.45	10.08	0.00	10.08	0.77	11.47	12.24
AP	25.04	2.55	27.59	8.69	11.51	20.20	28.99	4.00	32.99
RD	5.13	15.06	20.19	8.86	12.49	21.35	0.05	22.28	22.33
Fish Species									
anmit	16.47	4.61	21.08						
arfel				1.13	14.31	15.44			
chchr							1.01	0.14	1.15
cyare	34.76	2.83	37.59	10.97	44.43	55.40			
cynot							7.12	83.10	90.22
etcro				16.39	23.27	39.66	23.32	0.20	23.52
larho				0.61	11.31	11.92	0.00	0.40	0.40
lexan				29.48	0.73	30.21	7.98	1.60	9.58
meame				32.37	1.90	34.27	37.05	0.02	37.07
miund	28.69	0.95	29.64						
opogl	0.05	15.89	15.94						
pebur	5.62	71.68	77.30						
seset							0.72	2.09	2.81
sypla	14.38	4.01	18.39	9.02	4.02	13.04			
trmac							22.76	12.42	35.18

were observed for Gulf butterfish and Atlantic thread herring in 1988, 2004, and 2007; for Atlantic croakers in 1985 and 2005; and for sand seatrout, bay anchovy, and blackcheek tonguefish in 1983 and 1999. For the six species from group I, JAIs were generally lower for 10 out of the 26 years of the time series (years grouped in the top-right part of the PC1–PC2 plane; Figure 4a). These six species all presented total contributions greater than 5% on the PC1–PC2 factorial plane (Table 3).

The two first PCs of the PCA conducted on fish group II (species for which juvenile abundances peaked in late fall and winter; Figure 4b) explained 68.0% of interannual variability in juvenile abundances. Sand seatrout and spot presented relatively high JAIs in 1990, 1999, and 2001 and lower JAIs in 1992. Southern kingfish, fringed flounder, and blackcheek tonguefish had higher JAIs in 1983, 1984, and 1988 and lower JAIs in 1982 and 2002. Hardhead catfish and pinfish presented relatively high JAIs in 2000 and 2004 (Figure 4b). The seven species from group II were generally characterized by low JAIs for 13 out of the 26 years of the time series (years grouped on the bottom-left part of the PC1–PC2 plane; Figure 4b). All seven species presented total contributions greater than 5% on the PC1–PC2 plane (Table 3).

The two first PCs of the PCA conducted on fish group III (species for which juvenile abundances peaked in summer and fall; Figure 4c) explained 54.6% of interannual variability in juvenile abundances. Silver seatrout presented relatively high JAIs in 1995, 1996, 2000, 2002, 2005, and 2007 (Figure 4c). Hogchokers and spot had high JAIs in 1983, 1985, 1998, and 1999 (Figure 4c). Fringed flounder and southern kingfish JAIs were also generally higher in 1982, 1984, and 1987 (Figure 4c). Atlantic bumpers, pinfish, and Atlantic moonfish had minor contributions to interannual patterns in JAIs during this season, their contributions being less than 5% on the PC1–PC2 plane (Table 3). As a result, these three species were ignored for the COIA of environment–juvenile abundance relationships.

Interannual Variations in Environmental Conditions

The two first PCs of the PCA conducted on environmental averages from group I (Figure 5a) explained 48.0% of interannual variability in environmental conditions during early spring through early summer. Six variables had total contributions greater than 20% of the PC1–PC2 plane (Table 3). Years 1990, 1999, 2000, and 2006 were generally characterized by relatively higher water and air temperatures (Figure 5a). Higher river discharge and wind speeds were observed in 1991, 1995, 1997, 1998, and 2003, and the contrary was true in 1985, 1986, 1996, and 2007 (Figure 5a). High values of SOI and atmospheric pressure characterized 1982 and 1989, and the contrary was true in 1983 and 1987 (Figure 5a). In total, four variables were selected as representative of environmental interannual variability in early spring through early summer based on a compromise between their correlations and relative contributions (Figure 5a; Table 3) and consistency with variables selected for the two other seasonal groups (see below): SOI, water temperature, river discharge, and wind speed (Figure 5a).

The two first PCs of the PCA conducted on environmental averages from group II (Figure 5b) explained 50.9% of interannual variability in environmental conditions during late fall and winter. Six variables had total contributions greater than 20% on the PC1–PC2 plane (Table 3). Years 1986, 1989, 1992, and 1997 were characterized by high values of wind speed and river discharge and low values of SOI and atmospheric pressure, whereas the contrary was true for 1985 and 1999 (Figure 5b). The NAO presented relatively high values in 1994 and 2004 and relatively low values in 1995, 2000, and 2002 (Figure 5b). Relatively high water and air temperatures were observed in 1988, 1990, 1998, and 2007, and the contrary was true in 1983, 1987, 1991, 1993, 2003, and 2006 (Figure 5b). Four variables were selected as representative of environmental interannual variability in late fall and winter based on a compromise between their correlations and relative contributions (Figure 5b; Table 3): NAO, water temperature, river discharge, and wind speed (Figure 5b).

The two first PCs of the PCA conducted on environmental averages from group III (Figure 5c) explained 45.7% of interannual variability in environmental conditions during summer and fall. Five variables had total contributions greater than 20% on the PC1–PC2 plane (Table 3). Wind speed appeared relatively high in 1988, 1995, 1999, 2003, and 2005 and relatively low in 1982, 1984, 1985, 1986, 1990, 1993, and 2000 (Figure 5c). Water and air temperatures were relatively high in 1998, 2002, 2004, 2006, and 2007 and were relatively low in 1987, 1991, and 1992 (Figure 5c). Particularly low river discharge occurred in 1982 and 1986, and high river discharge occurred in 1997 (Figure 5c). Four variables were selected as representative of environmental interannual variability in summer and fall based on a compromise between their correlations and relative contributions (Figure 5c; Table 3): atmospheric pressure, water temperature, river discharge, and wind speed (Figure 5c).

Of noticeable interest is also the observation that for two out of the three seasonal groups, river discharge appeared highly negatively correlated with SOI (in early spring–early summer and in late fall–winter; Figure 5a, b). Similarly, a slight positive correlation was observed between NAO and water temperature in late fall and winter, and a strong negative correlation was observed between NAO and water temperature in summer and fall (Figure 5b, c).

Environment–Juvenile Abundance Relationships

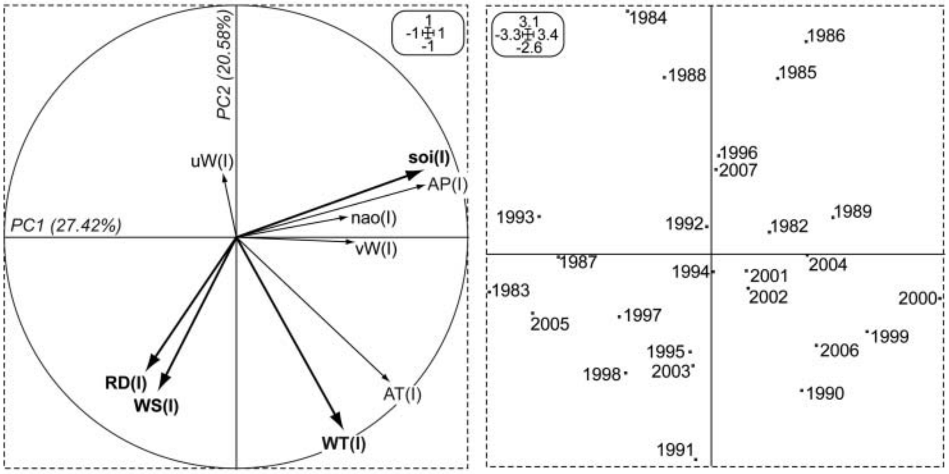
The three first axes of the COIA allowed 78.3% of the common structure between environmental and fish data sets to be visualized (Figure 6a, b). The significance level from the Monte Carlo permutation test was 0.027. However, the total inertia was 0.80, indicating a relatively low statistical agreement between the two data sets. Nevertheless, relationships emphasized by the COIA appeared to be of meaningful ecological sense. The common structure between fish and environmental data sets was mainly driven by river discharge during early spring through early summer, wind speed during late fall and winter, and water temperature during summer and fall (Figure 6a, b; Table 4). For brevity, only the clearest relationships linking environmental factors and species presenting total contributions greater than 10% on the three first axes of the co-inertia will be commented on further (Figure 6; Table 4).

Juvenile abundances of sand seatrout during early spring through early summer were positively associated with river discharge during this season (Figure 6a). Juvenile abundances of Atlantic croakers in early spring through early summer were negatively associated with river discharge and NAO, and to a lesser extent with water temperature, during late fall and winter (Figure 6a, b). Juvenile abundances of Gulf butterfish during early spring through early summer were positively associated with SOI and water temperature and negatively associated with river discharge during this season (Figure 6a, b).

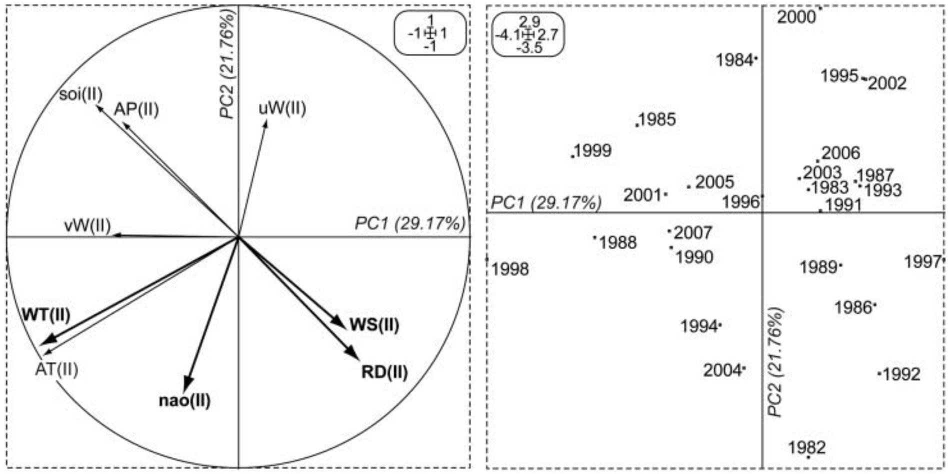
Juvenile abundances of sand seatrout during late fall and winter were positively associated with water temperature and NAO during late fall–winter and were negatively associated with river discharge during late fall–winter and early spring–early summer (Figure 6a, b). Juvenile abundances of fringed flounder during late fall and winter were negatively associated with water temperature and positively associated with river discharge during early spring through early summer (Figure 6a, b). Juvenile abundances of southern kingfish during late fall and winter were negatively associated with wind speed during this season, and were positively associated with river discharge during early spring through early summer (Figure 6a, b).

Juvenile abundances of silver seatrout during summer and fall were positively associated with water temperature and wind speed and negatively associated with atmospheric pressure

a) Early spring through early summer



b) Late fall and winter



c) Summer and fall

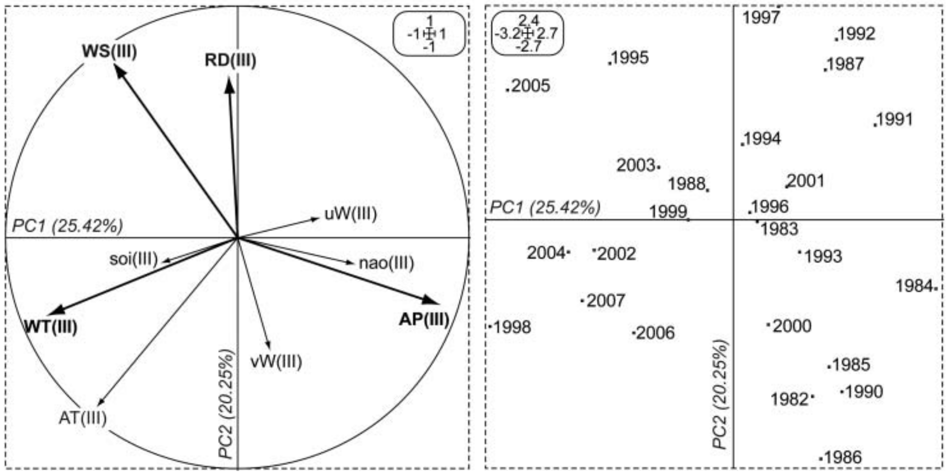


FIGURE 5. Principal components analyses conducted on normalized environmental factors averaged over **(a)** early spring through early summer (i.e., February–July; seasonal group I), **(b)** late fall and winter (November–February; seasonal group II), and **(c)** summer and fall (i.e., June–November; seasonal group III). Correlations between environmental factors and projections of years on the principal components 1 and 2 (PC1–PC2) are represented in the left and right columns, respectively. Bold labels indicate variables that were retained for co-inertia analysis of environment–juvenile abundance relationships (i.e., independent variables with a total contribution > 20% on PC1–PC2; Table 4). Scales are given in the rounded boxes. Codes for environmental factors are defined in Table 1.

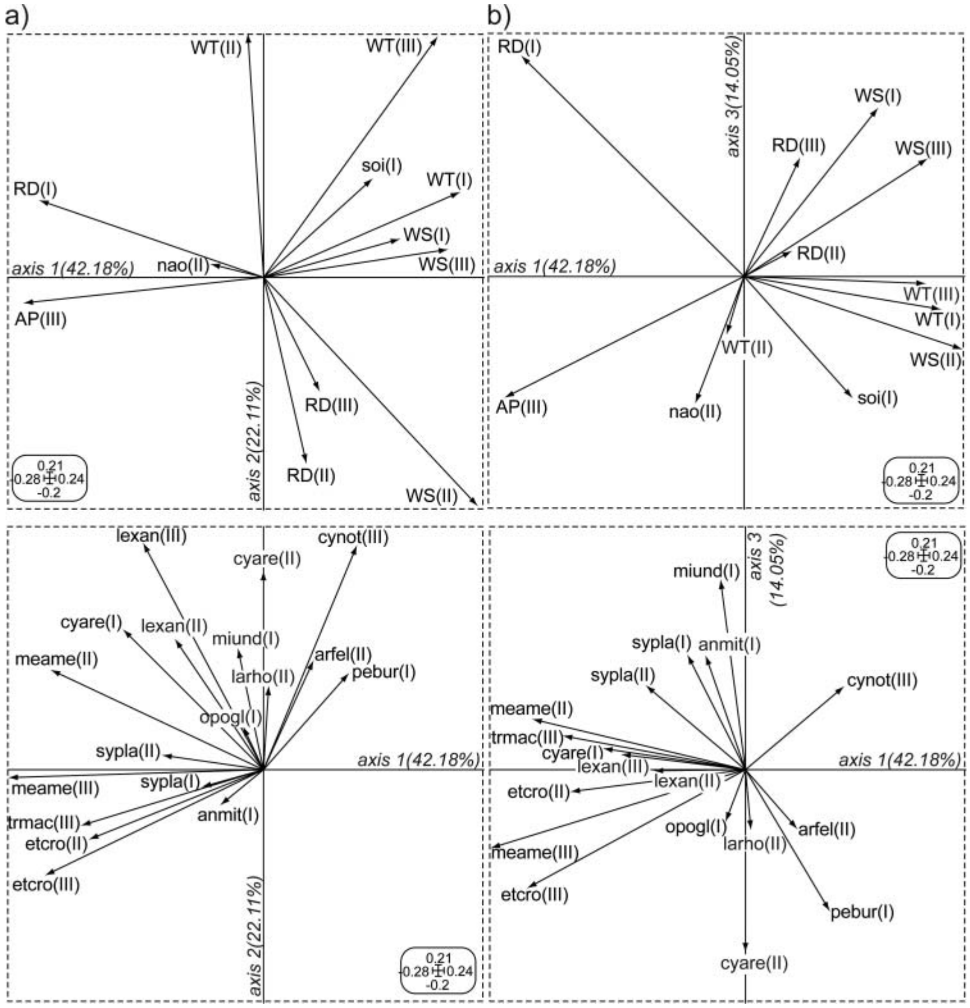


FIGURE 6. Co-inertia analysis (see Methods) coupling 12 normalized environmental factors (four variables/seasonal group) and $\log_{10}(x + 1)$ transformed standardized juvenile abundance indices of 18 fish species (six species from seasonal group I, early spring–early summer; seven species from seasonal group II, late fall–winter; and five species from seasonal group III, summer–fall; Table 2) on **(a)** axes 1 and 2 of the co-inertia and **(b)** axes 1 and 3 of the co-inertia. Projections of environmental variables and fish species are given in the top and bottom panels, respectively. Total inertia is 0.80, and the percentage of variance explained is 64.3% on axes 1 and 2 and 56.2% on axes 1 and 3. Significance level (*P*) of the fixed-*D* Monte Carlo permutation test with 1,000 permutations was 0.027. Fish species codes and seasonal groups are defined in Table 2; environmental factor abbreviations are defined in Table 1.

during this season (Figure 6a, b). Juvenile abundances of fringed flounder during summer and fall were positively associated with atmospheric pressure and negatively associated with wind speed during this season, and were positively associated with river discharge during early spring through early summer (Figure 6a, b). Juvenile abundances of spot during summer and fall were positively associated with river discharge during early spring through early summer (Figure 6a). Juvenile abundances of southern kingfish during summer and fall were positively associated with atmospheric pressure and negatively associated with wind speed during this season, and were positively associated with river discharge and negatively associated with wind speed during early spring through early summer (Figure 6a, b). Finally, juvenile abundances of hogchokers during summer and fall were positively associated with atmospheric pressure and negatively associated with wind speed during this season, and were positively associated with river discharge and negatively associated with water temperature and SOI during early spring through early summer (Figure 6a, b). Overall, river discharge during early spring through early summer appeared to be related to juvenile fish abundances of many species from several seasonal groups and also presented the highest total contributions of all environmental variables on the three first axes of the co-inertia (sum of axes 1, 2, and 3 = 50.4%; Table 4).

DISCUSSION

Whereas a variety of local environmental variables were identified as potential controls of juvenile fish abundances in our study, three of them appeared to affect juvenile dynamics of

TABLE 4. Absolute contributions (%) of fish species and environmental variables on the first three axes of the co-inertia analysis. Projections of environmental variables and fish species on axes 1–2 and axes 1–3 of the co-inertia are depicted in Figure 6a and 6b. Codes of environmental variables are given in Table 1; fish species codes are defined in Table 2 (seasonal groups: I = early spring–early summer; II = late fall–winter; III = summer–fall).

Species or variable	Axis 1	Axis 2	Axis 3
Fish Species			
anmit(I)	0.50	0.39	7.63
cyare(I)	6.50	7.77	0.28
miund(I)	0.21	5.47	22.43
opogl(I)	0.10	0.55	1.37
pebur(I)	2.29	3.52	12.21
sypla(I)	1.07	0.09	7.86
arfel(II)	0.77	4.42	1.91
cyare(II)	0.00	15.52	20.49
etcro(II)	10.09	1.91	0.28
larho(II)	0.00	2.47	1.82
lexan(II)	2.56	6.59	0.00
meame(II)	15.23	3.96	1.60
sypla(II)	3.18	0.07	4.18
cynot(III)	3.08	20.95	4.07
etcro(III)	16.09	4.45	8.87
lexan(III)	4.90	20.54	0.13
meame(III)	22.36	0.02	4.09
trmac(III)	10.99	1.21	0.69
Environmental Variables			
soi(I)	3.83	3.77	9.01
WT(I)	12.87	2.91	0.67
WS(I)	6.00	0.54	17.77
RD(I)	16.96	2.39	31.02
nao(II)	0.75	0.05	9.60
WT(II)	0.08	24.75	1.68
WS(II)	16.33	22.07	3.57
RD(II)	0.61	13.63	0.32
WT(III)	10.89	24.41	0.03
WS(III)	11.20	0.30	8.61
AP(III)	19.44	0.25	9.28
RD(III)	0.98	4.88	8.38

many species: river discharge, wind speed, and water temperature. Climatic indices that were representative of large-scale, oceanwide climatic conditions (e.g., SOI and NAO) were also found to play a role.

River Discharge

River discharge appeared to have a major effect on interannual variations in juvenile fish abundances in the Mobile Bay area. This result is consistent with previous studies reporting the influence of river discharge on larval or juvenile fish abundances (or both) along the East Coast (Crecco et al. 1986; Rulifson and Manooch 1990; North and Houde 2003) and West Coast (Turner and Chadwick 1972; Kimmerer et al. 2001) of the United States. However, the studies cited above were conducted on anadromous fish species (striped bass *Morone saxatilis*, white perch *Morone americana*, and American shad *Alosa sapidissima*) that directly utilize riverine habitats during the larval or juvenile stages. Our results indicate that juvenile abundances of nonanadromous coastal marine fish species are also affected by river discharge variability in waters off Mobile Bay, as has been suggested for Gulf menhaden *Brevoortia patronus*, king mackerel *Scomberomorus cavalla*, and Atlantic bumpers in the Mississippi River delta (Grimes and Finucane 1991; Govoni 1997). In Europe, variability in recruitment of European anchovy *Engraulis encrasicolus* (in the Mediterranean Sea, the Bay of Biscay, and the Black Sea), European whiting *Merlangius merlangus* (in the Black Sea), and European bass *Dicentrarchus labrax* (in Portugal) has also been linked to variability in river discharge within their respective water bodies (Daskalov 1999, 2003; Lloret et al. 2004; Planque and Buffaz 2008; Vinagre et al. 2009).

A likely explanation for the observed effect of river discharge on juvenile abundances of these nonanadromous species may be the stimulation of coastal marine primary and secondary production by terrestrial nutrient inputs (Day et al. 1989), which in turn affects the abundance and distribution of zooplanktonic prey of larval and juvenile fish (Kimmerer 2002; Martino and Houde 2010). Moreover, the inputs of the freshwater layer in coastal surface waters affect water column stratification, which also influences the distribution of fish larvae and juveniles and their zooplankton food in the estuaries (Mann 1993; Kimmerer 2002; Martino and Houde 2010). The influence of river discharge on juvenile fish abundances may thus result either from variable feeding conditions for larval and juvenile fish or from variability in salinity habitats associated with water column stratification. In the present study, among species for which juvenile abundances peaked in summer and fall (e.g., the fringed flounder, spot, southern kingfish, and hogchoker) or in late fall and winter (e.g., the Atlantic croaker, sand seatrout, fringed flounder, and southern kingfish), many were associated with river discharge during early spring through early summer, consistent with a probable effect of river discharge on larval and early juvenile feeding conditions.

The present study also demonstrated a correlation between river discharge and large-scale climatic conditions (SOI), illustrating the sensitivity of watershed processes to global climate variation (Nohara et al. 2006). More specifically, the fluctuations of El Niño–La Niña phases, reflected by SOI in the present study, have been shown to affect precipitation patterns in the study region, which in turn strongly affect river discharge interannual variability (Srivastava et al. 2010). Our results from the north-central Gulf of Mexico, along with those from other marine systems, thus suggest that large-scale variations in discharge arising from climate variability as well as from human watershed regulations (such as dams) can strongly affect coastal marine fish population dynamics.

Wind

The JAIs of four species—namely southern kingfish during late fall–winter and summer–fall and silver seatrout, fringed flounder, and hogchokers during summer and fall—were found to relate with wind speed in the study area. Variations in juvenile abundances of marine fishes from a wide diversity of coastal systems, including the U.S. East Coast (Hare and Cowen 1996; Luettich et al. 1999), South Africa (Hutchings et al. 1998), Denmark (Nielsen et al. 1998), and Japan (Nakata et al. 2000), have been linked to wind-driven mechanisms of larval transport. However, in contrast to larval fish, juvenile fish examined in the present study were well developed and able to control their swimming direction. Wind is also known to affect vertical mixing of the water column, thereby influencing primary and secondary production processes and leading to variable feeding conditions for juveniles (Mann 1993). Turbulence generated by wind stress also affects encounter rates of juvenile fish with their zooplanktonic prey (Mann 1993). In addition, wind stress can also be an important driver of coastal circulation, thus affecting the distribution of juvenile zooplanktonic prey (North and Houde 2003). However, most of the relationships found between wind speed and juvenile abundances in the present study were negative and were generally found to occur with no seasonal lags (e.g., juvenile abundances of silver seatrout and fringed flounder during late fall and winter were negatively related to wind speed during this season). This tends to suggest that strong winds resulted in smaller numbers of juveniles collected at the three sampling stations. Consequently, it remains difficult to disentangle an effect of wind stress on species catchability from its potential influence on water column structure and associated larval transport, larval and juvenile feeding, or both.

Temperature

In the present study, variations in juvenile abundances of many species were related to water temperature variations (e.g., the Atlantic croaker and Gulf butterfish during early spring through early summer; sand seatrout and fringed flounder during late fall and winter; and silver seatrout and hogchoker during summer and fall; Figure 6a, b). Temperature effects on juvenile fish abundances have been widely documented in a variety of marine ecosystems but primarily for fishes in northern latitudes, such as Atlantic cod *Gadus morhua* (North Atlantic), European anchovy and European whiting (Black Sea), walleye pollock *Theragra chalcogramma* (Alaska), European sprat *Sprattus sprattus* (Baltic Sea), and others (Daskalov 1999; Planque and Frédou 1999; MacKenzie and Köster 2004; Ciannelli et al. 2005). Temperature variations were also shown to be correlated with NAO in late fall–winter and summer–fall in the present study (Figure 5b, c). This is consistent with observations from the U.S. East Coast by Hare and Able (2007), who proposed that winter severity, and in particular minimum temperature (which tracked NAO variability well), was the main environmental control of winter-spawned Atlantic croaker recruitment success. In the present study, the relationship between Atlantic croaker abundance during early spring through early summer and water temperature during late fall and winter also reflected a similar relationship, tracking variations of NAO during late fall and winter (Figure 6b). However, this relationship was found to be negative, such that juvenile abundances of Atlantic croakers during early spring through early summer appeared to increase when water temperature and NAO during fall and winter decreased. This inconsistency between Hare and Able's (2007) result and our observations could be accounted for by the fact that Atlantic croakers are at the edge of the species' biogeographical range in the northeast continental shelf of the United States, where Hare and Able (2007) conducted their study. Conversely, the northern Gulf of Mexico is not only characterized by the highest relative probability of occurrence for this species (Froese and Pauly 2010) but also by much less severe winters, which could explain a different relationship between this species and temperature conditions than those observed elsewhere. This is consistent with the hypothesis that correlations between environmental factors and juvenile fish abundances vary as a function of relative locations within the biogeographical ranges of fish species (Myers 1998).

Other species' abundances were related to water temperature in our study: positive relationships were observed for Gulf butterfish in early spring through early summer, for silver seatrout in summer and fall, and for sand seatrout during late fall and winter (Figure 6a, b). Conversely, fringed flounder during late fall and winter and hogchokers during summer and fall were negatively associated with water temperature during early spring through early summer (Figure 6a, b). Gulf butterfish spawn from fall through spring in the study area (Pattillo et al. 1997; Hernandez et al. 2010a, 2010b). Growth and survival of larvae and early juveniles of this species could thus be favored by warm conditions during early spring through early summer, explaining the positive relationship we observed with water temperature during early spring through early summer for this species. Conversely, fringed flounder and hogchokers spawn in spring and summer in the region (Pattillo et al. 1997; Hernandez et al. 2010a, 2010b). Larval and early juvenile survival for these two species could thus be favored in years with cool water temperatures in spring and summer, contributing to higher juvenile abundances of fringed flounder in late fall and winter and of hogchokers in summer and fall. Such effects of water temperature on larval and early juvenile growth and survival during spring and summer (contributing to variable juvenile abundances in summer, late fall, and winter) were also reported for larval striped bass along the U.S. East Coast (Secor and Houde 1995; Rutherford et al. 1997).

Other Potential Drivers

Although the multivariate approach used in this study identified the major environmental variables involved in shaping multispecies patterns in juvenile fish abundances, the total inertia remained relatively low (0.80), indicating that other biological and environmental factors that have not been considered in the present study play an important role. For example, dissolved oxygen concentrations (particularly the occurrence of hypoxic water masses during summer) have been shown to contribute to the dynamic of coastal marine communities in the Mississippi River delta (Rabalais and Turner 1998). The higher probability of occurrence of hypoxic events during warm years may also further help in explaining some of the negative relationships between juvenile abundances and water temperature observed in the present study (e.g., for the fringed flounder and hogchoker). Such hypoxic events indeed occur every summer in Mobile Bay (Park et al. 2007) and the Mississippi–Alabama shelf (Brunner et al. 2006), and they may affect juvenile abundances of fish species whose larvae or juveniles (or both) are found during summer in the study area. Similarly, seasonal jellyfish invasions reported in coastal Alabama waters, which are also more frequent during warm conditions, could also influence juvenile abundance patterns for some coastal fish species (Graham et al. 2003).

Biological variables, such as spawning stock biomass, may further help to increase the amount of explained variability in juvenile abundances for some of the species examined (Clark and Hare 2002; Ottersen et al. 2006). Sand seatrout, Atlantic croakers, and southern kingfish, for example, are heavily harvested in our region (NOAA 2006), and all three species are bycatch of the shrimp industry (Diamond et al. 2000; Steele et al. 2002). The influence of general harvest pressure and shrimp fishery effort on juvenile abundance and survival of these fishes in our region is an interesting area of research and should be given particular attention in a separate analysis. Finally, single-species analyses need to be conducted to account for the potential additive effects of several environmental and biological factors on fish juvenile dynamics. Such single-species analyses should be conducted at first on species for which otoliths records are available and can be used to build the size-at-age relationships requested for the development of age-specific models (e.g., Atlantic croaker).

To conclude, this study provides the first investigation of environmental influences on juvenile fish dynamics by using a multispecies and multivariable approach in the north-central Gulf of Mexico, outside of the Mississippi River delta. It confirms the importance of river discharge for fish dynamics in the region and for nonanadromous coastal marine fish species in general. Consistent with previous studies, juvenile fish abundances in river-dominated, productive coastal ecosystems appear to track some of the large-scale climate patterns represented by synthetic indices such as the SOI or NAO and by local environmental conditions, among which river discharge is prevailing. This result has strong implications for management since it emphasizes the strong associations between watershed processes and the production of adjacent coastal fisheries.

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