

Patterns and drivers of the demersal fish community of Chesapeake Bay

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ABSTRACT: Large-scale research on the environmental, biological, and anthropogenic drivers of fish distributions, abundances, and community structure can identify patterns and trends within systems, provide mechanistic insight into ecosystem functioning, and contribute to ecosystem-based fisheries management. This study synthesized 10 yr of extensive fisheries-independent bottom trawl data (2002 to 2011) to evaluate drivers of demersal fish community structure in Chesapeake Bay, the largest estuary in the United States. Changes in community composition were assessed using constrained correspondence analysis. Also, aggregate community metrics (species richness, Simpson diversity, and catch-per-unit-effort [CPUE] of species groups) were modeled using generalized additive models. Five species (Atlantic croaker, white perch, spot, striped bass, and summer flounder) accounted for >75% of the total trawled biomass. The demersal fish community was primarily structured by the latitudinal salinity gradient that largely differentiated anadromous fishes from coastal shelf spawning species and elasmobranchs, with low overall CPUE and richness in mesohaline waters. Low dissolved oxygen concentrations (below ~4 mg l⁻¹) greatly suppressed CPUE and diversity metrics and appeared to displace fish biomass toward the northern and southern edges of the bay's mainstem channel. Water temperature and month strongly influenced the seasonal dynamics of community composition and metrics. Community composition and biomass shifted after 2007, with a substantial decline in annual CPUE of some species groups. Recruitment and fishing indices for the dominant species were the best predictors of the interannual patterns in community metrics, outperforming various other climatic and biological annual-scale covariates.

KEY WORDS: Community structure · Demersal fishes · Chesapeake Bay · Environmental conditions · Species richness · Species diversity · Hypoxia · Bottom trawl survey

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INTRODUCTION

Understanding the influences of environmental and biological factors on fish abundance, distribution, population dynamics, and catch has been an integral objective of fisheries science since the inception of the field (Smith 1994). Information on these ecological processes and relationships helps to determine management actions designed to promote sustainable use of fisheries resources, particularly in an ecosystem-based fisheries management (EBFM) context (Link 2010). The growing attention to (and even mandated utilization of) EBFM approaches has fos-

tered renewed appreciation of multispecies and community-based research within ecosystems. This highlights the need for continued research and monitoring to support ecosystem modeling efforts (Latour et al. 2003, Link 2010). Research linking environmental and anthropogenic drivers with fish dynamics is particularly important in estuarine and coastal waters, where productivity, fishing pressure, and anthropogenic stresses are most intense (Longhurst et al. 1995, Jackson et al. 2001, Worm et al. 2009).

Within the United States, Chesapeake Bay is a model system to study the many factors influencing fish dynamics in an estuarine environment because

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of its large area, high productivity, well-studied nature, and long fishing history. The Chesapeake Bay ecosystem supports a large number of fish species and is a critical nursery and foraging habitat for many migratory fishes (Murdy et al. 1997, Able & Fahay 2010). As with most estuarine and coastal environments, the system is influenced by a multitude of stressors that include eutrophication, fishing, and climate change. Eutrophication has promoted phytoplankton growth, shifted production from benthic to pelagic habitats, contributed to the growing hypoxia problems, decreased water clarity, and also degraded important submerged vegetated habitats (Nixon 1995, de Leiva Moreno et al. 2000, Kemp et al. 2005). Industrialized exploitation of finfish and shellfish since the late 19th century has drastically modified the fish community and fish habitat, as exemplified by the collapse of and subsequent moratorium on several fisheries (e.g. American shad, river herring, and Atlantic sturgeon), reductions of eastern oyster populations to ~1% of virgin abundance (Rothschild et al. 1994, Wilberg et al. 2011), and the collapse and recovery of striped bass populations (Richards & Rago 1999). Climate change is predicted to affect water temperature, CO₂ concentrations, water acidity, sea level, precipitation, and storm intensity in Chesapeake Bay, with consequences for the physiological suitability of the bay for species, the extent of juvenile fish habitats, the quality and timing of plankton production, and the severity of bottom hypoxia (Najjar et al. 2010). The various stressors of the bay combine with natural environmental conditions to structure the occupying fish community in terms of abundance, distribution, and diversity of member species. Evaluation of these ecological relationships and the dynamics of the fish community is an important component to facilitating EBFM (Link 2010), aiding in the ongoing development of ecosystem models (e.g. Christensen et al. 2009), and predicting community responses to changes in the severity of system stressors.

Despite the large research efforts within Chesapeake Bay, the majority of studies examining fish community structure have concentrated on smaller spatial and temporal scales (e.g. Orth & Heck 1980), riverine systems (Carmichael et al. 1992, Wagner 1999, Wagner & Austin 1999), or juvenile fishes (Jung & Houde 2003, Woodland et al. 2012). Only 1 study focused on bay-wide patterns in species assemblages and community structure (Jung & Houde 2003); however, it was restricted to ecological patterns of small (3 to 26 cm), non-benthic fishes as sampled with a mid-water trawl. To date, no published study has

quantitatively examined and described the factors influencing the community structure of the bay's benthic and demersal fish fauna at a large spatial scale, mostly due to the lack of available data. This monitoring and research gap contributed to the initiation in 2002 of the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAAP), a large-mesh bottom trawl survey designed to capture late juvenile and adult demersal fishes in the bay. The survey provides critical biological and ecological data in support of ecosystem modeling and fisheries management (Latour et al. 2003, Bonzek et al. 2011).

The current study utilized 10 yr of extensive ChesMMAAP trawl data to examine patterns in the community structure of fishes in the mainstem of the bay and evaluated the role of different environmental, biological, and anthropogenic factors in affecting structural changes. Several catch and biodiversity metrics were used to characterize community structure in a multispecies context. Community metrics were modeled as functions of various explanatory covariates hypothesized or documented to influence fish populations or system dynamics. Dominant species in Chesapeake Bay were grouped based on life history characteristics to capture different modes of bay utilization. The specific objectives were to (1) characterize spatial and temporal patterns in demersal fish community structure and aggregate community metrics, and (2) relate community structure and metrics to physical and biological factors at both smaller and larger spatio-temporal scales. These analyses benefit ongoing EBFM and modeling efforts in Chesapeake Bay by providing basic information on community ecology, time series of catch-per-unit-effort (CPUE) trends, simple indicators of ecosystem status, and a 10 yr frame of reference for evaluating ongoing community responses to natural and anthropogenic stressors.

MATERIALS AND METHODS

Study area

Chesapeake Bay, located in the mid-Atlantic region of the east coast of the United States (Fig. 1), is the largest estuary in the country and one of the largest in the world (Kemp et al. 2005). Large freshwater inputs from the Susquehanna River in the north and multiple rivers along the western shore generate an increasing salinity gradient along the bay's 320 km length. The bay is relatively shallow,

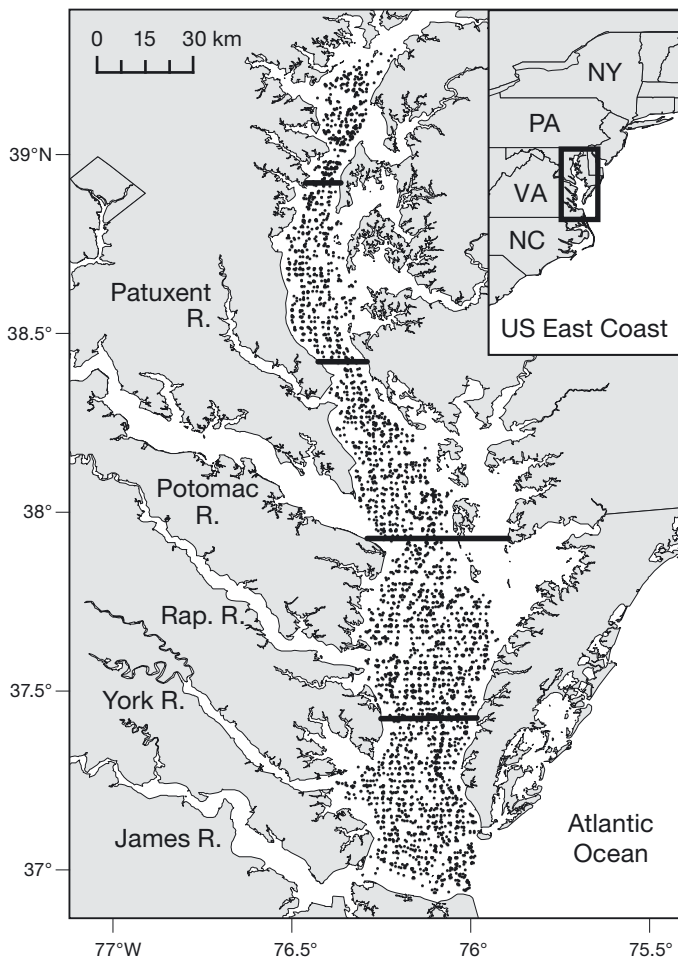


Fig. 1. All stations ($n = 3640$) sampled by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAAP) in March, May, July, September, and November from 2002 to 2011. Dark horizontal lines delineate 5 regional strata (Region 1 in the upper bay and Region 5 in the lower bay). Rap. R. = Rappahannock River

with an average depth of 6.5 m (Kemp et al. 2005), but a deeper, (20 to 30 m) narrow channel runs along its center north of the Rappahannock River. The annual temperature range of bay waters (0 to 30°C) is one of the most extreme of any coastal ecosystem (Murphy et al. 1997).

Field data

Data for this study were collected by the ChesMMAAP bottom trawl survey from 2002 to 2011. The survey operates 5 cruises a year (March, May, July, September, and November), sampling approximately 80 stations per cruise. Stations were selected based

on a stratified random design, with strata defined by water depth (3.0 to 9.1 m, 9.1 to 15.2 m, and >15.2 m) and latitude (5 latitudinal regions; Fig. 1). Sampling locations for each cruise were selected randomly (limited to trawlable areas), and sampling intensity was proportional to the surface area of the stratum. The survey utilizes a 13.7 m (headrope length), 4 seam balloon trawl with 7.6 cm mesh in the codend to target late juvenile and adult fishes (Bonzek et al. 2011). At each station, temperature, salinity, dissolved oxygen (DO), and depth were measured using a Hydrolab MS5 sonde prior to sampling. Real-time net mensuration equipment (NETMIND trawl monitoring system, Northstar Technical) was used to monitor net geometry, ensure consistent gear behavior, and to allow for accurate estimation of area swept. Tows were conducted in daylight hours in the direction of the tidal current at speeds of approximately 3 knots (5.6 km h⁻¹) and were typically 20 min in duration. However, duration of tows at stations with hypoxic bottom waters (DO < 2 mg l⁻¹) were generally restricted to 10 min to maximize cruise efficiency, as the catches at these stations are typically zero or very low. Some tows were also reduced to avoid interactions with commercial fishing gears. Immediately after collection, the catch was sorted by species and size class (if distinct size classes were evident), enumerated, and weighed. Subsamples of captured species and size classes were processed for individual length and weight.

For this study, analyses were restricted to demersal fishes and excluded pelagic fishes, which are not sampled effectively by the bottom trawl. Demersal species with <10 individuals or <1 kg captured were omitted from analyses, as these represent rare species or species that are not adequately sampled by the survey gear. CPUE (kg km⁻²) was calculated for each tow from area swept measurements (mean net width multiplied by towed distance measured by onboard GPS) for the following species groups: all fishes (FISH), anadromous fishes (ANAD), coastal shelf spawners (COAS), and elasmobranchs (ELAS). Catchability was assumed to be constant over time, space, and species. Species classified as ANAD or COAS were restricted to those that accounted for >5% of total biomass, and ELAS species were restricted to >0.5% of total biomass. The ANAD, COAS, and ELAS groupings were chosen because they (1) segregate species by life history characteristics, (2) exhibit differential recruitment patterns (Wood & Austin 2009), (3) represent distinct patterns of habitat usage (Murphy et al. 1997), and (4) account for >90% of the total biomass sampled.

Multivariate analysis

A multivariate statistical technique was used to explore patterns within the demersal fish community inhabiting Chesapeake Bay. Relationships among species CPUE and environmental variables were assessed using constrained (or canonical) correspondence analysis (CCA) (Ter Braak 1986). CCA, commonly used in ecological studies of communities, is an ordination technique that extracts the major gradients in a multivariate dataset that can be explained by different explanatory variables (McGarigal et al. 2000). CCA combines a weighted multiple linear regression with ordination and assumes that species have a unimodal response across the gradient of each explanatory variable (Borcard et al. 2011). The explanatory variables in the current study included physical characteristics of bottom water (temperature, salinity, DO), spatial attributes (depth, latitude), and temporal periods (month, year). Significance of explanatory factors (at the 5% significance level) was evaluated using a permutation test (Legendre & Legendre 1998). Prior to analysis, individual species that accounted for <0.5% of total trawled biomass were grouped together as minor species, as CCA can be sensitive to rare species (Borcard et al. 2011).

Univariate analyses

Community characteristics were summarized into 3 general univariate community metrics for analysis: species richness, Simpson's index of diversity, and aggregate CPUE (for FISH, ANAD, COAS, and ELAS groups). These metrics were chosen because they (1) describe different aspects of assemblages such as biological diversity and biomass; (2) are commonly measured and reported, facilitating comparisons with other studies; and (3) have been proposed (or are considered) as useful ecosystem indicators for EBFM and ecosystem modeling (Rice 2000, Methratta & Link 2006, Link 2010). Although aggregate CPUE metrics can be biased and hyper-responsive indices of community abundance if species catchabilities are not constant (Maunder et al. 2006, Kleiber & Maunder 2008), we chose to include them because they (1) rely on fishery-independent data that are less prone to temporal or spatial change in species catchabilities than fishery-dependent data, (2) have a precedent of use in EBFM literature (Rice 2000, Methratta & Link 2006, Link 2010), (3) preserve the directionality of community changes (Kleiber & Maunder 2008), and (4) accurately represent the trends

of the dominant individual species (A. Buchheister unpubl. data). Biological diversity was described with 2 common diversity metrics, species richness (S ; the number of species in a tow) and Simpson's diversity index (D), calculated at each station. D was calculated as:

$$D = 1 - \sum_{i=1}^S p_i^2 \quad (1)$$

where p is the fraction of the total biomass belonging to the i th species at a station, given that at least 1 species was captured (Magurran 2004). Diversity values, D , are constrained between 0 and 1 and increase with greater S or with a more even biomass distribution across captured species. As is commonly done, stations with no species captured ($S = 0$) were omitted from D calculations because they would result in high diversity estimates ($D = 1$) at those stations.

Generalized additive models (GAMs) were used to model the response of the 3 univariate community metrics as functions of explanatory variables. GAMs provide a general and powerful modeling framework that allows responses to be modeled with both a parametric component (equivalent to generalized linear modeling) and a non-parametric component (Wood 2006, Zuur et al. 2009). The non-parametric component relies on smoothing functions for covariates, permitting the covariates to have non-linear effects on the response that are dictated by the data and not by *a priori* assumptions of relationships among the response and covariates. Explanatory variables were identical to those used for the multivariate analyses. Year and month of sampling (YR and MO , respectively) were modeled parametrically as categorical factors. The continuous covariates included latitude (LAT , decimal degrees), depth (DE , m), bottom DO (DO , mg l⁻¹), bottom salinity (SA), and bottom water temperature (T , °C). These continuous covariates were smoothed non-parametrically and were chosen because they are commonly measured and known to influence fish distribution and abundance (Murdy et al. 1997). The full GAM was defined as:

$$y_i = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) \cdot MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i \quad (2)$$

where y_i is a given response variable for station i , α_1 and α_2 are the estimated mean effects for each level of YR and MO , and the g_1 to g_5 are nonparametric smoothing functions for each covariate. A space-time interaction was included in the model (i.e. separate latitude smoothers for each month) because this was the only first-order interaction of concern based on

thorough graphical analyses. Thin-plate regression splines were used as the basis to smooth all covariates. The intercept, a , scales the model prediction to the appropriate level of the response because each smooth estimate (g) is constrained to average to zero over the entire dataset (Ciannelli et al. 2008). The residual error, e_i , is assumed to be independent and identically distributed, with a mean of zero and constant variance. Both CPUE and D were modeled using a normal distribution; however, CPUE was log transformed [$\log_e(\text{CPUE} + 0.1)$] prior to analysis to account for the positively skewed distribution of these data. Species richness data were modeled with a negative binomial distribution, appropriate for overdispersed count data (Zuur et al. 2009). Graphical and statistical analyses indicated that differences in sampling effort (area swept) did not have discernible effects on S or D across stations and that all tows were sufficiently long to capture a representative sample of biological diversity; therefore no sampling effort adjustments were needed in GAMs for S or D (e.g. an offset *sensu* Zuur et al. [2009] was not included in the GAMs).

Model selection was employed to determine the best combination of explanatory variables for predicting changes in the response metrics. Akaike's information criterion (AIC) was used to determine whether reduced models were more strongly supported by the data than the full model in Eq. (2) (Burnham & Anderson 2002, Zuur et al. 2009). For all models, stations with incomplete water quality information ($n = 230$; 6.3% of stations) were omitted from the analysis. Collinearity among covariates was examined with Pearson correlation coefficients and variance inflation factors (VIF) (Zuur et al. 2009). Although correlated, salinity and latitude were both retained because VIF values were not above the cutoff of 5 (Zuur et al. 2009) and because they provide information on different environmental characteristics.

Examining interannual patterns in data

Several annual-scale covariates were hypothesized to contribute to interannual variability in species composition and community metrics of the Chesapeake Bay demersal fish fauna (Table 1). Model selection approaches were used to compare among different annual covariates to infer which variables best explained the interannual trends in the community metrics and to evaluate the strength of evidence for different mechanisms influencing fish community structure.

Annual-scale covariates were classified into categories representing the predominant mode of influence on fishes: climate, fishing, population size, and recruitment (Table 1). Climate variables included the principal components-based index of the North Atlantic Oscillation for winter months (Hurrell 2012); mean daily discharge from the Susquehanna River (the bay's largest tributary) from February to May (Schubel & Pritchard 1986, Kemp et al. 2005, USGS 2012); summertime volume of hypoxic water ($\text{DO} < 2 \text{ mg l}^{-1}$) in the bay (D. Scavia & M. A. Evans pers. comm.); minimum of monthly mean temperatures for winter months (December to March) at Gloucester Point, VA, following Hare & Able (2007) (SERCC 2012, VIMS 2012); and mean daily chlorophyll a ($\mu\text{g l}^{-1}$) estimates (March to August) of bay-wide surface waters interpolated from Chesapeake Bay Program data (M. Brush unpubl. data). The fishing category of covariates included annual Chesapeake Bay (MD and VA) and coast-wide (NC to MA) landings calculated as the sum of recreational and commercial catches as reported by the National Marine Fisheries Service (NOAA 2012). The sum of female spawning stock biomasses (SSBs) was used as an indicator of coast-wide population size for the ANAD and COAS groups. SSB estimates were restricted to species with available data from stock assessments: Atlantic croaker, summer flounder, and striped bass (ASMFC 2010, ASMFC 2011, Terceiro 2011). Recruitment covariates included composite young-of-the-year (YOY) recruitment indices for the ANAD and COAS separately and for the 2 groups combined (ANAD + COAS). Composite indices were calculated as the average of z-standardized recruitment indices for appropriate species weighted by each species' relative biomass from all ChesMMAP cruises. Recruitment indices were obtained from the Maryland Department of Natural Resources (ANAD species; Durell & Weedon 2011) and the Virginia Institute of Marine Science (VIMS) Juvenile Fish and Blue Crab Trawl Survey (COAS species; Tuckey & Fabrizio 2011). All annual covariates were standardized to have a mean of zero and standard deviation of 1 for consistency in model comparisons.

The community metrics (S , D , CPUE) were aggregates of many species and year classes of fishes. Effects of annual covariates on adult and community metrics may have been delayed by several years if the mechanism of control was through recruitment processes. To account for multiple year classes and delayed effects, annual covariates were calculated as a single year value or a mean of 2 yr (i.e. a span of 1 or 2 yr). Covariates were also lagged 0, 1, or 2 yr. All

Table 1. Details and justifications for the annual-scale covariates included in statistical models of fish community patterns in Chesapeake Bay. Annual covariates were grouped into 4 categories (climate, fishing, population size, and recruitment) and were calculated for different lags (yr) and spans (yr) using data for identified months. As described in 'Materials and methods', population size and recruitment covariates were calculated separately for anadromous species (ANAD), coastal shelf spawners (COAS), and both of these groups combined. YOY: young-of-the-year

Covariate	Months	Lag	Span	Data source	Justification	Literature examples
Climate						
North Atlantic Oscillation index	Dec–Mar	0, 1, 2	1, 2	Hurrell (2012)	Indicator of climate conditions; linked to changes in fish communities and stocks	Hofmann & Powell (1998), Attrill & Power (2002), Hurrell et al. (2003), Hare & Able (2007)
River discharge	Feb–May	0, 1, 2	1, 2	USGS (2012)	Alters availability of low-salinity habitat; affects nutrient loading, hypoxia, and food web structure	Jung & Houde (2003), Kemp et al. (2005), Purcell & Decker (2005)
Hypoxic volume	Jul	0	1	D. Scavia & M. A. Evans pers. comm.	Alters habitat quality, fish distribution, prey availability; potential increase in mortality	Pihl et al. (1991), Keister et al. (2000), Breitburg (2002), Stierhoff et al. (2006)
Minimum winter temperature	Dec–Mar	0, 1, 2	1, 2	SERCC (2012), VIMS (2012)	Affects overwinter mortality; linked to croaker recruitment	Norcross & Austin (1981), Hare & Able (2007), Lankford & Targett (2001)
Chlorophyll <i>a</i>	Mar–Aug	0, 1, 2	1, 2	M. Brush pers. comm.	Proxy for primary productivity; influences food availability; related to eutrophication intensity	Harding et al. (2002), Kemp et al. (2005)
Fishing						
Landings, bay	All	0	1	NOAA (2012)	Direct biomass removal and source of mortality (local scale)	Richards & Rago (1999), Worm et al. (2009)
Landings, coast-wide	All	0	1	NOAA (2012)	Direct biomass removal and source of mortality (larger scale)	Richards & Rago (1999), Worm et al. (2009)
Population size						
Spawning stock biomass	All	0	1	ASMFC (2010, 2011), Terceiro (2011)	Estimate of coast-wide population size	Richards & Rago (1999), Worm et al. (2009)
Recruitment						
YOY index	Vary ^a	0, 1, 2	1, 2	Durrell & Weedon (2011), Tuckey & Fabrizio (2011)	Measure of age 0 production; source of biomass for population	Hare & Able (2007)

^aMonths used for index calculation vary depending on the species included in the index

combinations of these spans and lags were calculated. Some covariates (hypoxic volume, landings, and SSB) were restricted to a 0 yr lag and 1 yr span (Table 1), as these covariates were hypothesized to have weak or negligible delayed effects on the measured response variables. GAMs of ANAD and COAS CPUE did not include the landings, SSB, or YOY indices for the opposing group.

The evaluation of the annual covariates involved replacing the year factor of the best GAM with each of the annual covariates individually. Each annual covariate was modeled with a smoothing function but was constrained to have no more than 2 degrees of freedom to avoid over-parameterization of the 10 yr time series. Competing models for each response variable were fitted and ranked using AIC and Akaike weights (Burnham & Anderson 2002). Pearson product-moment correlations were calculated between the estimated effect of each annual covariate and the original estimated year effect to indicate the strength and directionality of the relationships. All statistical analyses for this study were performed using the 'vegan' and 'mgcv' libraries in the software package R (version 2.13.2; R Development Core Team 2012).

RESULTS

Basic catch information

ChesMMAp sampled 3640 stations during 48 cruises from 2002 to 2011. Two cruises were not conducted (September 2007, May 2009), and upper bay stations were not sampled during the May 2003 and July 2010 cruises. A total of 98 species were collected during this 10 yr period; however, the analyses were limited to 50 demersal species based on the previously specified criteria (Tables 2 & 3). The number of spe-

Table 2. Catch information for demersal fish species captured in Chesapeake Bay by the ChesMMA survey. Values are totals of all cruises from 2002 to 2011. The top 5 species are classified as either a coastal shelf spawner (COAS) or an anadromous species (ANAD). Elasmobranchs (ELAS) contributing at least 0.5 % of the total biomass were also classified as a distinct group. Mean body size (\pm SD) was calculated from fork length for teleosts, pre-caudal length for sharks, and disc width for batoids

Species	Group	No. of stations	Biomass (kg)	Biomass (%)	Count (no. of fish)	Count (%)	Size (mm)
<i>Micropogonias undulatus</i> (Atlantic croaker)	COAS	1347	22068.7	38.1	104624	38.5	239 \pm 52
<i>Morone americana</i> (white perch)	ANAD	522	8347.8	14.4	61230	22.5	188 \pm 30
<i>Leiostomus xanthurus</i> (spot)	COAS	1574	5228.4	9	56715	20.8	162 \pm 33
<i>Morone saxatilis</i> (striped bass)	ANAD	994	5166.5	8.9	7275	2.7	347 \pm 117
<i>Paralichthys dentatus</i> (summer flounder)	COAS	1517	3035.3	5.2	6097	2.2	329 \pm 103
<i>Raja eglanteria</i> (clearnose skate)	ELAS	356	2447.3	4.2	1678	0.6	404 \pm 62
<i>Cynoscion regalis</i> (weakfish)		1119	2105.1	3.6	17023	6.3	213 \pm 61
<i>Dasyatis say</i> (bluntnose stingray)	ELAS	175	1607.8	2.8	424	0.2	395 \pm 128
<i>Rhinoptera bonasus</i> (cownose ray)	ELAS	113	990.6	1.7	196	0.1	585 \pm 216
<i>Gymnura altavela</i> (spiny butterfly ray)	ELAS	110	918.3	1.6	318	0.1	566 \pm 220
<i>Myliobatis freminvillii</i> (bullnose ray)	ELAS	96	825.6	1.4	234	0.1	511 \pm 215
<i>Pogonias cromis</i> (black drum)		92	766.7	1.3	178	0.1	448 \pm 326
<i>Dasyatis americana</i> (southern stingray)	ELAS	85	655.3	1.1	151	0.1	423 \pm 164
<i>Mustelus canis</i> (smooth dogfish)	ELAS	137	439.1	0.8	368	0.1	593 \pm 162
<i>Archosargus probatocephalus</i> (sheepshead)		65	427.6	0.7	115	<0.05	478 \pm 155
<i>Gymnura micrura</i> (smooth butterfly ray)	ELAS	114	412.3	0.7	220	0.1	514 \pm 156
<i>Squalus acanthias</i> (spiny dogfish)	ELAS	33	376.5	0.7	147	0.1	727 \pm 97
<i>Menticirrhus</i> spp. (kingfish)		407	336.0	0.6	1905.5	0.7	233 \pm 63
<i>Sphoeroides maculatus</i> (northern puffer)		408	223.1	0.4	1941	0.7	151 \pm 34
<i>Dorosoma cepedianum</i> (gizzard shad)		127	195.1	0.3	420	0.2	285 \pm 88
<i>Ictalurus punctatus</i> (channel catfish)		40	178.6	0.3	159	0.1	382 \pm 78
<i>Stenotomus chrysops</i> (scup)		355	137.3	0.2	3158	1.2	120 \pm 22
<i>Dasyatis sabina</i> (Atlantic stingray)		52	130.4	0.2	73	<0.05	314 \pm 102
<i>Chaetodipterus faber</i> (Atlantic spadefish)		182	129.9	0.2	409	0.2	126 \pm 103
<i>Carcharhinus plumbeus</i> (sandbar shark)		43	104.6	0.2	54	<0.05	555 \pm 109
<i>Sciaenops ocellatus</i> (red drum)		6	101.9	0.2	11	<0.05	892 \pm 185
<i>Tautoga onitis</i> (tautog)		21	73.2	0.1	48	<0.05	419 \pm 68
<i>Chilomycterus schoepfii</i> (striped burrfish)		127	54.9	0.1	166	0.1	191 \pm 48
<i>Opsanus tau</i> (oyster toadfish)		103	50.0	0.1	151	0.1	226 \pm 90
<i>Prionotus carolinus</i> (northern searobin)		405	49.6	0.1	2252	0.8	121 \pm 23
<i>Scophthalmus aquosus</i> (windowpane)		251	48.5	0.1	427	0.2	191 \pm 53
<i>Dasyatis centroura</i> (roughtail stingray)		7	48.1	0.1	16	<0.05	440 \pm 44
<i>Trinectes maculatus</i> (hogchoker)		344	46.5	0.1	974	0.4	124 \pm 24
<i>Urophycis regia</i> (spotted hake)		255	39.4	0.1	1216	0.4	137 \pm 44
<i>Ameiurus catus</i> (white catfish)		21	38.2	0.1	42	<0.05	346 \pm 129
<i>Centropristis striata</i> (black seabass)		163	21.3	<0.05	285	0.1	155 \pm 50
<i>Leucoraja erinacea</i> (little skate)		16	19.4	<0.05	25	<0.05	288 \pm 33
<i>Bairdiella chrysoura</i> (silver perch)		156	17.1	<0.05	396	0.1	140 \pm 26
<i>Prionotus evolans</i> (striped searobin)		162	11.7	<0.05	257	0.1	135 \pm 43
<i>Larimus fasciatus</i> (banded drum)		36	10.1	<0.05	142	0.1	157 \pm 60
<i>Ameiurus nebulosus</i> (brown bullhead)		4	5.6	<0.05	28	<0.05	244 \pm 18
<i>Orthopristis chrysoptera</i> (pigfish)		43	5.6	<0.05	84	<0.05	147 \pm 27
<i>Astroscopus guttatus</i> (northern stargazer)		17	5.1	<0.05	17	<0.05	220 \pm 72
<i>Synodus foetens</i> (inshore lizardfish)		28	3.5	<0.05	34	<0.05	223 \pm 42
<i>Lagodon rhomboides</i> (pinfish)		9	3.0	<0.05	39	<0.05	139 \pm 14
<i>Selene vomer</i> (lookdown)		30	3.0	<0.05	72	<0.05	110 \pm 23
<i>Selene setapinnis</i> (Atlantic moonfish)		73	2.4	<0.05	200	0.1	81 \pm 21
<i>Cynoscion nebulosus</i> (spotted seatrout)		15	2.2	<0.05	17	<0.05	224 \pm 60
<i>Etropus microstomus</i> (smallmouth flounder)		9	2.0	<0.05	13	<0.05	115 \pm 93
<i>Trichiurus lepturus</i> (Atlantic cutlassfish)		20	1.2	<0.05	59	<0.05	290 \pm 93

Table 3. Fishes excluded from analyses due to low catches or poor sampling by the ChesMMA bottom trawl. P: pelagic; D: demersal. (–) Biomass not collected

Species	Habitat	Count (no. of fish)	Biomass (kg)
<i>Peprilus triacanthus</i> (butterfish)	P	5502	378.6
<i>Peprilus paru</i> (harvestfish)	P	5502	285.3
<i>Brevoortia tyrannus</i> (Atlantic menhaden)	P	1422	257.9
<i>Pomatomus saltatrix</i> (bluefish)	P	562	138.7
<i>Cyprinus carpio</i> (common carp)	D	9	82.0
<i>Alosa pseudoharengus</i> (alewife)	P	624	79.8
<i>Acipenser oxyrinchus</i> (Atlantic sturgeon)	D	4	17.2
<i>Alosa aestivalis</i> (blueback herring)	P	138	14.1
<i>Carcharias taurus</i> (sand tiger shark)	P	3	13.0
<i>Anchoa mitchilli</i> (bay anchovy)	P	13299	10.2
<i>Alosa sapidissima</i> (American shad)	P	69	10.0
<i>Alosa mediocris</i> (hickory shad)	P	40	9.4
<i>Rachycentron canadum</i> (cobia)	P	1	6.5
<i>Carcharhinus brevipinna</i> (spinner shark)	P	1	6.4
<i>Leucoraja ocellata</i> (winter skate)	D	1	5.2
<i>Trachinotus carolinus</i> (Florida pompano)	P	30	4.8
<i>Squatina dumeril</i> (Atlantic angel shark)	D	2	4.1
<i>Scomberomorus maculatus</i> (Spanish mackerel)	P	7	3.3
<i>Sphyrna tiburo</i> (bonnethead)	D	1	3.2
<i>Rhizoprionodon terraenovae</i> (Atlantic sharpnose shark)	D	1	2.7
<i>Caranx hippos</i> (crevalle jack)	P	22	1.6
<i>Clupea harengus</i> (Atlantic herring)	P	9	1.5
<i>Caranx crysos</i> (blue runner)	P	24	1.2
<i>Notropis hudsonius</i> (spottail shiner)	P	1	0.8
<i>Symphurus plagiatus</i> (blackcheek tonguefish)	D	43	0.7
<i>Opisthonema oglinum</i> (Atlantic thread herring)	P	37	0.7
<i>Hippocampus erectus</i> (lined seahorse)	D	33	0.6
<i>Urophycis chuss</i> (red hake)	D	12	0.4
<i>Merluccius bilinearis</i> (silver hake)	D	3	0.4
<i>Pseudopleuronectes americanus</i> (winter flounder)	D	1	0.4
<i>Anchoa hepsetus</i> (striped anchovy)	P	120	0.3
<i>Perca flavescens</i> (yellow perch)	D	4	0.3
<i>Etropus</i> spp.	D	9	0.1
<i>Mugil</i> spp.	P	1	0.1
<i>Lepomis gibbosus</i> (pumpkinseed)	D	1	<0.5
<i>Hippoglossina oblonga</i> (fourspot flounder)	D	1	<0.5
<i>Eucinostomus argenteus</i> (spotfin mojarra)	D	3	<0.5
<i>Syngnathus fuscus</i> (northern pipefish)	D	30	<0.5
<i>Hypsoblennius hentz</i> (feather blenny)	D	23	<0.5
<i>Fistularia tabacaria</i> (bluespotted cornetfish)	D	1	<0.5
<i>Gobiosoma bosc</i> (naked goby)	D	17	<0.5
<i>Sardinella aurita</i> (Spanish sardine)	D	1	<0.5
Serranidae (unidentified sea basses)	D	1	<0.5
<i>Gobiesox strumosus</i> (skilletfish)	D	7	<0.5
<i>Stellifer lanceolatus</i> (star drum)	D	1	<0.5
<i>Sphyrna borealis</i> (northern sennet)	D	1	<0.5
<i>Acipenser brevirostrum</i> (shortnose sturgeon)	D	1	–
<i>Ammodytes</i> spp.	D	1	–

cies captured at each station ranged from 0 to 19 species, with an overall mean of 3.4 species. Simpson's diversity averaged 0.30 across all stations and 0.42 if diversity values of zero were excluded. A total of 57.9 t and 272 084 individuals were collected from Chesapeake Bay. The top 5 species ranked by weight

(Atlantic croaker, white perch, spot, striped bass, and summer flounder) accounted for 75 % of all trawled biomass, with Atlantic croaker alone contributing 38 % by both biomass and abundance (Table 2).

Species composition of trawl catches varied considerably across year, month, region, and depth strata, reflecting the dynamic spatiotemporal characteristics of the Chesapeake Bay fish community (Fig. 2). Monthly differences in species composition were dominated by changes in Atlantic croaker, striped bass, white perch, and spot. Atlantic croaker accounted for over 50 % of sampled fish biomass in May and July, but relative contributions decreased in the fall (September and November), as this species is known to migrate to the continental shelf for spawning. Biomass proportions of striped bass and white perch were highest in November and March, corresponding with their winter-spring spawning. Although proportional spot catches were high from July to November, their contribution to total biomass peaked in September. Trawled biomass peaked in July, with that month accounting for 31 % of the total. Species dominance in the 5 survey regions shifted spatially from white perch in the upper bay to striped bass in the mid-bay area and Atlantic croaker in the lower bay. Region 5 in the lower bay accounted for 43 % of total trawled biomass and had a more equitable contribution from various species. Patterns by depth stratum indicated higher catches of white perch in the shallow reaches of the

bay, whereas croaker dominated in intermediate and deeper bay areas. Relative to the other factors, annual variability in catch composition was less pronounced but showed decreased contribution by Atlantic croaker in the later years. Concomitant increases in proportional biomass contributions by ELAS and

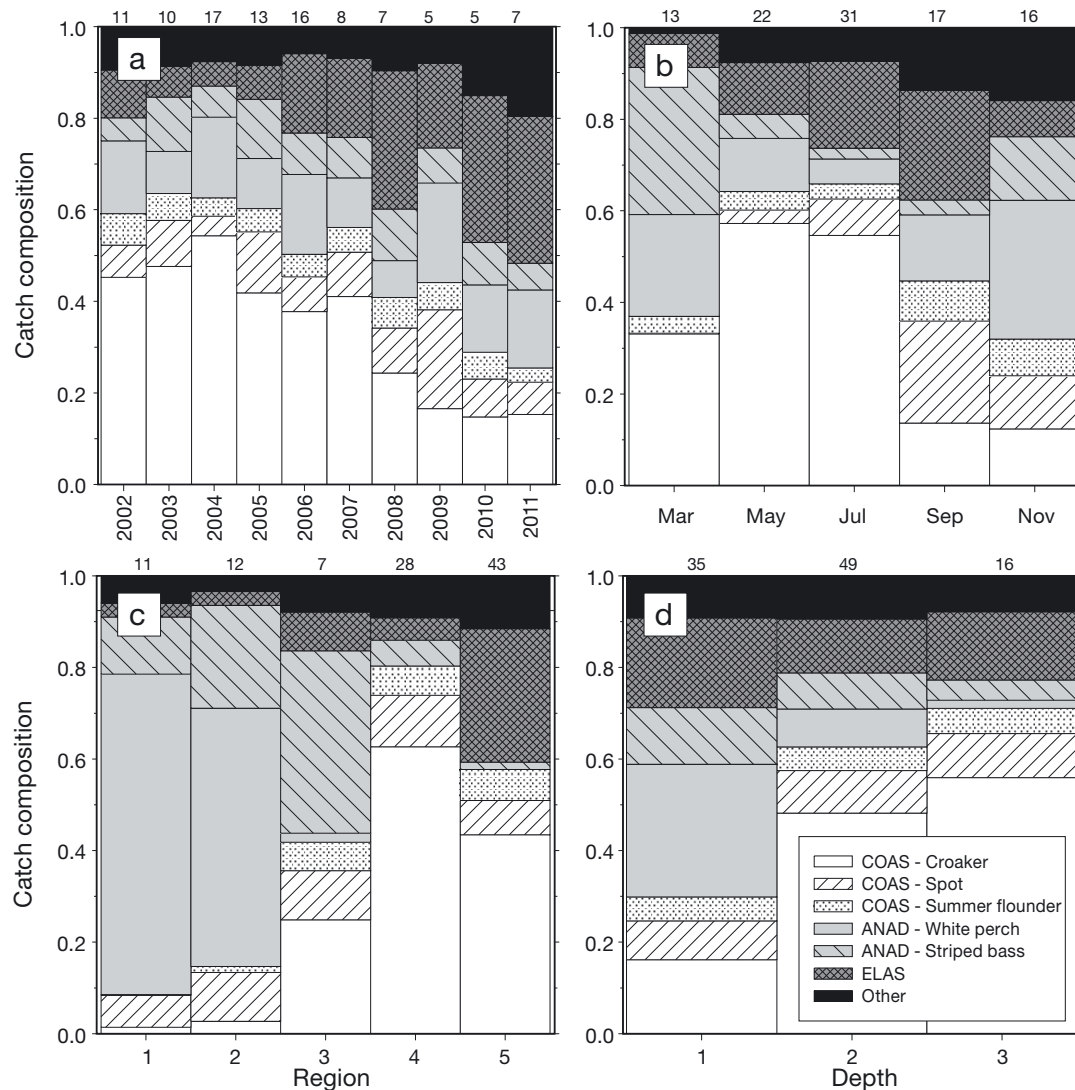


Fig. 2. Fish biomass composition from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) bottom trawls by (a) year, (b) month, (c) region, and (d) depth stratum. Species groups are identified by bar color—white: coastal shelf spawners (COAS); gray: anadromous species (ANAD); dark gray: elasmobranchs (ELAS); black: other species. Region values are for 30 min latitude intervals from the upper bay (Region 1) to the lower bay (Region 5). Depth strata 1, 2, and 3 are defined as 3.0 to 9.1, 9.1 to 15.2, and >15.2 m, respectively. Numbers on the top of each bar represent the percentage of total biomass captured for that factor level

other fishes were also observed in later years. Overall, trawled biomasses were higher before 2007 (with peaks in 2004 and 2006), whereas 2008 to 2011 had relatively low biomasses. However, these trends were slightly confounded due to the missing and incomplete cruises in 2009 and 2010, respectively.

Constrained correspondence analysis of community composition

Species composition within the Chesapeake Bay community was largely driven by latitudinal and

salinity gradients, which were strongly correlated with the first CCA axis (CCA1; Fig. 3). The CCA explained 18% of the total inertia in the multivariate dataset due to the high variability and noise common in survey catch data. ANAD species (white perch and striped bass) had strong negative loadings on CCA1, highlighting their higher catch rates in the lower salinity waters of the upper bay, especially during November and March. Cownose ray, spot, and the minor species held an intermediate position, reflecting a broader and more equitable distribution throughout the bay. The second CCA axis (CCA2) differentiated among the many marine-dominated

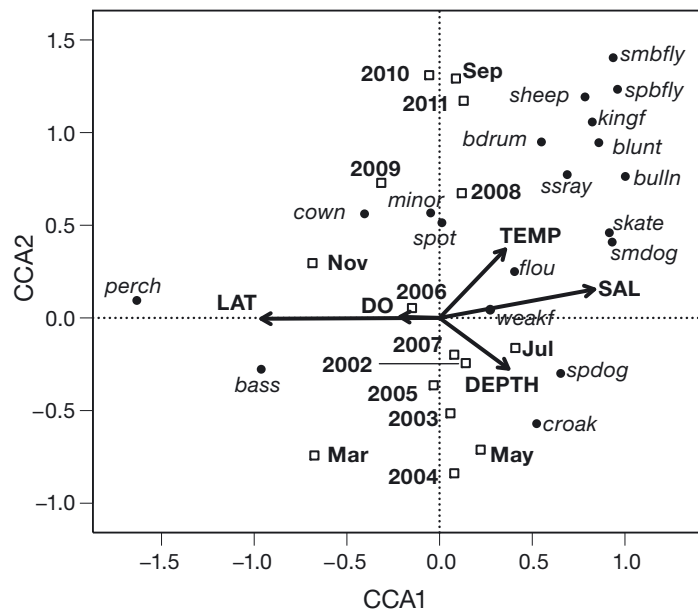


Fig. 3. Constrained correspondence analysis (CCA) ordination diagram for station-level catch-per-unit-effort of species captured by the ChesMMA survey from 2002 to 2011. Arrows indicate the increasing gradient of the significant continuous explanatory variables (LAT: latitude; DEPTH; TEMP: temperature; SAL: salinity; DO: dissolved oxygen). Squares and bold text identify the centroids for each year and month of sampling. Species scores in ordination space are indicated by dots (*bass*: striped bass; *bdrum*: black drum; *blunt*: bluntnose stingray; *bulln*: bullnose ray; *cown*: cownose ray; *croak*: Atlantic croaker; *flou*: summer flounder; *kingf*: kingfish; *minor*: species <0.5% total biomass; *perch*: white perch; *sheep*: sheepshead; *skate*: clearnose skate; *smbfly*: smooth butterfly ray; *smdog*: smooth dogfish; *spbfly*: spiny butterfly ray; *spdog*: spiny dogfish; *spot*: spot; *ssray*: southern stingray; *weakf*: weakfish)

species that tend to be centered in the higher salinity waters of the lower bay. One of the strongest factors driving the patterns in community composition along this axis was a clear separation among years before and after 2008 (2002 to 2007 and 2008 to 2011 with more negative and positive loadings, respectively). There was also separation among spring and early fall (September) catches. Atlantic croaker loaded negatively on CCA2 corresponding with higher CPUE in the early period (2002 to 2007) of the time series, while the relative contribution of many other species to total catch increased in the later period of the time series. September also was a strong driver of species composition, with many of the elasmobranchs loading with warmer water in September. Although a significant factor in the model, DO did not correspond strongly with gradients in species composition.

Generalized additive models of community metrics

With only 2 exceptions, the full generalized additive model provided the best fit to the univariate community metrics (Table 4). Inclusion of a space-time interaction helped account for the dynamic seasonal movements of different species within Chesapeake Bay. Models explained between 33.9 and 51.2% of the null deviance.

Species richness exhibited the largest changes in magnitude as a function of latitude, with mid-latitudes having substantially lower values, particularly in July and September (Fig. 4). DO also strongly depressed *S* at values below $\sim 4 \text{ mg l}^{-1}$ (Fig. 5). Species richness was greatest at intermediate depths (~ 16 to 22 m) and greater depths ($>30 \text{ m}$), but precision at the greater depths was poor. Mean station-level *S* increased at lower salinities and increased

Table 4. Best-fit generalized additive models (GAMs) of species richness (*S*), Simpson's diversity (*D*), and catch-per-unit-effort (CPUE, kg km^{-2}) from bottom trawl survey data in Chesapeake Bay for different species groups (FISH: all fishes; ANAD: anadromous fishes; COAS: coastal shelf spawners; ELAS: elasmobranchs). Models include an intercept (*a*), coefficients for the parametric components (α), smoothing functions for the nonparametric components (*g*), residual error (*e*) for each station (*i*), and various explanatory variables: year (*YR*), month (*MO*), latitude (*LAT*), salinity (*SA*), water temperature (*T*), dissolved oxygen (*DO*), and water depth (*DE*). Percent of total deviance (% Dev.) explained by each model is also presented

Metric	Group	Model	% Dev.
Richness	FISH	$S_i = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i$	50.9
Diversity	FISH	$D_i = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) MO + g_2(T) + g_3(DO) + g_4(DE) + e_i$	33.9
CPUE	FISH	$\log_e(\text{CPUE}_i + 0.1) = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i$	35.0
	ANAD	$\log_e(\text{CPUE}_i + 0.1) = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i$	51.2
	COAS	$\log_e(\text{CPUE}_i + 0.1) = a + \alpha_1(YR) + \alpha_2(MO) + g_1(LAT) MO + g_2(SA) + g_3(T) + g_4(DO) + g_5(DE) + e_i$	48.3
	ELAS	$\log_e(\text{CPUE}_i + 0.1) = a + \alpha_1(YR) + g_1(LAT) MO + g_2(SA) + g_3(T) + g_4(DO) + e_i$	47.6

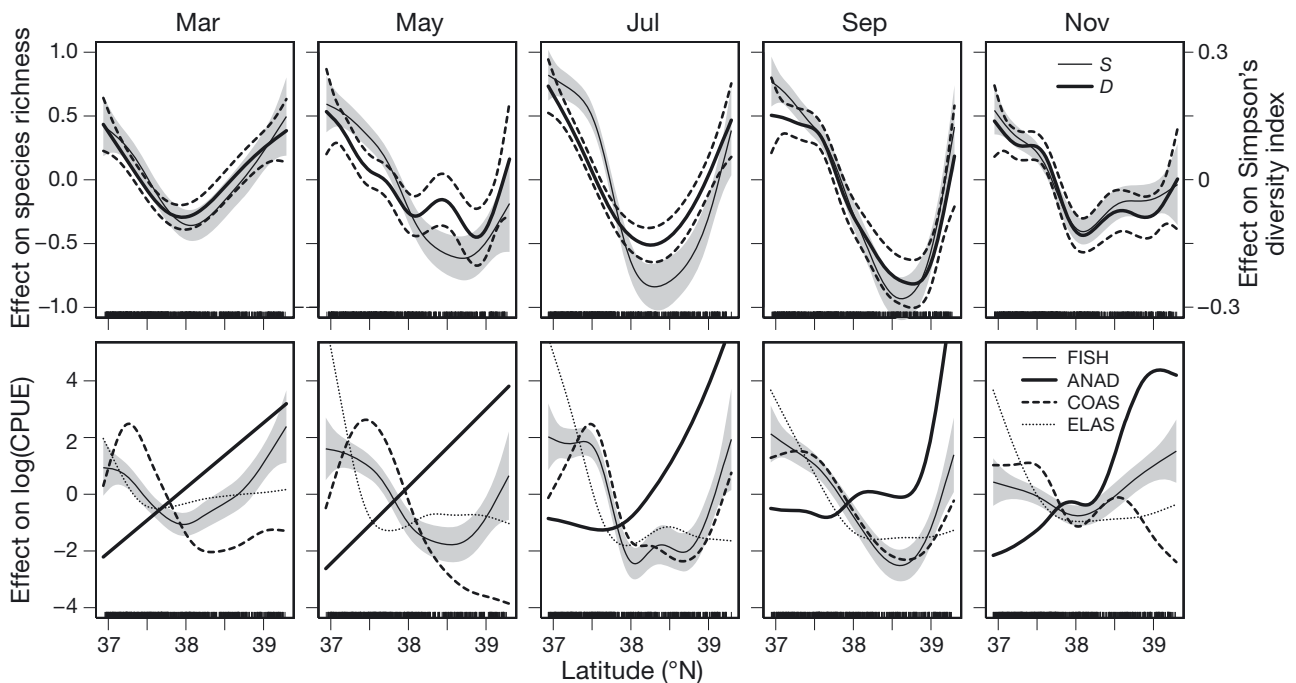


Fig. 4. Partial, smoothed effects of latitude on diversity metrics (upper panels) and log-transformed catch-per-unit-effort [$\log_e(\text{CPUE}+0.1)$] (lower panels) by sampling month, as estimated from generalized additive models of Chesapeake Bay trawl survey data. Upper panels display mean partial effects (± 2 SE) of latitude on species richness (S ; thin line with gray shading; left scale) and Simpson's diversity index (D ; thick lines, right scale) for each month separately. Lower panels display mean monthly partial effects on CPUE of different species groups: all fishes (FISH; thin solid line), anadromous fishes (ANAD; thick solid line), dominant coastal shelf spawners (COAS; dashed line), and elasmobranchs (ELAS; dotted line). For clarity, confidence intervals (± 2 SE; gray shading) are only plotted for FISH, but the magnitudes were similar for other species groups. Sampling intensity for each covariate is indicated by the rug plot on the x-axis

linearly with warmer temperatures (Fig. 4). Species richness progressively increased by month, with the largest positive effect in November (Fig. 6). Annually, S peaked in 2007, but the magnitudes of the year effects were generally low (Fig. 6).

The model for Simpson's diversity index only explained 33.9% of the deviance, but had similar responses to the modeled covariates as did S (Table 4). For example, D increased with temperature and depth, decreased as DO declined below $\sim 4 \text{ mg l}^{-1}$ (Fig. 4), and exhibited minima at mid-latitudes (Fig. 5). Salinity was dropped from the GAM as a non-significant covariate (Table 4). Temporally, November yielded the highest relative effect on D , but D was relatively consistent across years (Fig. 6).

Results of GAMs fitted to CPUE data clearly demonstrated different influences of environmental and spatial factors on catch rates of different species groups (Figs. 4 to 6). Trends for the FISH group were generally a combination of the predicted patterns for the other groups, but the FISH trends tended to mirror COAS patterns more closely (e.g. Fig. 4) due to the biomass dominance of COAS fishes in the total

catch (Table 2). Catches of COAS and ANAD fishes generally showed contrasting trends with temperature and latitude; ANAD fishes preferred colder waters below 15°C and higher latitudes, opposing the trends for COAS species (Figs. 4 & 5). These inverse trends acted to dampen the responses of the FISH patterns with these factors. The Potomac River mouth (at 38°N) represented a transitional point for COAS below which catches increased dramatically in most months, with a clear peak at approximately 37.5°N in the spring and summer months (Fig. 4). Catches of ELAS increased monotonically with decreasing latitude. Salinity had strong positive effects on CPUE of ANAD and ELAS fishes in low and high salinities, respectively, whereas the effect on COAS fishes was only slightly positive at lower salinities (Fig. 5). COAS fishes preferred intermediate depths whereas ANAD fishes preferred shallower waters. The effect of DO was detected only at levels $< 3.5 \text{ mg l}^{-1}$, but this was most strongly evident with the COAS group. Month effects on CPUE were generally smaller than other factors and lacked precision (Fig. 6), suggesting that the majority of changes by

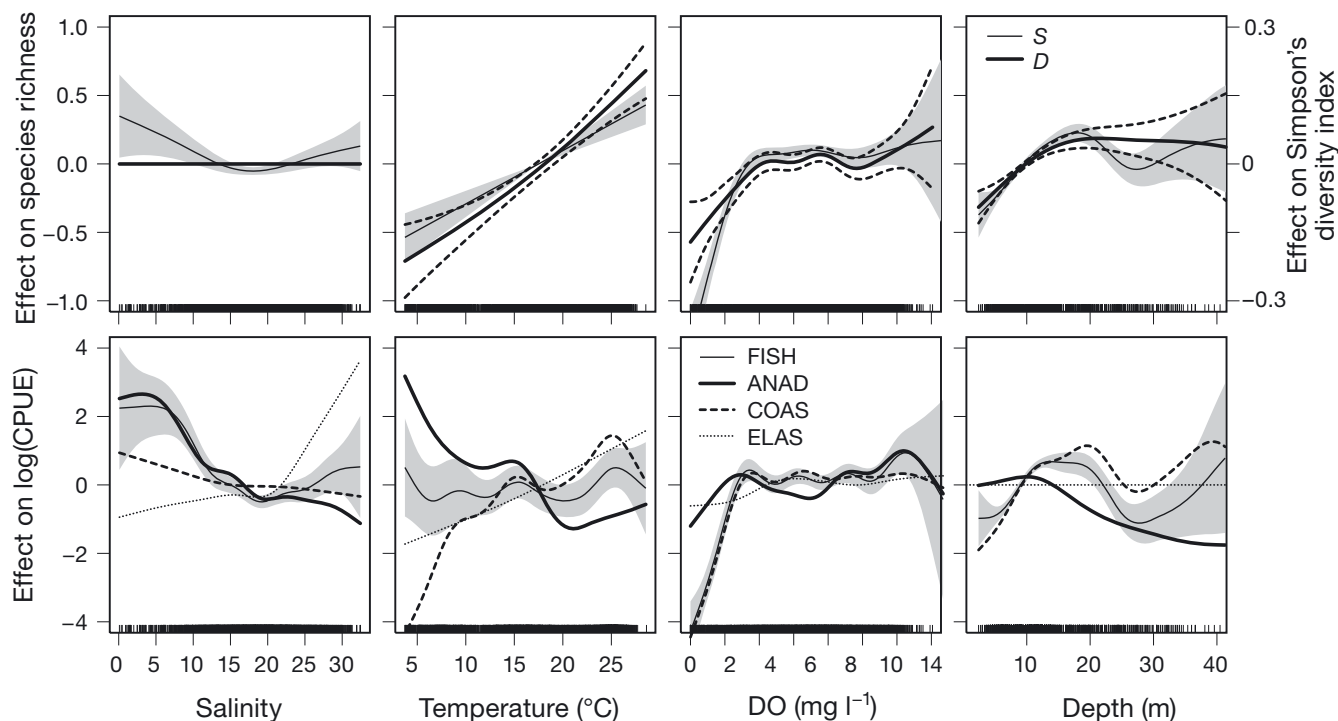


Fig. 5. Effects of salinity, temperature, dissolved oxygen (DO), and depth on diversity metrics (upper panels) and log-transformed catch-per-unit-effort [$\log_e(\text{CPUE}+0.1)$] (lower panels), as estimated from generalized additive models of Chesapeake Bay trawl survey data. Upper panels display mean partial effects (± 2 SE) of covariates on species richness (S ; thin line with gray shading; left scale) and Simpson's diversity index (D ; thick lines; right scale). Lower panels display mean partial effects of each covariate on CPUE of different species groups: all fishes (FISH; thin solid line), anadromous fishes (ANAD; thick solid line), dominant coastal shelf spawners (COAS; dashed line), and elasmobranchs (ELAS; dotted line). For clarity, confidence intervals (± 2 SE; gray shading) are only plotted for FISH, but the magnitudes were similar for other species groups. Sampling intensity for each covariate is indicated by the rug plot on the x-axis

month were captured by water temperature or by the latitude-month interaction. The annual trends showed peaks in ANAD, COAS, and FISH catches in 2005 and 2006 followed by declines during the latter half of the time series. Back-transformed, bias-corrected CPUE values (calculated at the medians of all the explanatory variables) indicated that COAS and ANAD catch rates (in kg km^{-2}) declined dramatically from their respective peaks (90% decline in COAS CPUE from 2005 to 2011; 80% decline in ANAD CPUE from 2005 to 2009). These estimates of percent decline exceeded estimates for individual COAS species (declines of 85 to 88%) and ANAD species (declines of 43 to 77% for white perch and striped bass, respectively) (A. Buchheister unpubl. data), likely due to the characteristics of aggregate CPUE metrics (Kleiber & Maunders 2008); however, all of these values represent substantial decreases in catch rates in recent years, especially for COAS species. ELAS CPUE remained more consistent over the time series although values were slightly higher after 2005.

Annual covariates

The categorical year factor typically described annual trends in community metrics far better than the various covariates hypothesized to influence community dynamics (Table 5). Of the examined covariates, fishery landings and recruitment indices tended to have greater predictive power across metrics and species groups. Landings tended to be positively correlated with interannual trends in FISH, ANAD, and COAS CPUE, suggesting that fisheries may have been responding to changes in fish abundance as represented by ChesMMAP data. YOY indices ranked within the top 3 models for several metric-group combinations, but effects could be positive or negative. For example, ANAD CPUE was positively correlated with the ANAD YOY index (with a relatively longer lag and span), whereas COAS CPUE was negatively correlated with a composite YOY index (i.e. high levels of recruitment corresponded with lower predicted COAS catch).

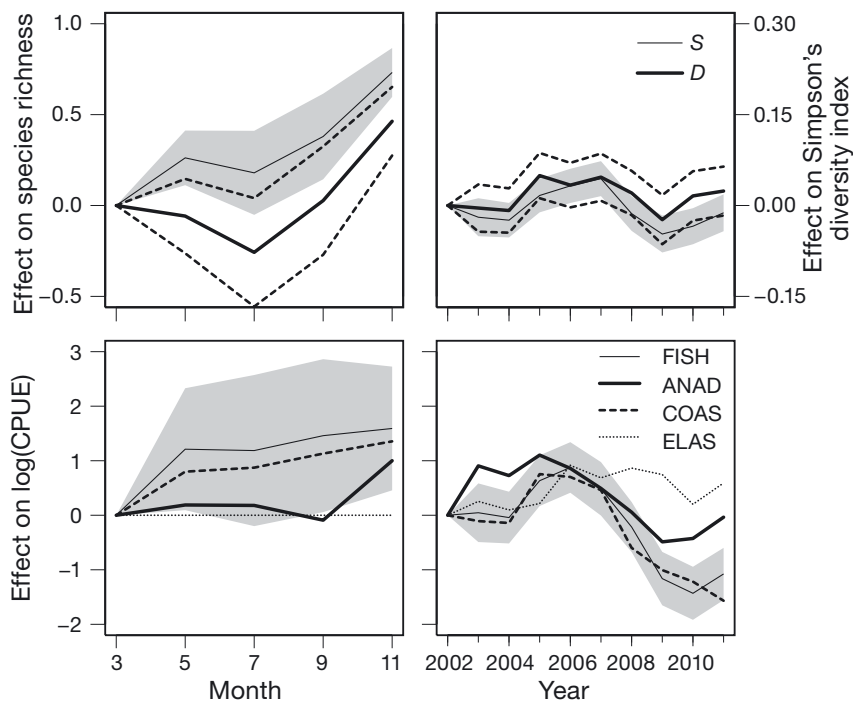


Fig. 6. Parametric partial effects of month and year on diversity metrics (upper panels) and log-transformed catch-per-unit-effort [$\log_e(\text{CPUE} + 0.1)$] (lower panels), as estimated from generalized additive models of Chesapeake Bay trawl survey data. Upper panels display mean partial effects (± 2 SE) on species richness (S; thin line with gray shading; left scale) and Simpson's diversity index (D; thick lines; right scale). Lower panels display mean partial effects on CPUE of different species groups: all fishes (FISH; thin solid line), anadromous fishes (ANAD; thick solid line), dominant coastal shelf spawners (COAS; dashed line), and elasmobranchs (ELAS; dotted line). For clarity, confidence intervals (± 2 SE; gray shading) are only plotted for FISH in the lower panels, but the magnitudes were similar for other species groups. Note that standard errors are inestimable for the reference (i.e. first) level of each factor

DISCUSSION

Environmental filtering of Chesapeake Bay demersal fish community

Salinity was the major environmental gradient structuring community composition, biodiversity, and catch rates within Chesapeake Bay. This gradient was captured by 2 related covariates: (1) direct measures of salinity and (2) latitude. Latitude indicated the general salinity regime (e.g. oligohaline to polyhaline) and acted as a spatial locator, whereas salinity was a higher-resolution (and more variable) measure of water quality. Particularly in estuarine environments, salinity is frequently found to be a dominant structuring factor (Day et al. 1989), separating freshwater and marine species. Typically, species richness and total biomass tend to have parabolic, nonlinear relationships with salinity, displaying a minimum in mesohaline waters because of the physiological demands of living in these brackish waters (Odum 1988, Wagner 1999). Consequently, mesohaline waters act as an obstacle to marine and freshwater species that limits the distribution of those species groups within the bay, translating to the documented parabolic trends in *S*, *D* and total fish CPUE (with a transitional point at ~ 20 psu and 38 to 38.5°N). These patterns suggest that bay-wide community assembly is largely driven through environmental filtering processes (i.e. general habitat suitability) whereby species inhabit-

ing the different regions of the bay are restricted by unique tolerances to and preferences for certain habitat and environmental characteristics (e.g. Mouillot et al. 2007). Mid-bay reductions in fish biomass indices were also observed consistently over years for the pelagic fish community (Jung & Houde 2003). Thus, both demersal and pelagic environments of the mesohaline Chesapeake Bay mainstem act as suboptimal habitats for bay fishes and support a relative paucity of fish biomass.

The mid-bay minima in biomass and diversity metrics may also be related to reduced habitat quality stemming from hypoxia. Fitted GAMs accounted for the direct effects of low DO concentrations (see 'Discussion—Community responses to hypoxia'), but other indirect effects are possible. Research suggests that benthic macro- and meiofauna (important food for benthivorous species like Atlantic croaker, spot, and white perch) are degraded in the mid-bay relative to other bay regions due to hypoxia and eutrophication stress (Hagy 2002, Kemp et al. 2005). Prolonged exposure of the mesohaline benthos to hypoxic conditions could have lasting consequences on the quality of foraging habitat for benthivores that restrict the suitability of the region even after bottom waters become oxygenated.

The spatial gradient in community composition was largely driven by the ANAD species (white perch and striped bass) but also reflected broader spatiotemporal trends in biodiversity. Ecologists frequently partition

Table 5. Summaries of the highest-ranking competing generalized additive models of species richness, species diversity, and catch-per-unit-effort (CPUE) modeled with different annual covariates. Models were constructed by replacing the Year factor from the best-fit models of Table 4 with each annual covariate from Table 1. Response metrics were modeled separately for each species group (FISH: all species combined; ANAD: anadromous species; COAS: coastal shelf spawners; ELAS: elasmobranchs). Covariates were calculated for different lags (yr), spans (yr), and species groups (A+C represents ANAD and COAS groups combined). Akaike weights (w) provide the weight of evidence or probability that a model is the best model of the models compared within each metric-group pair. Pearson product-moment correlations (R) between the covariate and the estimated year effect in the null model (as plotted in Fig. 6) indicate the strength and direction of the relationship of the covariate and the response variable.

YOY: young-of-the-year

Metric and Group	Rank	Covariate	Lag	Span	w	R
Richness						
FISH	1	Year	0	1	0.994	1.00
	2	Landings, coast-wide (COAS)	0	1	0.003	0.32
	3	YOY Index (A+C)	1	2	0.001	−0.75
Diversity						
FISH	1	River discharge	2	2	0.504	0.73
	2	YOY Index (ANAD)	1	1	0.092	−0.26
	3	Landings, coast-wide (ANAD)	0	1	0.079	0.62
CPUE						
FISH	1	Year	0	1	0.991	1.00
	2	Landings, coast-wide (A+C)	0	1	0.009	0.81
	3	Landings, coast-wide (COAS)	0	1	0.000	0.73
ANAD	1	Year	0	1	0.811	1.00
	2	Landings, coast-wide (A+C)	0	1	0.172	0.94
	3	YOY Index (ANAD)	2	2	0.016	0.90
COAS	1	Year	0	1	0.983	1.00
	2	YOY Index (A+C)	0	2	0.013	−0.92
	3	Landings, coast-wide (COAS)	0	1	0.003	0.75
ELAS	1	Year	0	1	0.511	1.00
	2	Landings, Bay (COAS)	0	1	0.462	−0.38
	3	YOY Index (ANAD)	1	2	0.010	−0.66

biodiversity into various components (α , β , and γ diversity) to better understand the processes that structure communities, particularly along environmental gradients (Magurran 2004). The demersal fish community of Chesapeake Bay exhibits an overarching trend of increasing regional species richness (i.e. γ diversity) from the upper bay to the lower bay (19 vs. 45 species encountered, respectively; A. Buchheister unpubl. data); however, our station-level estimates of S (i.e. α diversity) were highest in the upper bay based on the GAMs. Thus, upper bay stations tend to have a consistently higher number of species caught at each station despite a smaller regional species pool than other bay regions. This pattern indicates that species turnover (i.e. β diversity — a measure of the change in species biodiversity over time or space) is low; in other words, species composition is more consistent and the

fish community more homogenous across upper bay stations, likely due to the relative ubiquity of white perch throughout the year in the upper bay. The mid-bay stations had a lower predicted S , a higher regional pool, and thus a much higher species turnover across stations. Generally, the middle and lower bays have a more diverse and dynamic fauna due to the migration of many species, making these regions more heterogeneous over space and time. Higher turnover in the mesohaline portion of the bay mainstem opposes the patterns documented in the Chesapeake Bay tributaries for smaller littoral fishes, where turnover was highest at the tidal freshwater interface (Wagner 1999). Thus, community patterns in species turnover may differ by estuarine region (tributaries vs. mainstem) or by the size range of the fish assemblage.

Seasonal regulation of community patterns

As in most temperate estuaries, the fish assemblage within Chesapeake Bay is known to be seasonally dynamic as different species migrate into and out of the bay given their life history strategies (Murdy et al. 1997, Able & Fahay 2010). Dividing the biomass-dominant species into ANAD, COAS, and ELAS groups effectively separated ~90% of the assemblage's biomass into different modes of life history and estuarine usage. Spawning by striped bass and white perch in freshwater and tidal tributaries during spring concentrates anadromous individuals in the upper bay, especially when water temperatures are low. For white perch, this is due to fish residing in deeper channels and bay areas during winter prior to their upstream spawning migration in the spring. Striped bass are also caught in higher numbers during cold months (March), when the resident contingent (mostly male fish) is overwintering in Chesapeake Bay and as coastal migrants are moving to the rivers for spawning (Fay et al. 1983). Catches of ANAD fishes also increased in November, as white perch and

striped bass residents generally aggregate in deeper waters in preparation for winter.

Both the COAS and the majority of the ELAS species demonstrated alternative usage of the bay's mainstem (relative to ANAD fishes), with greatest residence and utilization during summer and fall when water temperatures are the warmest. The COAS trends are likely linked to (1) the migrations of COAS species that forage in the estuary during warmer months prior to offshore spawning (Murdy et al. 1997, Able & Fahay 2010), (2) the movement of winter/spring-settled juveniles from shallow estuarine nursery areas and tributaries to the mainstem during ontogeny (Rogers et al. 1984, Sackett et al. 2008), and (3) the recruitment of age 0 COAS juveniles to the trawl gear when sufficient fish sizes (~100 to 150 mm) are attained in the summertime (Bonzek et al. 2011). ELAS life histories are more varied given the larger number of species; however, several species spawn in spring or summer within estuarine waters or forage in the bay in summer and fall (Wourms 1977, Murdy et al. 1997).

The warmest temperatures (in July) promote greater bay utilization by many species, including ELAS, COAS, and subtropical species that use the bay as a foraging ground. Late summer and early autumn temperatures also allow rarer tropical species to join the warm-temperate and subtropical summer residents in the bay (Murdy et al. 1997), thus increasing biological diversity. Despite cooler temperatures, species richness and Simpson diversity was relatively high in November because cold temperate and even boreal species (e.g. striped bass, spotted hake) become more prevalent in the bay while many species are migrating out to overwinter in coastal waters.

Community responses to hypoxia

Low DO produced one of the strongest negative responses of any of the modeled variables. Within Chesapeake Bay, the effects of hypoxia on distribution and abundance of zooplankton and fish larvae have been demonstrated in several locations (Roman et al. 1993, Keister et al. 2000, Ludsin et al. 2009). However, research on the effects of hypoxia on adult fishes has been restricted to tributaries and smaller areas within the bay (Pihl et al. 1991, Carmichael et al. 1992, Breitburg et al. 2001) or has focused on effects on pelagic and mainly planktivorous fishes (Jung & Houde 2003, Ludsin et al. 2009). To our knowledge, this is the first study in Chesapeake Bay

to document the large effects on demersal fish biodiversity and catch rates that are predominantly driven by chronic influence of low DO concentrations. The drastic decline in *S*, *D*, and CPUE documented here was consistent with work from other systems (e.g. Breitburg 2002, Eby & Crowder 2002, Keller et al. 2010) and suggests that from a multi-species, community perspective, there is a strong threshold avoidance response that begins when DO drops below ~4 mg l⁻¹. This threshold suggests that habitat quality for the demersal fish assemblage begins to be reduced at values >2 mg l⁻¹ (the typical definition for hypoxia), as fish exhibit elevated respiration and metabolism, reduced growth, or other signs of physiological stress that drive mobile animals to emigrate from the affected area (Breitburg 2002, Gray et al. 2002).

Emigration from and avoidance of low DO waters was detected in the spatial distribution of fishes in July, when hypoxic conditions are most extreme. The latitudinal effects predicted by the GAMs (Fig. 4) included apparent indirect effects of low DO (i.e. after the direct DO effects were explicitly accounted for by the models). FISH CPUE, COAS CPUE, and species richness showed the steepest declines with latitude in July at ~37.75° N near the southern edge of the bay's deeper mainstem channel (Fig. 1), suggesting an aggregated edge effect due to the southern displacement of fishes. The bathymetry of this area near the mouth of the Rappahannock River promotes a strong oxycline (Hagy et al. 2004), and similar aggregations of fish catch rates have been shown surrounding hypoxic areas in the Gulf of Mexico (Craig 2012). A concurrent northward displacement of fishes was evidenced by the steep increase in FISH CPUE in July and September at the northern edge of the mainstem channel (at ~39°N). These patterns in CPUE combined the effects of multiple species which may respond differently to low DO. For example, the northward displacement of COAS fishes was caused almost exclusively by spot in July and September. Interestingly, the displacement of ANAD fishes did not appear as drastic in July (more so in September). However, these ANAD trends may be a result of a longitudinal displacement resulting from greater utilization of shallower stations and habitats at those latitudes (e.g. Eby & Crowder 2002). Additionally, the lack of a steeper increase in ANAD CPUE to the north could be the result of the smoothing function fitting data from 2 species; white perch catch rates alone (without striped bass) were much greater north of 39°N where the mainstem channel ends and hypoxia is less problematic. Slightly elevated CPUE

(FISH, ANAD, and COAS groups) at DO levels of ~ 4 mg l⁻¹ also provide some support for aggregation of fish biomass at DO levels that are sufficiently oxygenated.

Biomass and biodiversity trends with DO and latitude primarily reflect the seasonally chronic, large-scale effects of low DO. This study documented notable, drastic shifts in large-scale fish distributions and catches, which represents a substantial reduction in available fish habitat for demersal fishes. From a system-wide perspective, it remains unclear whether the tradeoffs of increased production from eutrophication combine with the negative effects of low DO to hinder or promote overall secondary fish production (Caddy 1993, Breitburg et al. 2009). Jung & Houde (2003) found bay-wide pelagic fish biomass to increase as mean annual depth-integrated DO decreased, which is supported by large-scale studies documenting higher pelagic productivity with increased eutrophication (de Leiva Moreno et al. 2000, Breitburg et al. 2009). However, it is also possible that the Jung & Houde (2003) patterns could be influenced by vertical displacement of fishes away from hypoxic bottom waters (Hazen et al. 2009). Demersal production does not benefit as much from eutrophication-induced increases in pelagic productivity due to the resulting degradation of benthic habitats (de Leiva Moreno et al. 2000, Breitburg et al. 2009). In our study, the localized negative effects of hypoxia were strongly evident in the demersal community, but there was little evidence of annual patterns in demersal productivity being strongly related to hypoxic volume or other climatic variables related to eutrophication (e.g. river discharge, chlorophyll *a*).

Large-scale factors influencing inter-annual community patterns

Species composition and community metrics changed dramatically within the 10 yr dataset, with later years characterized by low CPUE of COAS, ANAD, and FISH species groups and decreased proportional contributions by Atlantic croaker. Strong annual shifts in community composition and structure have previously been documented for the bay's pelagic fish community (Jung & Houde 2003). The pelagic community exhibited resilience to a strong environmental perturbation (in the form of very high annual precipitation), progressively returning to the pre-disturbance structure as time passed (Jung & Houde 2003). In this study, several climate, fishing, population size, and recruitment covariates were

evaluated to identify the dominant drivers of the documented interannual patterns for the demersal community, based on different hypotheses. Multiple ecosystem processes act simultaneously on the various constituents of the community (species, age classes, etc.) and can complicate relationships between covariates and community metrics. Given this complexity and the greater flexibility (i.e. degrees of freedom) of the categorical year factor, models with single covariates tended to be outperformed by models with the year factor. However, there is value in ranking the relative explanatory power of considered variables to help elucidate and evaluate different underlying mechanisms regulating community dynamics (e.g. Jung & Houde 2003, Keller et al. 2012). Overall, the annual patterns were most strongly linked to fishing pressure and recruitment processes, but it is unclear whether the trends represent natural fluctuations in community dynamics or if these changes are symptomatic of continued stresses on the bay ecosystem (e.g. Boesch et al. 2001, Kemp et al. 2005).

Coastwide landings ranked as some of the best annual predictors of CPUE and biodiversity metrics. Coastwide landings for the COAS group (primarily Atlantic croaker and summer flounder) have been decreasing since ~ 2004 and 2005, while landings of white perch and striped bass have remained relatively consistent during the study period (ASMFC 2010, 2011, Terceiro 2011). The positive correlation between fishery landings and survey CPUE is complicated by the vagaries of using landings data (e.g. lack of effort data, influence of management regulations, discards); however, part of these concerns are minimized as landings for Atlantic croaker (the dominant species) are not restricted by a catch quota as they are for some of the other species (ASMFC 2010). The correlated pattern in coastwide landings and CPUE metrics underscores the fact that relationships among independent and dependent variables in the GAMs are not necessarily causative, but they may be both responding to some other latent variable(s). Interestingly, the general decline in COAS CPUE (since 2005/2006) and COAS landings does not appear to be driven by changes in total population size given that SSB for Atlantic croaker and summer flounder have continued to grow (ASMFC 2010, Terceiro 2011). A likely explanation is that spatial and distributional dynamics of species could alter the theoretically positive relationship among survey CPUE, landings, and SSB. Such changes in fish distributions can occur at large scales as a consequence of environmental climate drivers (Nye et al. 2009, Pinsky & Fogarty 2012), or they could result from local factors

such as habitat quality and prey availability (e.g. Caddy 1993, Craig 2012). Linkages between survey CPUE, landings, and the coastwide stock are also influenced by the degree of spatial connectivity and exchange among the many estuarine and coastal systems that contribute to the total stock of each species.

Recruitment indices also ranked highly as some of the best predictors of CPUE. Surprisingly, the sign of the relationship was not positive for COAS fishes, contrary to the typical expectation. Given the dominance of Atlantic croaker in the ChesMMA catch and the weighting scheme of the YOY composite index calculations, the Atlantic croaker YOY index drove the patterns in the COAS and ANAD + COAS YOY indices. The negative relationship between recruitment and future adult CPUE could be indicative of density-dependent effects on mortality (Rose et al. 2001); however, recent work has demonstrated a relatively weak correspondence between YOY Atlantic croaker indices and future CPUE of croaker age classes using the ChesMMA data (Woodward 2009). This poor correlation may be related to low site fidelity by adult Atlantic croaker and highlights the importance of spatial scale in looking at such relationships. CPUE of ANAD fishes was positively correlated with the group's recruitment index with a longer lag, which is consistent with ANAD fishes recruiting to the trawl gear at slightly older ages (approx. age 2 to 3; Bonzek et al. 2011). The strong correlation between ANAD CPUE and the ANAD recruitment index may also have been influenced by the spatially constrained nature of the white perch population, whose migrations are smaller in scale; any white perch recruitment signals would be more easily detected in adults with less environmental and ecological noise.

Within Chesapeake Bay and other coastal systems, several studies have linked climatic variables with patterns in fish populations and community metrics (e.g. Hofmann & Powell 1998, Attrill & Power 2002, Nye et al. 2009). Despite the several climatic covariates examined and the multiple iterations of time lags and spans for each, these covariates consistently performed worse than variables related to fishing and recruitment. The only exception was river discharge, but it was used to model Simpson diversity which lacked variability and contrast among years. These general patterns do not negate the importance of climatic variables as important drivers of community metrics but instead indicate that other processes such as recruitment (which can be influenced by climate) may be more directly related over the 10 yr time scale investigated. Additionally, community responses to

climatic forcing may be harder to detect than responses for individual species. For example, Hare & Able (2007) linked recruitment indices, adult abundance, and landings of Atlantic croaker to the North Atlantic Oscillation and to minimum winter temperatures at decadal time scales. These relationships were not strongly evident in our analysis, perhaps due to our shorter time series or to the added influence of the other COAS species.

Implications and significance

Concerns over long-term environmental and anthropogenic stressors and their impacts on the Chesapeake Bay ecosystem have helped foster interest in EBFM in Chesapeake Bay (Houde 2006). Management of Chesapeake Bay in an ecosystem-based framework will rely on a suite of suitable indicators to capture the many components that define ecosystem status (Brodziak & Link 2002, Link 2002) and to overcome the limitations of any individual metric (e.g. Kleiber & Maunder 2008). Given its distinct annual and spatial trends in Chesapeake Bay and emphasis on biomass-dominant species, total fish CPUE (as an index of demersal fish biomass) appears to be a useful ecosystem indicator as suggested by many authors in other systems (e.g. Rice 2000, Methratta & Link 2006). However, we have demonstrated that aggregate biomass metrics for anadromous fishes, coastal spawners, and elasmobranchs provide greater resolution of community patterns, capturing distinct life history and bay utilization patterns for dominant demersal species. Both species richness and Simpson diversity were sensitive to the environmental covariates and exhibited similar functional responses to the modeled variables, suggesting that both are useful indicators of general biological diversity of the Chesapeake Bay fish community.

This study provides a 10 yr frame of reference for the bay-wide demersal fish community that can be used to evaluate future changes to species composition, distribution, or abundance at a large scale. The documented trends and influences of each explanatory factor may also provide tentative relationships to help inform predictions regarding the influence of different stressors on the Chesapeake Bay fish community. Continued large-scale monitoring of Chesapeake Bay will be critical for detecting ecosystem-level responses to continued stresses and is an essential component to a successful management strategy for the many resources of Chesapeake Bay and western Atlantic waters.

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