

Fish and Blue Crab Assemblage Structure in a U.S. Mid Atlantic Coastal Lagoon Complex

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ABSTRACT: Variability in assemblages of organisms in contiguous lagoons is dependent upon component bays and their connections to the ocean and terrestrial watersheds. Fish and blue crab assemblage structure of Maryland's coastal lagoon complex, which consists of Assawoman, Isle of Wight, Sinepuxent, and Chincoteague Bays, was analyzed for spatial and seasonal patterns for the period 1991–2002. Nonmetric multidimensional scaling ordinated sites from a Maryland state trawl survey into discrete groups associated with each embayment. Dominant species included *Callinectes sapidus*, *Anchoa mitchilli*, *Leiostomus xanthurus*, *Bairdiella chrysoura*, and *Brevoortia tyrannus*. The relative abundance of these and other dominant species were significantly higher in the two bays north of the ocean inlet than in bays south of the inlet. Ninety-two species were identified in the survey, with total species richness highest in the southern-most bay (Chincoteague: $S = 83$) and lowest in the northern most bay (Assawoman: $S = 59$). On a catch per unit effort basis, the northern two bays were more diverse and productive. These bays were most affected by anthropogenic eutrophication, but also exhibited higher connectivity to the ocean inlet. There was clear seasonality in assemblage structure with peak abundance and diversity in the summer compared to spring and fall. Factors that influenced seasonal and spatial structure of Maryland's coastal lagoon complex included temperature, degree of eutrophication, and proximity to oceanic exchange. The arrangement of the bays in their exposure to oceanic and watershed influences specify that habitat management actions should occur at a bay-level scale rather than across the lagoon complex.

Introduction

Coastal lagoons are often highly productive systems that function as nursery areas and feeding grounds for coastal fishes, potentially supporting important commercial and recreational fisheries. Although coastal lagoons represent one type of estuary, they often do not typify larger estuaries that are characterized by strong salinity gradients due to higher freshwater input (Yáñez-Arancibia et al. 1994). Fish assemblages in estuaries are largely structured by abiotic gradients (Kupschius and Tremain 2001) that include salinity (Wagner 1999; Martino and Able 2003), temperature (Maes et al. 2004), dissolved oxygen (Weisberg et al. 1996; Eby and Crowder 2004), habitat heterogeneity and structure such as reefs or submerged vegetation (Heck Jr. et al. 2003; Martino and Able 2003), and turbidity (Cyrus and Blaber 1992). Coastal lagoons are particularly influenced by oceanic exchange via inlets. Lagoon fish assemblages may be structured differently with less influence from watershed effects and greater influence from oceanic proximity.

Like other lagoon systems, the coastal embayments of Maryland, USA (Fig. 1), located on the Delmarva Peninsula (the coastal plain peninsula

between Chesapeake Bay and Atlantic Ocean) support a diverse array of fish and invertebrates (Cargo 1958; Schwartz 1961, 1964; Wazniak et al. 2004; Murphy 2005). These four coastal embayments each have distinct characteristics related to flow, area, depth, connectivity to ocean waters, and anthropogenic habitat alterations. The embayments share connections with the ocean and are well connected as a series of lagoons. The degree of similarity of fish assemblage between embayments is the topic of our study, a question that should have application to similar lagoon systems elsewhere.

Previous investigations examining ichthyofaunal assemblages in coastal areas have identified several environmental parameters that affect structural components of the assemblage (Whitfield 1999; Desmond et al. 2002; Perez-Ruzafa et al. 2004). The primary variables affecting species in nearshore regions are salinity (Wagner 1999; Martino and Able 2003; Poizat et al. 2004), temperature (Desmond et al. 2002), chlorophyll *a* (Perez-Ruzafa et al. 2004), oxygen (Eby and Crowder 2004), and habitat heterogeneity, particularly with regard to structural components such as vegetation or reef systems (Whitfield 1999; Martino and Able 2003). In typical drowned river valley estuarine systems, environmental gradients are often steep due to the large watershed to surface area ratio and associated freshwater influence. This can cause dramatic shifts in salinity and temperature that estuarine organisms

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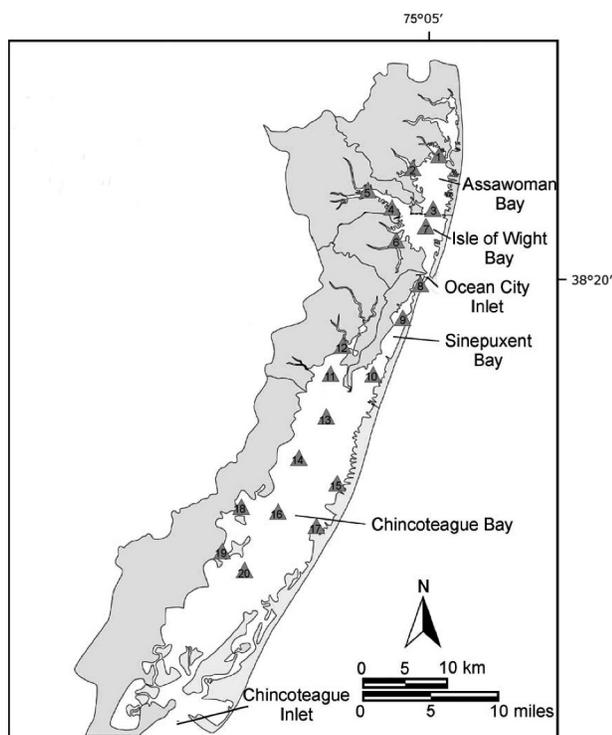


Fig. 1. Map of study location with trawl sampling sites denoted by triangles (map courtesy of the Maryland Department of Natural Resources).

must either adapt to or avoid (Vernberg 1982). Coastal lagoons are less influenced by high freshwater flow (e.g., less stratification) but are influenced by winds, tides, and location of oceanic input (Mariani 2001; Poizat et al. 2004). Assemblages in these systems must contain those species capable of thriving under dynamic conditions or shift structure as conditions vary. Many species use estuaries facultatively at different phases of their life cycles that include nursery (Gillanders et al. 2003), reproduction (Hagan and Able 2003), and opportunistic foraging (Franzoi et al. 1993). Many of these life history traits are ontogenetic in nature such that a species will occupy multiple niches throughout its life (Able and Fahay 1998). Seasonal turnover in species in temperate estuaries and lagoons is expected; the phenology (seasonal appearance of species) is often a characteristic attribute of lagoon and estuarine systems.

In Maryland's coastal bay complex, Schwartz (1964) speculated that there were differences in the faunal composition of the northern bays (Assawoman and Isle of Wight) versus the southern bays (Sinepuxent and Chincoteague) due largely to the stronger currents deflected north from the inlet at Ocean City (Fig. 1). Because of the various influences on the specific embayments including eutro-

phication (Boynton et al. 1996), abiotic variability, habitat variation including submerged macrophyte coverage (Wazniak et al. 2004), wetland acreage, anthropogenic alteration (Maxted et al. 1997), and differing geomorphologies (Pritchard 1960; Cerco et al. 1978), we hypothesized that each embayment would support a distinct, identifiable fish and macroinvertebrate community. Because this is a temperate system, we also hypothesized that spatial differences in assemblage structure will vary seasonally.

The Delmarva coastal lagoon complex represents an opportunity to analyze assemblage structure related to season and habitat attributes specific to constituent embayments. We analyzed a moderately long-term data set (12 yr, 1991–2002) available from Maryland Department of Natural Resources. Our objectives were to evaluate differences in assemblage structure among the four primary embayments in Maryland and identify the discriminating species, contrast metrics of biodiversity across the four embayments and compare these metrics to other assemblage characteristics, characterize seasonal changes in assemblage structure, and contrast biological attributes of Maryland coastal bays to similar systems of the mid Atlantic region.

Materials and Methods

STUDY AREA

The Maryland coastal lagoon complex extends along the entire Atlantic coast of the state behind the barrier islands of Assateague and Fenwick. The system consists of four major embayments: the southern embayments of Chincoteague and Sinepuxent, and the northern embayments of Assawoman and Isle of Wight (Fig. 1). A large urban resort community, Ocean City, is located on Fenwick Island. These embayments are connected to several smaller tidal creek systems with low freshwater discharge and exhibit little stratification due primarily to wind-driven mixing (Cerco et al. 1978).

The coastal bays and associated tributaries are shallow, with an average depth of 1.2 m. The watersheds of the embayments are relatively small compared to open water areas (45,246 ha, or about 1.7 times the area of the bays; Boynton et al. 1996). The coastal bays maintain only two connections through relatively small inlets to ocean waters: Ocean City Inlet, which separates the northern and southern embayments, and a series of southern channels received by Chincoteague Bay. The combination of reduced freshwater input and limited oceanic exchange results in low water replacement times and causes these systems to retain nutrients, sediments, and other inputs from the watershed. The northern coastal bays (Assawoman and Isle of

Wight) are relatively enriched with nitrogen (median N [2000–2002] > 1 mg l⁻¹) while the southern bays (Sinepuxent and Chincoteague) exhibit lower total nitrogen concentrations (median N [2000–2002] < 1 mg l⁻¹; Wazniak et al. 2004). Seagrass coverage varies between the four systems, with Chincoteague showing substantially higher areal coverage. Over the course of the survey corresponding to this study, seagrass coverage in each of the bays has increased dramatically (Wazniak et al. 2004).

SURVEY DESIGN

Beginning in 1972, the Maryland Department of Natural Resources initiated a biological survey of the four coastal embayments. The survey methodology was standardized in 1991 and this analysis consists of data collected from 1991 to 2002. Twenty fixed trawl stations were established throughout the four embayments (Fig. 1). Trawl samples were collected by a 4.8 m semi-balloon trawl with tickler chain towed at ca. 3 knots for 6 min. The mean estimated area sampled per tow was 1,864 m². Samples were sorted by species and identified in the field. Water quality collected at each sampling event included dissolved oxygen (mg l⁻¹), salinity, and temperature. Trawl sites were sampled seasonally: spring (April–May), early summer (June–July), late summer (August–September), and autumn (October).

STATISTICAL ANALYSES

Because sampling effort was uneven between the four embayments, catch per unit effort (CPUE; i.e., catch per tow or haul) statistics were calculated for each bay. Water quality parameters were tested for significance using a two-way analysis of variance (ANOVA) with site nested within embayment and embayment nested within season (Sokal and Rohlf 1995). Assumptions for the ANOVA (normality and homogeneity of variances) were examined both visually and using the Shapiro-Wilkes test statistic. Water quality data met the assumptions of the ANOVA model and did not require transformations.

Variations in individual species abundance were analyzed for differences among bays and seasons and for possible associations with environmental variables. For this analysis, CPUE was calculated for each site with sample catches pooled across years. Individual species abundance was transformed if necessary and analyzed for potential embayment or seasonal effects. If normality was not achieved through data transformation, a Kruskal-Wallis (K-W) nonparametric test was used to determine departure from the null hypothesis (Sokal and Rohlf 1995).

COMMUNITY ANALYSIS

As a complement to the more generally applied species richness and the Shannon-Weiner indices (Peet 1974), we also constructed k-dominance curves to show structure relative to dominant species and number of individuals (Lambhead et al. 1983). Species composition analysis was conducted using nonmetric multidimensional scaling (MDS), which is appropriate in ordination of nonparametric data (Fasham 1977; Clarke 1993; Clarke and Ainsworth 1993). MDS plots were based on similarity matrices, constructed using an abundance weighted Bray-Curtis similarity index. Sample sites were used as the sampling unit (pooled across season and year) to look for patterns among embayment assemblages. The goodness of fit of the data distributed across two composite axes was indexed by the stress coefficient, which tends towards zero when the data are perfectly represented. Stress represents the distortion involved in representing multidimensional data in two dimensions (Field et al. 1982). MDS plots are deemed an acceptable representation of the data when stress values are < 0.2 (Clarke 1993).

Differences in assemblage structure between embayments or seasons identified by MDS was further analyzed by permutation-based, one-way analysis of similarity (ANOSIM; Clarke 1993). Where appropriate, R statistic values were used to determine the dissimilarity of groups. R values were protected for pairwise comparisons and represent the extent of similarity between two groups. Values close to 1 indicated very different composition between samples, while values near zero are expected to exhibit little difference. ANOSIM was used to test the null hypothesis that within seasons, no changes in community structure were observed between the embayments, and to test that within single embayment assemblages, there was no difference between seasons. To establish which species most contributed to community structure, the similarity percentage analysis (SIMPER) approach was used (Clarke 1993). This method identifies which species (due to their relative abundances) are contributing most to the overall dissimilarity between defined (a priori) groups. Multivariate community analyses were carried out in the Community Analysis and Species Richness and Diversity Packages (Pisces Conservation, Ltd., 1997).

Results

WATER QUALITY

During the period April–October (1991–2002), salinity varied between 8.1 to 37.4, water temperatures varied from 9.9°C to 32.3°C, and dissolved oxygen concentrations ranged from 1.8 to

TABLE 1. Number of species, individuals, and mean catch per site for each embayment and season, 1991–2002.

Season	Bay	No. Species Caught	No. Sites	No. Individuals	Mean Catch per Site (no. Individuals)
Spring	All	51	20	52,874	2,644
Early summer	All	76	20	135,385	6,769
Late summer	All	77	20	92,214	4,611
Fall	All	59	20	21,238	1,062
All	Assawoman	59	3	81,439	27,146
All	Isle of Wight	80	4	84,936	21,234
All	Sinepuxent	60	3	9,236	3,079
All	Chincoteague	83	10	126,100	12,610

11.2 mg l⁻¹. Salinity and temperature were significantly different between bays and seasons ($p \leq 0.001$, $df = 3$) whereas dissolved oxygen differed only between seasons ($p \leq 0.001$). Salinity was the only parameter that differed significantly ($p \leq 0.001$, $df = 65$) between sites (as a nested component of ANOVA). Mean salinity was highest in Sinepuxent (mean = 29.3) and lowest in Isle of Wight (mean = 26.8). Pairwise comparisons between bays indicated no difference in salinity between Assawoman and Isle of Wight. Sinepuxent bay was typically cooler (mean temp = 20.5°C) than the other three embayments; temperatures did not differ significantly among these three bays (mean temp = 21.7°C). Each embayment had seasonal differences in all water quality parameters.

CATCH CHARACTERISTICS

From 1991 to 2002, 1744 tows were made collecting 286,486 specimens and 96 species (Table 1). Trawl samples were dominated by 9 species comprising 95% of the catch. These were in descending order of abundance: *Callinectes sapidus*, *Anchoa mitchilli*, *Leiostomus xanthurus*, *Cynoscion regalis*, *Clupea harengus*, *Micropogonias undulatus*, *Paralichthys dentatus*, *Bairdiella chrysoura*, and *Brevoortia tyrannus*. Catch per site (CPS) differed between bays and seasons with the northern bays of Assawoman and Isle of Wight exhibiting higher CPS than the southerly bays of Sinepuxent and Chincoteague. The trawl data also indicated a seasonal pattern in CPS, with lower numbers of species and organisms caught in the spring and fall than in summer months.

SINGLE SPECIES

Dominant species differed significantly among bays, seasons, and years. *C. sapidus* (species rank = 1; Table 2) abundance was significantly different between seasons ($p < 0.0001$) consistently showing peaks in the early summer across all years (Fig. 2), but exhibiting fairly low interannual variability (coefficient of variation [CV] of annual means = 0.33). *C. sapidus* distribution was also different between bays ($p < 0.0001$) with ca. twofold less

abundance observed in Sinepuxent than in other bays. Interannual variation was low to moderate for all of the dominant species (Table 2). *A. mitchilli* abundances showed moderate interannual variation, with significant differences occurring between seasons and bays ($p < 0.0001$ each). Similar to *C. sapidus*, *A. mitchilli* mean abundance was c. 50% lower in Sinepuxent than the other bays. This same spatial distribution pattern was observed for *L. xanthurus*, a schooling demersal species, where Sinepuxent was significantly lower than the other systems ($p < 0.0001$) and a seasonal shift was evident with peaks in the early summer.

C. regalis, another demersal species, showed significant seasonal and embayment differences ($p < 0.0001$ each). Abundance tended to peak in summer months, and the northern bays of Assawoman and Isle of Wight exhibited ca. twofold higher abundances than the Chincoteague or Sinepuxent. *C. harengus* was a dominant springtime species, which again exhibited lower abundances in Sinepuxent Bay than other embayments ($p < 0.01$).

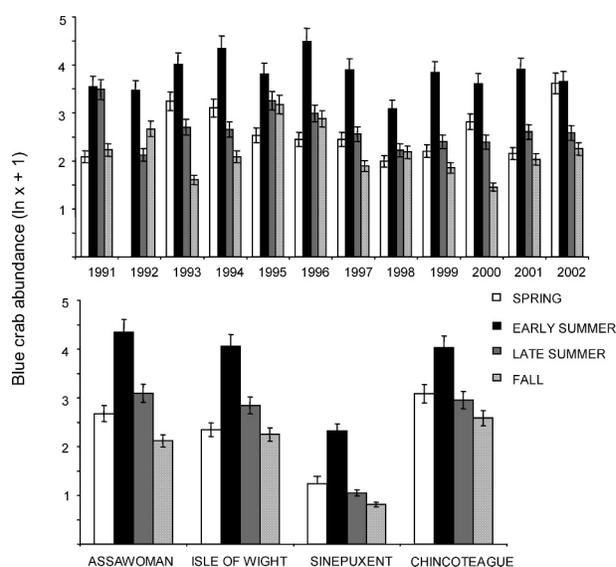


Fig. 2. Blue crab abundance transformed ($\ln x + 1$) across years (top) and embayments (bottom). Bars indicate standard error.

TABLE 2. Ranked list of 9 dominant species (those comprising 95% of abundance) caught 1991–2002 in descending order, with coefficients of variation (CV). All other species accounting for < 5% are listed below table.

Common Name	Scientific Name	Species Rank (% Catch)	CV
Blue crab	<i>Callinectes sapidus</i>	1 (28.6)	0.33
Bay anchovy	<i>Anchoa mitchilli</i>	2 (25.5)	0.6
Spot	<i>Leiostomus xanthurus</i>	3 (24.3)	1.68
Weakfish	<i>Cynoscion regalis</i>	4 (6.7)	0.74
Atlantic herring	<i>Clupea harengus</i>	5 (3.2)	0.99
Croaker	<i>Micropogonias undulatus</i>	6 (2.7)	0.72
Summer flounder	<i>Paralichthys dentatus</i>	7 (2.2)	0.44
Silver perch	<i>Bairdiella chrysoura</i>	8 (1.1)	0.61
Atlantic menhaden	<i>Brevoortia tyrannus</i>	9 (0.6)	1.19

Trinectes maculatus, *Synodus foetens*, *Pleuronectes americanus*, *Menidia menidia*, *Centropristis striata*, *Sphoeroides maculatus*, *Syngnathus fuscus*, *Apeltes quadracus*, *Prionotus carolinus*, *Etropus microstomus*, *Gobiosoma bosc*, *Anchoa hepsetus*, *Urophycis regia*, *Lucania parva*, *Scophthalmus aquosus*, *Mustelus canis*, *Raja eglanteria*, *Gymnura micrura*, *Dasyatis americana*, *Rhinoptera bonasus*, *Anguilla rostrata*, *Conger oceanicus*, *Dorosoma cepedianum*, *Alosa aestivialis*, *Opsanus tau*, *Gobiosox strumosus*, *Pollachius virens*, *Urophycis chuss*, *Ophidion marginatum*, *Strongylura marina*, *Cyprinodon variegatus*, *Fundulus diaphanus*, *Fundulus heteroclitus*, *Fundulus majalis*, *Menidia beryllina*, *Membras martica*, *Hippocampus erectus*, *Syngnathus floridae*, *Fistularia tabacaria*, *Prionotus evelans*, *Peprilus alepidotus*, *Peprilus triacanthus*, *Ammodytes americanus*, *Selene setapinnis*, *Selene vomer*, *Caranx hippos*, *Trachurus lathami*, *Rachycentron canadum*, *Scomberomorus cavalla*, *Scomberomorus maculatus*, *Upeneus parvus*, *Mugil cephalus*, *Mugil curema*, *Sphyrna borealis*, *Astroscopus guttatus*, *Cynoscion nebulosus*, *Menticirrhus saxatilis*, *Pogonias chromis*, *Chaetodipterus faber*, *Pomatomus saltatrix*, *Microgobius thalassinus*, *Chasmodes bosquianus*, *Hypsoblennius hentz*, *Morone americana*, *Morone saxatilis*, *Chaetodon ocellatus*, *Eucinostomus argenteus*, *Archosargus probatocephalus*, *Diplodus holbrooki*, *Lagodon rhomboids*, *Stenotomus chrysops*, *Lutjanus campechanus*, *Lutjanus griseus*, *Orthopristis chrysoptera*, *Tautoga onitis*, *Tautoglabrus adspersus*, *Mycteroperca microlepis*, *Balistes capricus*, *Aluterus schoepfi*, *Monacanthus hispidus*, *Chilomycterus schoepfi*, *Lagocephalus laevigatus*, and *Symphurus plagiatus*.

M. undulatus (rank = 6) distribution was significantly different between bays and seasons (K-W nonparametric test, $p < 0.0001$ for each factor). *M. undulatus* abundance was generally highest in the fall, but this pattern was variable between years (Fig. 3). Its abundances in the northern two bays were twofold higher than those in the southern two bays. *P. dentatus* (rank = 7) showed highest abundances during early summer (seasonal effect; K-W, $p < 0.0001$). Its distribution varied significantly between bays (K-W, $p < 0.0001$), with generally lower abundances in the Sinepuxent than elsewhere. The species exhibited relatively low intrannual variation across the bays (CV = 0.44). *B. chrysoura* differed in abundance significantly by bay and season (K-W, $p < 0.0001$) with a peak abundance in late summer and higher abundances in Assawoman and Isle of Wight bays. *B. tyrannus* abundance tended to peak in early summer. CPS was significantly influenced by embayment (K-W, $p < 0.001$) and season (K-W, $p < 0.001$). No *B. tyrannus* were observed for Sinepuxent samples, and the Isle of Wight showed significantly higher abundances than elsewhere.

ASSEMBLAGES AND EMBAYMENTS

The MDS plots for trawl data indicated fairly tight ordination of specific embayments (Fig. 4). The stress statistics were all low, signifying that the two-dimensional plots were representative of the relationship between sites. The northern bays of Assawoman and Isle of Wight ordinated together along axis 1 whereas Sinepuxent ordinated along

both axes, remaining separate from the other embayments along axis 1. Chincoteague sites generally clustered together with dispersion along both axes. Individual sites 20 and 12 were discrete from other Chincoteague sites, while site 7 (Isle of Wight) was separate from the other sites of that

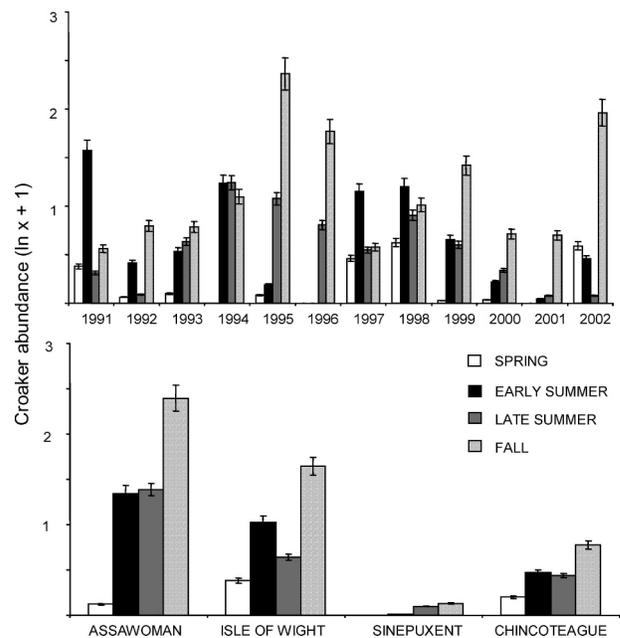


Fig. 3. Atlantic croaker abundance transformed ($\ln x + 1$) across years (top) and embayments (bottom). Bars indicate standard error.

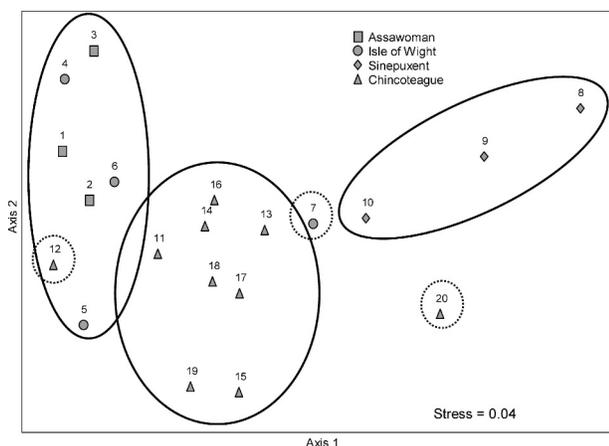


Fig. 4. Nonmetric multidimensional scaling (MDS) plots of trawl sites based on species abundances, 1991–2002. Site identification numbers are referenced in Fig. 1. Solid line ovals outline groups according to embayment, while dotted line ovals delineate sites termed anomalous from their respective system. Note that the two northern bays, Assawoman and Isle Wight, are classified together in this ordination.

embayment. When data for each embayment were compared on a seasonal basis, separation of sites according to bays remained apparent.

The separation of sites by embayment was supported by the ANOSIM analysis ($r = 0.45$, $p < 0.004$; Table 3). Pairwise comparisons (Bonferroni adjusted significance level to account for multiple [$n = 6$] comparisons) were significant between Assawoman and Chincoteague and between Sinepuxent and each of the other bays. MDS plots by season showed moderate separation between early and summer samples, but broad overlap across

TABLE 3. Analysis of similarity by embayment and season for the trawl survey, 1991–2002. Pairwise tests between bays are protected at $\alpha = 0.005$ level. See text for discussion of interpretations for R values. The number in parentheses by each embayment indicates number of sites used in analysis (bay and season).

1st Group	2nd Group	p	Sample R
By bay (sample R = 0.45, $p < 0.004$)			
Assawoman (3)	Chincoteague (10)	0.04	0.42
Assawoman (3)	Isle of Wight (4)	0.85	-0.19
Assawoman (3)	Sinepuxent (3)	0.05	1
Chincoteague (10)	Isle of Wight (4)	0.08	0.25
Chincoteague (10)	Sinepuxent (3)	0.01	0.7
Isle of Wight (4)	Sinepuxent (3)	0.05	0.78
By season (sample R = 0.30, $p < 0.001$)			
Early summer (20)	Fall (20)	0.001	0.53
Early summer (20)	Late summer (20)	0.001	0.22
Early summer (20)	Spring (20)	0.001	0.31
Fall (20)	Late summer (20)	0.001	0.24
Fall (20)	Spring (20)	0.001	0.25
Late summer (20)	Spring (20)	0.001	0.26

TABLE 4. Results from similarity percentage (SIMPER) analysis for the trawl survey, 1991–2002. Diagnostic species are listed in descending order of percent contribution to overall bay similarity. Those species that contribute to the top 90% ranked species are shown. Mean abundance is mean number of individuals per embayment over the 10-yr survey.

Typifying Species	Mean Abundance	% Contribution	Cumulative %
Assawoman			
<i>A. mitchilli</i>	7,930.3	30.2	30.2
<i>L. xanthurus</i>	7,038.0	27.2	57.4
<i>C. sapidus</i>	4,739.7	19.3	76.7
<i>C. regalis</i>	3,690.0	12.2	88.9
<i>M. undulatus</i>	1,164.0	3.6	92.5
Isle of Wight			
<i>L. xanthurus</i>	5,205.8	30.0	30.0
<i>C. sapidus</i>	5,201.0	26.4	56.4
<i>A. mitchilli</i>	5,892.8	24.6	81.0
<i>C. regalis</i>	1,657.7	7.4	88.4
<i>P. dentatus</i>	3,95.0	2.9	91.3
Sinepuxent			
<i>C. sapidus</i>	944.3	31.9	31.9
<i>A. mitchilli</i>	937.7	23.1	55.0
<i>L. xanthurus</i>	339.7	9.5	64.5
<i>P. dentatus</i>	129.0	7.3	71.7
<i>S. maculatus</i>	77.4	4.2	75.9
<i>P. carolinus</i>	75.6	4.1	80.0
<i>S. foetens</i>	73.3	3.7	83.7
<i>E. microstomus</i>	83.0	3.0	86.7
<i>S. aquosus</i>	55.0	2.1	88.8
<i>C. striata</i>	46.7	2.0	90.8
Chincoteague			
<i>C. sapidus</i>	4,849.3	43.6	43.6
<i>L. xanthurus</i>	3,030.6	24.7	68.3
<i>A. mitchilli</i>	2,677.5	20.7	89.0
<i>P. dentatus</i>	322.2	2.7	91.7

other seasons. The ANOSIM procedure confirmed this pattern in that there was a significant difference between seasons, but a low R value ($r = 0.30$; $p < 0.001$) indicated high overlap (Table 3). The SIMPER analysis showed that each bay had distinctive species in terms of their relative abundances. The higher relative abundances of *A. mitchilli*, *L. xanthurus*, and *C. sapidus* distinguished the fauna of Assawoman Bay (Table 4) from other bays. In general the relative abundance of these three species, in addition to *C. regalis* and *P. dentatus*, were diagnostic among the bays. Note that these dominant species were consistently higher in relative abundance in the northern two bays than in the southern two bays. In this analysis, Sinepuxent required the greatest number of species (10) to meet the 90% similarity measure.

DIVERSITY

Species richness (Fig. 5) showed significant differences between bays (ANOVA, $F = 58.5$, $p < 0.0001$) and seasons ($F = 153.3$, $p < 0.0001$). The

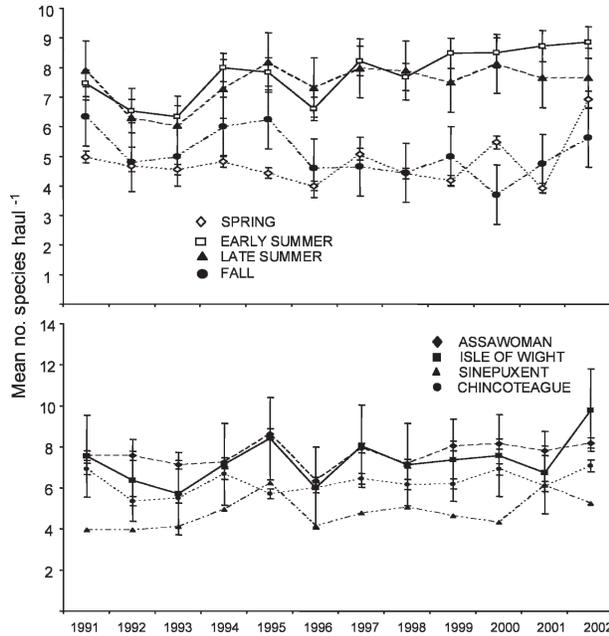


Fig. 5. Mean number of species per haul for 1991–2002 Maryland Department of Natural Resources coastal finfish trawl survey by season (top) and embayment (bottom). Bars represent standard error.

northern bays of Assawoman (mean = 7.6) and Isle of Wight (mean = 7.3) were higher in species richness compared to those of Sinepuxent (mean = 4.8) and Chincoteague (mean = 6.2). The two summer periods were not statistically different from each other, but each was significantly higher than spring and fall samples based on Tukey's protected pairwise comparisons. The mean species richness per haul was without trend during the survey period, but showed a small peak in all bays except Chincoteague in 1995. A second peak was evident for 2002 for Isle of Wight (Fig. 5).

The Shannon-Wiener diversity index H' varied across years and was statistically different between bays ($F = 5.5$, $p < 0.001$) and seasons ($F = 67.9$, $p < 0.0001$). Similar to species richness, H' was highest in the northern bays and higher during summer months than during spring or fall. The k -dominance curves (Fig. 6) overlapped, curtailing clear interpretations. Greater dominance by just a few species in Chincoteague Bay was indicated by a higher y -intercept. The Sinepuxent curve flattened out sooner indicating less dominance and perhaps a greater number of rare species. The k -dominance curves showed good separation among seasons (Fig. 6). The fall curve was consistently lower indicating greater diversity and less dominance in comparison to summer seasons.

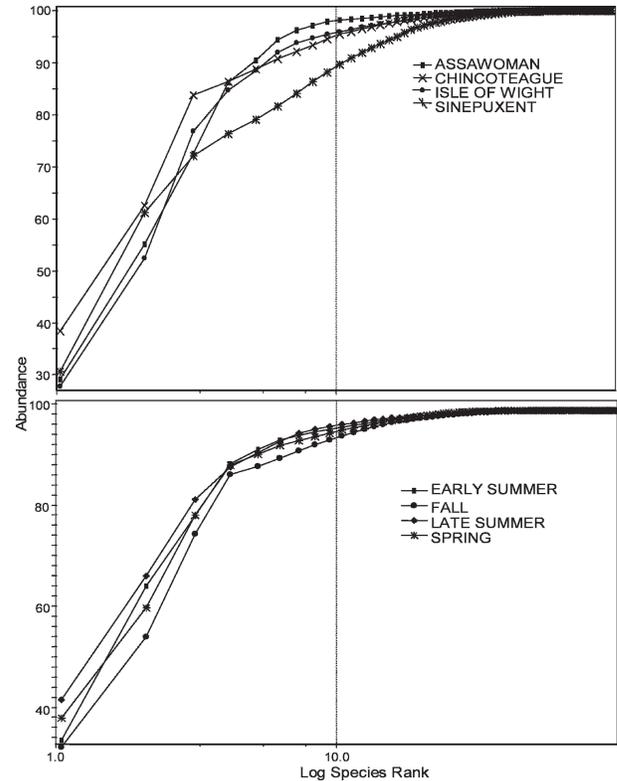


Fig. 6. K -dominance curves by embayment (top) and season (bottom).

Discussion

FISH ASSEMBLAGES BY EMBAYMENT

The particular abiotic attributes of lagoons (shallowness, high turbidity, nature of the substrate, temperature fluctuation, salinity, and oxygen levels) associated with their high biotic productivity often offer excellent conditions for colonization by many marine species of fish (Pollard 1994; Yáñez-Arancibia et al. 1994; Nixon et al. 2001; Poizat et al. 2004; Vega-Cendejas and Hernandez de Santillana 2004). Considerable evidence supports the role of the lagoon-estuarine environment in the life cycles of coastal species (Day and Yáñez-Arancibia 1985; Yáñez-Arancibia et al. 1994; Secor and Rooker 2005), and various explanations have been proposed to link abundances with environmental parameters (Nixon 1982; Whitfield 1999; Martino and Able 2003). The coastal bays of Maryland support a diverse array of fish species comparable to other estuarine systems of the Mid Atlantic Bight (Table 5). Ordination and cluster analyses demonstrated that each bay harbors a distinct assemblage of finfish and *C. sapidus*, and that these differences between systems were due to the relative abundances of relatively few dominant species. There also was a general pattern of higher diversity and

TABLE 5. Comparison of species richness between adjacent coastal systems along the mid Atlantic coast.

System	No. Species	Duration of Study (yr)	Sampling Gear	Source
Chesapeake Bay	57	5	Mid water trawl	Jung and Houde 2003
Delaware River	63	14	Beach seine	Weisberg et al. 1996
Delaware Coastal Bays	46	3	Beach seine and otter trawl	Derickson and Price 1973
Maryland Coastal Bays	94	12	Beach seine and otter trawl	This study
Great Bay, New Jersey	26	3	Otter trawl	Martino and Able 2003
Atlantic Ocean surf zone, Virginia	12	3	Surf seine	Layman 2000
Pamlico Sound, North Carolina	78	2	Otter trawl	Ross and Eppersly 1985

abundance of dominant species in the two northern bays in comparison to the two southern bays.

Inlets are the major, if not exclusive source for marine transients into coastal lagoons (Mariani 2001). While each of the Maryland embayments supports distinct assemblages, it is apparent that there is a discrete effect produced by the inlets on those sites closest to them. Most of the sites align with other sites of the same embayment suggesting that the sites represented the assemblage of each embayment. Yet, some sites were distinctly ordinated away from their respective embayment and these may have been related to proximity to direct connections to coastal and freshwater inputs. Sites 12 and 20 were anomalous from other sites in Chincoteague Bay (Fig. 4). Site 12 lies within the northwestern portion of the bay in the subembayment of Newport Bay. This watershed (fed by Trappe and Ayres Creeks) drains the town of Berlin and the water quality is marginal to poor (Wazniak et al. 2004). This site is more aligned with those of the northern bays presumably due to similar water quality conditions supportive of similarly tolerant species (e.g., *B. tyrannus*). Site 20 is the southernmost site and while it was an outlier across all bay sites, it loosely ordinated with Sinepuxent sites. This site was most proximate to the southern inlet (Chincoteague) and increased marine influence may have caused this site to ordinate close to Sinepuxent Bay, which is most proximate to the marine influence of Ocean City Inlet. Site 7 was anomalous among Isle of Wight sites and appeared to be more associated with the Sinepuxent sites. Again, this may reflect the proximity of this site to the Ocean City Inlet and the marine influence on the assemblage there.

Previous studies comparing assemblages in estuarine and coastal systems have focused on trends in species richness along gradients (Wagner 1999; Jung and Houde 2003; Martino and Able 2003), but rarely make direct comparisons between constituent systems using community metrics (Weinstein 1985). Maryland's coastal embayment assemblages were characterized broadly by the species richness trends, Shannon-Weiner index, and k-dominance curves. There were significant differences in the number of species taken per sample

between each of the bays, with the northern bays (Assawoman and Isle of Wight) supporting a higher richness than the southern bays. No difference occurred between the two northern bays, while Chincoteague and Sinepuxent were different, with a particularly low number of species found in Sinepuxent (ca. 4.8 haul⁻¹). Assawoman Bay consistently supported a higher number of species and individuals per unit effort even though the total number of species caught in the system was lowest (59 total). This presents an interesting contrast: Assawoman Bay is supporting high diversity at the sample level, but overall, not as many species are coming into the system. Assawoman Bay is supporting a resident assemblage that is fairly diverse, but fewer species exploit the bay over time. Causal factors of these differences could include eutrophication and associated water quality, habitat heterogeneity, or disturbance.

The northern bays exhibit higher nutrient loads coupled with reduced habitat heterogeneity due to relatively low coverage of seagrasses (predominantly *Zostera marina*) and increased development of the surrounding resort community (Wazniak et al. 2004). The higher abundances in the northern bays are consistent with the view that increased nutrient loads lead to increased fish productivity (Lee and Jones 1991; Nixon and Buckley 2002). Eutrophication can also significantly affect the types of fish present in a waterbody (Caddy 2000). Highly eutrophic water bodies tend to have dominant populations of rough or pelagic fish that feed at lower trophic levels (Lee and Jones 1991; Price 1998). As a mechanism underlying this community shift, some authors (Lee and Jones 1991; Jeppesen et al. 2000) have suggested reduced foraging by piscivorous species, brought about by increased turbidity from increased concentrations of phytoplankton. Median annual values for phytoplankton stocks offer some support for this view (2001–2004; chlorophyll *a* [$\mu\text{g l}^{-1}$]): Assawoman = 15, Isle of Wight = 11, Sinepuxent = 5, Chincoteague = 5, from Wazniak et al. 2004).

Price (1998) compared patterns of littoral species assemblages in the Maryland embayments with those of Delaware (heavily eutrophied and lacking seagrass habitat) and concluded that the eutrophied

systems in Delaware shifted to a *Fundulus*-dominated system in contrast to *B. tyrannus*, *L. xanthurus*, and *Menidia menidia* in more oligotrophic systems. CPS (seine) for *F. heteroclitus* and *F. majalis* was generally higher in Sinepuxent Bay (Murphy 2005) than the other bays contrary to an expectation of higher abundances in the two northern bays. Caddy (2000) proposed that eutrophication may cause a shift in dominance from demersal species to pelagic species that are better equipped to exploit increases in primary production, which is consistent with observed higher abundance of *B. tyrannus* and *L. xanthurus* in the Northern embayments.

SEASONAL VARIABILITY

Peak catches occurred in the summer seasons, with abundances much reduced in spring and fall. The pairwise comparisons between seasons, although all statistically significant, resulted in low R values, indicative of strong overlap in species composition. This suggests that while the seasons were discrete in terms of assemblage structure, many species were using these embayments for longer than one season, with the notable exception of *C. harengus* that only occurred in the spring.

C. sapidus showed a consistent peak in abundance in early summer (Fig. 3), and this pattern occurred across all embayments. *C. sapidus* exhibit migratory patterns in the coastal embayments (Cargo 1958) although gradients in salinity are small. Cargo (1958) showed through tagging experiments that crabs migrated to the southern inlet at Chincoteague although tagged crabs were released much nearer to the inlet at Ocean City. Cargo also noted that there may be a resident population that completes its life cycle entirely within the embayments without migrating into coastal waters. The seasonal patterns in abundance in this study supported a possible late summer emigration to southern Chincoteague Bay (not sampled) or the ocean, although another possible explanation is harvest depletion by fishermen during the summer months.

COMMUNITY STRUCTURE

Simple area or volume of habitat can explain substantial variability in species richness across ecosystems (Wootton 1999; Frank and Shackell 2001). Wootton (1999) asserts several hypotheses that may account for a positive correlation between species richness and area. Large areas by definition provide more space and are more likely to support rare species. Chincoteague Bay (area = 189×10^6 m² from Boynton et al. 1996) is by far the largest embayment and did exhibit the highest overall species count (Table 1). Larger areas also are more

likely to support diverse habitats (e.g., oyster reefs, seagrass, and channel edges), supporting more species that exploit these niches. Chincoteague has a greater amount of seagrass coverage than the other three embayments, but all are devoid of reef structure (Wazniak et al. 2004). The third possible reason for the area-richness relationship suggested by Wootton (1999) is that assemblages in small areas are more likely to incur high rates of extinction and lower rates of immigration. The extinction scenario is unlikely in the coastal bays due to the proximity of alternative habitats; differential immigration may be a plausible explanation for the low mean species per haul seen in Sinepuxent Bay, if this bay receives less oceanic influence due to reduced immediate ocean flow (through Ocean City inlet). Alternatively, species are arriving in high diversity to Chincoteague. It is possible that the southern Chincoteague route for immigration is a dominant determinant of diversity throughout the Chincoteague. Chincoteague Bay diversity indices may have been higher due to the increased sampling effort there compared to the other three embayments.

Maryland coastal lagoons harbor large regions of seagrass coverage, predominantly *Ruppia maritima* and *Z. marina*. Chincoteague and Sinepuxent Bays are well vegetated (32% and 36%, respectively) compared to Assawoman and Isle of Wight (8% and 6%, respectively; Wazniak et al. 2004). Although seagrass is known as important fish habitat (Orth and Heck 1980; Olney and Boehlert 1988; Heck et al. 2003), we did not observe a significant affect of seagrass coverage on either species richness ($p = 0.19$) or CPUE ($p = 0.10$). Seagrass coverage may be important in many coastal systems, but other factors appear to be reducing its effect; e.g., seagrass can affect sampling efficiency and lead to underrepresented estimates of diversity and abundance (Serafy et al. 1988).

Most species encountered in mid Atlantic coastal bays are spawned elsewhere and enter the coastal bays either passively (via oceanic transport; Warlen et al. 2002) or actively as they search for foraging regions or refugia (Heck et al. 2003). Recruitment (e.g., *B. tyrannus* and *C. sapidus*) is often driven externally by oceanic circulation and wind patterns (Epifanio and Garvine 2001; Warlen et al. 2002). The assemblages of these systems are structured by large-scale external processes that affect the four connected bays similarly. In this respect, the embayments respond as open systems, mediated by oceanic influences through the Ocean City Inlet and to a lesser extent, the Chincoteague Inlet. On a smaller scale, the embayments may exhibit attributes of closed systems. The northern bays are affected to a greater degree by anthropogenic

eutrophication and shoreline modification than the southern bays. Interestingly, on a site-specific basis, the more productive and diverse assemblages are those exposed to higher rates of eutrophication and habitat alteration.

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