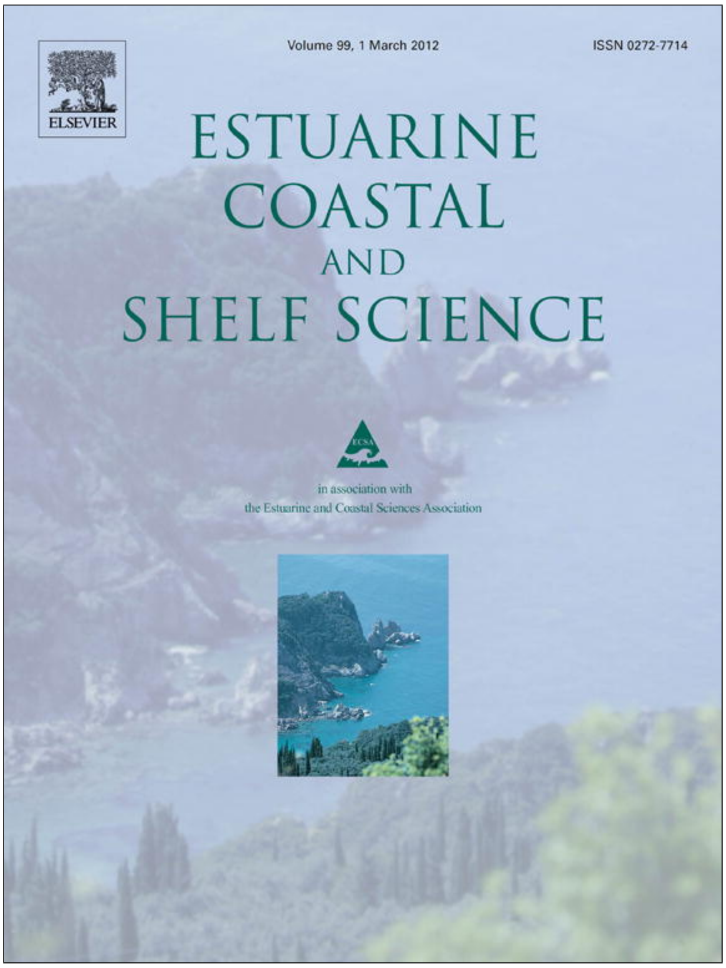
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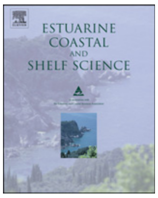

Comparing the nursery role of inner continental shelf and estuarine habitats for temperate marine fishes

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ABSTRACT

The marine-estuarine transition represents an important biogeographic boundary, yet juvenile marine finfish have been observed in both temperate inner continental shelf (ICS) and estuarine habitats during the summer nursery period. In a direct comparison of ICS and estuary nurseries, spatial and temporal patterns in species composition, biodiversity, size structure, and relative abundance of age-0 fishes were tested using contemporaneous data from multiyear (2004–2006) trawl surveys of the Maryland ICS near Assateague Island, MD, and lower Chesapeake Bay, VA (estuary). Survey data from both habitats showed similar seasonal progression of assemblage structure, biodiversity phenologies, and dominant species identities. Late summer densities for four of five numerically dominant species varied by habitat. Densities of bay anchovy *Anchoa mitchilli*, weakfish *Cynoscion regalis*, and Atlantic butterfish *Peprilus triacanthus* were higher in the ICS; whereas summer flounder *Paralichthys dentatus* density was higher in the estuary. Density of spot *Leiostomus xanthurus* did not differ between habitats. Apparent daily growth rates of these five species, as estimated by modal length progression, were not significantly different between the two habitats. Although individual species displayed varying affinities for ICS versus estuarine habitats, this study provides strong evidence that the ICS of the Middle Atlantic Bight is capable of functioning interchangeably with polyhaline estuarine regions as nursery habitat for a diverse group of marine finfish.

1. Introduction

Coastal habitats play a critical role as nurseries in the early life history of many marine fish species (Ray, 2005) but juvenile production varies with heterogeneity in biotic and abiotic properties across space and time. Within the mosaic of coastal habitats, the relative importance of estuaries versus inner continental shelf (hereafter "ICS") habitats has received recent attention (see Able, 2005 for a review) despite a longstanding recognition that faunal similarities can arise between these habitats (e.g., McHugh, 1967). The traditional view that the marine-estuarine transition functions as an important biogeographic boundary between the coastal ocean and estuarine nursery habitats has been revised due to evidence of recruitment of the same species to both estuarine and coastal marine habitats (Lenanton, 1982; Bennet, 1989; McBride and Conover, 1991; Blaber et al., 1995; Able et al., 2006). In contrast, a continuum model of biotic structuring (consistent with the ecocline concept, van der Maarel, 1990; Yarrow and Marin, 2007) suggests that these species are responding to the marine-estuarine transition as a zone of suitable habitat types nested within one or more gradients.

Conceptualizing the marine-estuarine transition as a coastal continuum emphasizes that nekton assemblages are structured by a gradient of similar physicochemical conditions (e.g., salinity, temperature, turbidity) arising from the mixing of estuarine and shelf water masses (Ray, 1991; Able, 2005; Elliott et al., 2007 and references therein). Despite these physicochemical similarities, there are evident (e.g., bathymetry, wave action, circulation dynamics), as well as hypothesized (e.g., predator prevalence), differences between these two habitats. Still, direct comparisons of juvenile habitat use patterns are relatively scarce due to logistical constraints associated with concurrent sampling of estuarine and ICS habitats and the paucity of coastal ocean monitoring relative to established estuarine surveys (Able, 2005).

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One of the most striking features of the coastal ocean environment in comparison to estuaries is the vast areal extent of the ICS. For example, the ICS of the Middle Atlantic Bight (MAB) extends roughly 1000 linear km from the southern terminus of Cape Cod, MA to Cape Hatteras, NC (Townsend et al., 2004) with a 20-m isobath that is widest in the central bight and averages 16 km offshore (c. 20,000 km^2). The ICS could substantially increase potential nursery area beyond the physical confines of estuaries; yet the function of the ICS habitats for individual species and the implication for population and community-level dynamics remains largely uninvestigated (Able, 2005; Fodrie et al., 2009). In fact, Beck et al.'s (2001) proposed nursery definition based on per-unit-area productivity has stimulated specific debate regarding the role of spatially expansive habitats capable of contributing greater overall recruitment to adult stocks despite lower per-unit-area juvenile productivity (Kraus and Secor, 2005; Dahlgren et al., 2006; Fodrie and Mendoza, 2006).

At the individual level, larger nursery areas can reduce competition and thereby foster higher growth rates (McCall, 1990; Beck et al., 2001); rapid growth during early life stages leads to larger size-at-age and can reduce size-dependent mortality (Sogard, 1997; Houde, 2009). The spatial or temporal separation of juvenile cohorts across multiple nurseries can dampen interannual recruitment variability by hedging against the inherent variability in biotic and abiotic conditions encountered during early life history (Secor, 2007; Planque et al., 2010). Thus, the availability of multiple nursery habitats can promote stability and persistence of populations and assemblages (Hilborn et al., 2003; Kraus and Secor, 2005; Kerr et al., 2009) or sustain remnant populations.

In estuaries and ICS habitats of the temperate MAB, seasonal residence by juveniles during the summer months followed by a southward or offshore autumnal migration is the predominant early life-history strategy among transient marine fish species (Able and Fahay, 1998; Nordlie, 2003). The predominance of this phenology provides a temporal context in which to evaluate patterns in juvenile habitat use within and across species. The seasonally pulsed arrival and departure of juveniles (often observed as discrete seasonal cohorts; e.g., Callihan et al., 2008) contributes to a dynamic mixture of predator, prey and competitor species. Habitat-specific variations in recruitment patterns alter local assemblage structure and can thus modulate the magnitude and ecological importance of interactions between species, which are often size-, age-, or density-dependent. These changes in assemblage composition can affect production cycles (Allen, 1982), the magnitude of functional niche redundancies (Micheli and Halpern, 2005), the strength of benthic-pelagic coupling (Vander Zanden et al., 2005), predator-prey dynamics (Hixon and Beets, 1993), carbon cycling and nutrient flux pathways (Vanni et al., 1997; Hjerne and Hansson, 2002).

In this study, we evaluated the null hypothesis that ICS and lower estuary environments are functionally equivalent in temperate waters, affording a nursery continuum rather than discrete habitats supporting biogeographically distinct juvenile assemblages. If the same temperate marine fish species are simultaneously using ICS and estuary nursery habitats, then assemblages in these habitats should exhibit similar temporal patterns and population characteristics such as growth and size structure. We used contemporaneous catch data from two multi-year trawl surveys (one survey conducted in inner continental shelf waters near Assateague Island, MD, and the other conducted in lower Chesapeake Bay, VA) to compare spatial and temporal patterns in composition and biodiversity of the juvenile fish assemblage in each of these habitats. Further, we compared size structure, growth, and relative abundance of five dominant species.

2. Methods

2.1. Field methods

2.1.1. Inner continental shelf

Species abundance data were collected during a bottom trawl survey of Maryland's (USA) ICS that sampled the nearshore neritic zone (5–20 m) from Ocean City inlet, MD southward for 22 km along the Assateague Island National Seashore (Fig. 1). Bottom habitats are relatively unstructured, typified by unconsolidated sediments and sandy swale bottom with scattered sandy shoals providing macrostructural vertical relief (Steimle and Zetlin, 2000). The coastline is dominated by high intensity beach zones and submerged macrophytes and macroalgae patches are generally absent although biogenic structure (e.g., polychaete tubes, shell hash) recovered during sampling suggests patch-scale microstructure habitats are present in some areas.

Depth stratified (shoal: 5–10 m, deep: 10–20 m) random sampling was conducted approximately bimonthly from June–November of 2004–2006 ($N = 120$ samples; Table 1). A Yankee demersal otter trawl with 28.5-m footrope and 6.4-mm codend mesh was deployed from either the *R/V Seawolf* or the *F/V Tony & Jan*. The gear was towed at 3 knots for 20 min along north-to-south transects that generally followed depth contours. In 2006, sampling was restricted to the northern portion of the sampling area (north of 38° 13′ 13″N) because of vessel costs; previous analysis showed no discernible difference in composition of catch

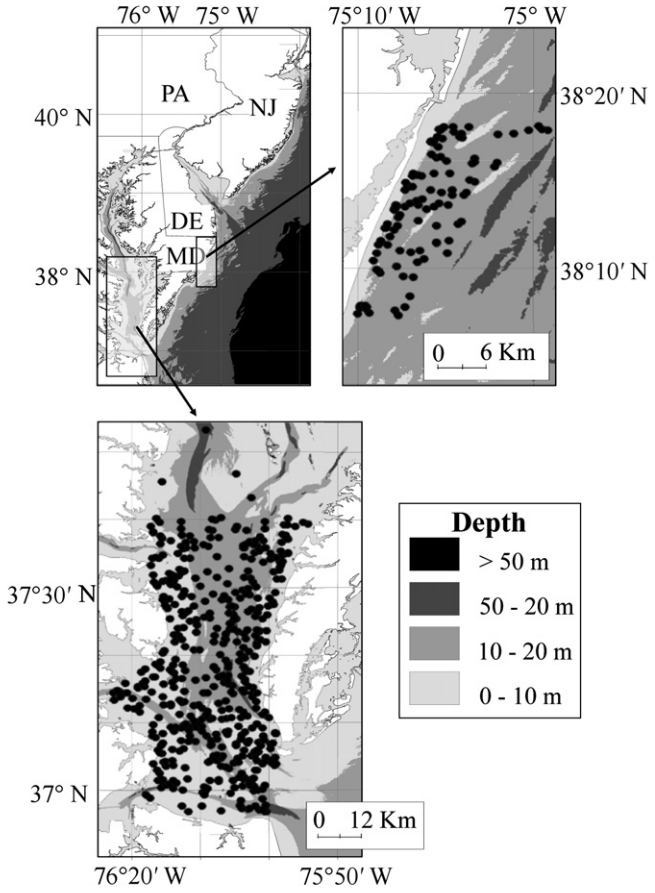

Fig. 1. Map of Chesapeake Bay and the Delmarva Peninsula including insets of the study areas: Maryland's inner continental shelf and lower Chesapeake Bay. Trawl locations are indicated by solid circles (some sites were sampled during multiple monthly cruises).

Table 1
Monthly sampling effort of Maryland's inner continental shelf (ICS) and lower Chesapeake Bay (estuary) per year (hauls [total distance trawled, km]) and ambient bottom conditions (mean [SD]): temperature (T, °C), salinity (Sal), percent dissolved oxygen saturation (DO) and depth (z, m).

Year	Month	Effort		ICS				Estuary			
		ICS	Estuary	T	Sal	DO	z	T	Sal	DO	z
2004	Jul	16 (14.0)	45 (16.8)	21 (0.4)	30 (0.2)	104 (3)	10 (3)	26 (1.4)	20 (2.9)	92 (11)	9 (4)
	Aug	12 (20.0)	45 (17.9)	22 (2.0)	31 (0.5)	85 (21)	14 (5)	25 (1.0)	19 (3.1)	95 (10)	10 (5)
	Sep	16 (27.8)	45 (16.6)	21 (3.4)	31 (0.6)	91 (18)	13 (3)	25 (0.3)	19 (2.5)	102 (9)	10 (5)
	Oct	–	45 (17.9)	–	–	–	–	22 (1.7)	18 (3.7)	107 (10)	9 (4)
	Nov	10 (19.3)	–	20 (3.4)	31 (0.4)	86 (19)	12 (3)	–	–	–	–
2005	Jun	12 (22.0)	45 (16.5)	17 (1.6)	31 (0.6)	109 (22)	14 (3)	22 (1.3)	20 (3.4)	104 (14)	9 (4)
	Jul	12 (23.1)	43 (16.6)	21 (1.9)	31 (0.5)	88 (24)	13 (3)	25 (1.3)	20 (2.5)	99 (15)	9 (5)
	Aug	12 (21.0)	44 (16.3)	21 (2.0)	31 (0.5)	88 (19)	12 (3)	27 (1.4)	20 (2.4)	100 (18)	9 (4)
	Sep	12 (21.0)	47 (17.4)	21 (2.9)	30 (0.6)	90 (24)	9 (1)	26 (0.5)	22 (2.9)	99 (12)	9 (4)
2006	Jul	6 (12.3)	45 (16.3)	20 (4.6)	30 (1.5)	83 (40)	11 (3)	25 (1.9)	20 (3.0)	102 (12)	9 (4)
	Sep	6 (10.7)	47 (17.5)	18 (2.8)	31 (0.6)	87 (13)	12 (5)	23 (1.0)	21 (3.0)	100 (10)	9 (5)
	Oct	6 (10.8)	45 (16.4)	20 (3.3)	31 (0.8)	84 (7)	11 (5)	20 (0.6)	20 (2.5)	105 (9)	10 (4)

between northern and southern portions of the sampling region (i.e., multivariate species-abundance characteristics; 2-way analysis of similarity (ANOSIM, Clarke, 1993) blocked by latitudinal and depth strata, R-statistic $= 0.017$, $p = 0.23$).

2.1.2. *Estuary*

Estuary survey data were collected by the Virginia Institute of Marine Science Juvenile Fish Trawl Survey. Monthly sampling within the estuary was based on a stratified random design delineated by depth and latitudinal zone (Tuckey and Fabrizio, 2009). The estuary survey data included in this study were constrained to sites located in the lower main stem of the estuary (Fig. 1; 37° 53′ 10″N to 36° 56′ 20″N; depth range: 1.5–29.9 m; salinity range: 11.5–29.2 [practical salinity scale]) and to those months and years in which contemporaneous ICS sampling was conducted. Trawlable bottom types in lower Chesapeake Bay are predominantly unconsolidated sediments punctuated by biotic (macrophytes and macroalgae), biogenic (e.g., polychaete tubes, sponges, hydroids) and abiotic (e.g., rubble) patch-scale habitats. Anecdotal evidence during estuarine trawling suggests that bottom habitats were more complex than in the ICS; yet, we lacked the data to directly compare aspects of bottom composition or heterogeneity between the estuary and ICS sampling areas. The estuary survey gear was a 9.1-m footrope demersal semi-balloon otter trawl with 6.4-mm codend mesh; the trawl was towed for 5 min at approximately 2.4 knots ($N = 496$ samples).

In both surveys, individual fish were identified to the species level, sorted, and total weight for each species was recorded. When feasible, the entire catch of each species was counted; otherwise, large catches of individual species were subsampled (by species) and total catch estimated via gravimetric (ICS) or volumetric (estuary) methods. Length (mm) data were collected for a subsample ($n = 30$) of each species, or size class if different size classes were present. In addition to depth (m), water temperature (°C), salinity, and percent dissolved oxygen saturation (DO) were collected prior to trawl deployment with a Seabird© CTD (water column profile) in the ICS and handheld YSI© sonde (surface and near-bottom values) in the estuary.

Due to differences in sampling design (e.g., gear deployment – ICS: 20 min, estuary: 5 min) and trawl dimensions (e.g., vertical gape – ICS ~3.2 m (Callihan et al., 2008), estuary ~1.3 m (M. C. Fabrizio *unpublished data*)), a gear calibration experiment was conducted in August 2008. A paired-haul experimental design was conducted between one of the ICS survey vessels (*R/V Seawolf*) and the estuary survey vessel (*R/V Fish Hawk*) in the ICS sampling area near Assateague Island, MD. The paired-haul experimental design and results are described in the online supplementary material.

2.2. *Data analysis*

2.2.1. *Environmental data*

To investigate the relationship between age-0 fish assemblage structure and the ambient physical environment, we calculated monthly mean and standard deviation (SD) of depth, temperature, salinity and DO at or near the bottom of each sampled site. The daily coefficient of variation (CV) was calculated for each variable, allowing approximately equivalent weighting between habitats (daily $n_{\mathrm{ocean}} = 3–12$ sites, $n_{\mathrm{estuary}} = 1–17$ sites), and averaged within seasons to estimate relative variability for each habitat.

2.2.2. *Assemblage analysis*

All fork length data were converted to total length (TL) and the age-0 fraction of the catch separated from older age classes using published length-at-age information (Grosslein and Azarovitz, 1982; Smith and Wenner, 1985; Sutter and McIlwain, 1987; Ross, 1988; Rountree and Able, 1993; Able and Fahay, 1998; Packer et al., 2003). If length distributions indicated that the age-0 length threshold differed from the published value, a normal distribution was fitted to the putative age-0 and adjacent age-1+ cohorts via a maximum likelihood procedure (FiSAT II v1.2.2©; www.fao.org/fishery). If the distance between length modes exceeded twice the larger SD, the cohorts were considered separate and the anti-modal length used as the age-0 length threshold. Numerical catch data from each haul were standardized to area-swept (ha^{-1}) catch-per-unit-effort CPUE using global positioning system measured tow distance and manufacturer-specified footrope length (ICS = 30 m, estuary = 10 m).

To prepare the catch-site matrix for multivariate analysis, species CPUE data from each survey were $\log_e(x+1)$ transformed to reduce weighting due to absolute differences between numerous and less abundant species (Clarke, 1993). Three separate matrices of Bray–Curtis site similarities were calculated from the $\log_e$-transformed CPUE data: one for each survey to examine assemblage structure within each habitat type and a third based on the merged site data from both surveys to allow inter-habitat comparisons. Prior to merging CPUE data from both surveys, we examined paired catch data from the gear calibration experiment and found that the two trawls had similar relative efficiencies in sampling dominant species and groups of species with similar ecomorphological attributes (e.g., shape, locomotion, size, habitat affinity; Fig. 2). This result indicated that a rank-based approach to direct comparisons of CPUE between surveys was appropriate. An alternative analytical approach using a more conservative intra-haul standardization of CPUE prior to multivariate analysis (% species contribution to total catch per haul; Wood et al., 2009) yielded nearly identical results.

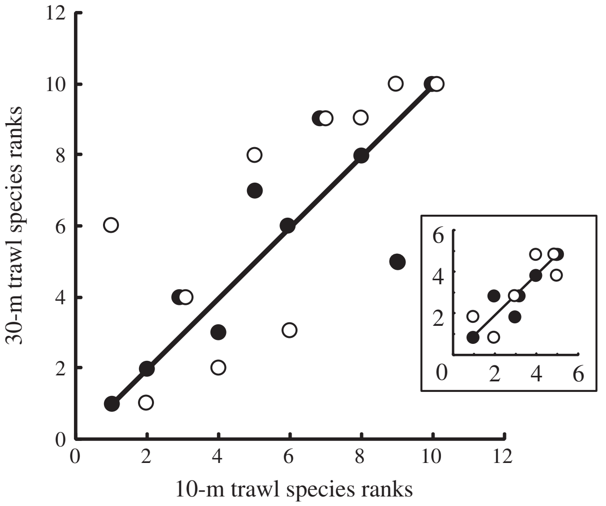

Fig. 2. Rank-order of individual species catch-per-unit-effort (catch ha^{-1}) from a paired-haul gear calibration experiment (1:1 line provided for reference). Empty circles denote paired ranks for 10 species captured in both trawls and solid circles denote paired ranks following inter-calibration (see online supplementary material for model details) of the paired catches (overlapping points have been jittered). Inset plot shows the same relationship for aggregate catches of ecomorphological species groups before (empty circles) and after (solid circles) gear inter-calibration (B).

Monthly sampling data were aggregated into three seasons: June, July = early summer, August, September = late summer, and October, November = fall. Analysis of similarity (ANOSIM, Clarke, 1993) was used to test for seasonal changes in assemblage structure within and between the ICS and estuary habitats. To account for interannual variability, we used 2-way ANOSIM to test for patterns within (seasonal) and between (spatial) habitats with year included as a block effect. The *R*-statistic from ANOSIM typically ranges from 0 to 1; a higher value indicates greater average similarity of samples within a group of interest (e.g., all sites within a season) relative to the average similarity across all sites (values from −1 to 0 are also possible, see Clarke, 1993 for details). The percent contribution of individual species to differences in average site similarities was assessed using SIMPER analysis (Clarke, 1993). Assemblage structure was also visually examined using non-metric multi-dimensional scaling (nMDS) which, in this case, provided a visual representation of within and between habitat patterns in assemblage structure based on species composition. All multivariate analyses were performed using PRIMER v-6 software.

Within each habitat, species richness *S* and Pielou's evenness index *J* were analyzed for seasonal differences with year included as a block effect using 1-way blocked ANOVA. Due to differences in area-swept per survey, these indicators of biodiversity could not be directly compared between habitats. Assumptions of residual normality and homoskedasticity were tested and for all contrasts (here and in other analyses) *p*-values were adjusted for multiple comparisons using a Bonferroni correction (a priori $\alpha = 0.05$). Univariate parametric and non-parametric tests were conducted using SAS v-9.2.

2.2.3. Species CPUE comparisons

Bay anchovy (*Anchoa mitchilli*), weakfish (*Cynoscion regalis*), spot (*Leiostomus xanthurus*), summer flounder (*Paralichthys dentatus*), and Atlantic butterfish (*Peprilus triacanthus*) were identified as diagnostic of assemblage trends (see *Results* Section 3.3) and were selected for species-level analysis. Inter-survey comparisons of species density that rely on area-swept CPUE data can yield spurious results due to differences in gear selectivity (Gunderson, 1993); therefore, gear-calibration models derived from the paired-haul experiment (*Methods* Section 2.1.2) were used to calibrate catch data for the five diagnostic species. Briefly, logistic and linear gear calibration models were alternatively fitted to length-specific (5-mm length-classes) paired-haul data for five groups of ecomorphologically similar species using the SELECT method (Millar, 1992; see online supplementary material). An information theoretic model selection criterion ($QAIC_C$; Burnham and Anderson, 2002) was used to identify the best length-specific model (logistic vs. linear) for each ecomorphological species group. Catch data from the estuary survey were calibrated to the ICS gear using the selected gear calibration model for that species, then standardized to catch-per-unit effort on an area basis ($CPUE_{Gear}$, catch ha^{-1}).

Attempts to normalize residuals through data transformation did not correct for symptomatic right-skewness in the $CPUE_{Gear}$ data; therefore differences in age-0 $CPUE_{Gear}$ within each habitat were examined using Kruskal–Wallis non-parametric ANOVA or the Wilcoxon rank-sum test (Quinn and Keough, 2003). Comparisons of catch rates between habitats (Wilcoxon rank-sum test) were restricted to the late summer season to limit potential bias arising from seasonal movements between habitats. The geometric mean (GM), calculated as the mean of $\log_e$-transformed $CPUE_{Gear}$, was selected as a conservative estimator of central tendency (McConnaughey and Conquest, 1993).

Note that two types of CPUE calculations were used in the analyses described above – an area-swept standardization (multi-species assemblage analysis), and a gear-calibrated area-swept standardization (single species analysis). There was insufficient paired-catch data from the gear calibration experiment to support full gear calibration of all species catches between the two trawls. Still, the use of the area-swept standardization is supported by the similarities in rank-abundance of dominant species in both trawls (Fig. 2) and the rank-based statistical methods used to analyze the multispecies data. Conversely, gear-calibration models were available for the abundant species selected for growth and density comparisons. For these species-level analyses, all catch-at-length data were gear-calibrated to maximize the comparability between ICS and estuary samples.

3. Results

3.1. Environmental conditions

Environmental conditions, particularly salinity and water temperature, differed consistently between the ICS and estuary habitats. In the ICS habitat, monthly average salinities near bottom ranged from 30.4 to 30.7, water temperatures from 17 to 21 °C, and DO saturations from 83 to 109% (Table 1). Average near bottom estuary conditions ranged from 21 to 23 (salinity), 20–26 °C (water temperature), and 92–107% DO saturation. Salinity in the estuary declined from the early summer to the fall months in 2004, yet showed no consistent pattern in 2005 or 2006. In the ICS, salinity increased slightly from early summer to the fall in 2004 and 2006 (salinity in 2005 was relatively constant). Monthly temperature peaked whereas DO saturation was lowest during August in both habitats. Seasonal temperature and DO saturation were more variable in the ICS (temperature: $CV_{ICS} = 9–17\%$, $CV_{estuary} = 1–4\%$; dissolved oxygen: $CV_{ICS} = 20–25\%$, $CV_{estuary} = 8–9\%$) while salinity was more variable in the estuary ($CV_{ICS} = 2\%$, $CV_{estuary} = 6–9\%$).

3.2. Species collections

Taxonomically (30 families, 46 genera, 54 species) and ecologically (e.g., pelagic, demersal, and epibenthic species) diverse assemblages of juvenile fishes were collected in each habitat (Appendix A). Age-0 juveniles accounted for 31% ($N = 323{,}634$) and 64% ($N = 132{,}809$) of the ocean and estuary survey catches, respectively, by number. Age-0 bay anchovy, weakfish, summer flounder, and a 2-species congeneric kingfish group (*Menticirrhus* spp.; including southern [*Menticirrhus americanus*] and northern kingfish [*Menticirrhus saxatilis*]), were numerically dominant in both habitats (species catch frequency $\geq$ 38%). These 3 species and the kingfish group contributed 56% and 25% of the total catch in numbers from the ICS and estuary survey, respectively. Although catches showed marked similarity in species composition with >50% ($n = 29$) of species present in both surveys, there were species-specific differences between habitats. For example, Atlantic butterfish, windowpane flounder (*Scophthalmus aquosus*), bluefish (*Pomatomus saltatrix*), and smooth dogfish (*Mustelus canis*) were captured more frequently in the ICS ($\geq$69% frequency) than in the estuary ($\leq$29% frequency). Conversely, smallmouth flounder (*Etropus microstomus*), Atlantic croaker (*Micropogonias undulatus*), and inshore lizard fish (*Synodus foetens*) each occurred in $\geq$14% of the estuary samples but < 6% of the ICS samples. Species that occurred in only one of the sampled habitats were infrequent (<14% frequency of occurrence) and contributed little to the total catch of either survey. These included thirteen species, (e.g., northern sennet *Sphyraena borealis*, black drum *Pogonias cromis*, clearnose skate *Raja eglanteria*, round scad *Decapterus punctatus*, rough scad *Trachurus lathami*) that were only captured in the ocean, and twelve species (e.g., North Atlantic harvestfish *Peprilus alepidotus*, Atlantic spadefish *Chaetodipterus faber*, lined seahorse *Hippocampus erectus*, northern searobin *Prionotus carolinus*) that were observed only in the estuary (Appendix A).

3.3. Multispecies assemblage structure

Seasonal changes in juvenile fish assemblages within the ICS and the estuary were significant (Global $R \geq 0.25$, $p = 0.001$) but showed similar trends between the two habitat types. In both habitats, the early summer juvenile fish assemblage was different from the late summer ($R \geq 0.33$, $p = 0.001$) and fall assemblage ($R \geq 0.29$, $p = 0.001$). Much of the difference between early summer and the other seasons was explained by high incidence and abundance of spotted hake (*Urophycis regia*) and Atlantic butterfish in the ICS (Fig. 3) and by Atlantic butterfish and spot in the estuary. Conversely, there was no significant difference ($R \leq 0.09$, $p \geq 0.14$) between the late summer and fall juvenile fish assemblages in either habitat. The high abundances of bay anchovy and weakfish during the late summer-fall seasons in both habitats were primarily responsible for the lack of a significant difference between those seasons. Other species, such as kingfish, summer flounder, and bluefish also contributed to the similarity in late summer and fall assemblages within habitats. The seasonal progression of assemblage structure was visually apparent in nMDS plots of depth-

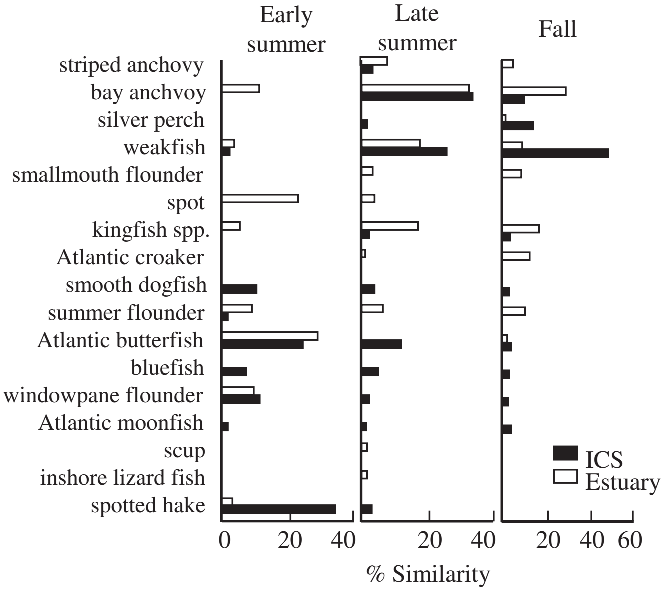

Fig. 3. Percent contribution of 17 diagnostic species to average seasonal Bray–Curtis site similarities for an age-0 finfish assemblage from Maryland's inner continental shelf (ICS, solid bars) and lower Chesapeake Bay (Estuary, empty bars). Seasons are defined as: early summer (June, July), late summer (August, September) and fall (October, November).

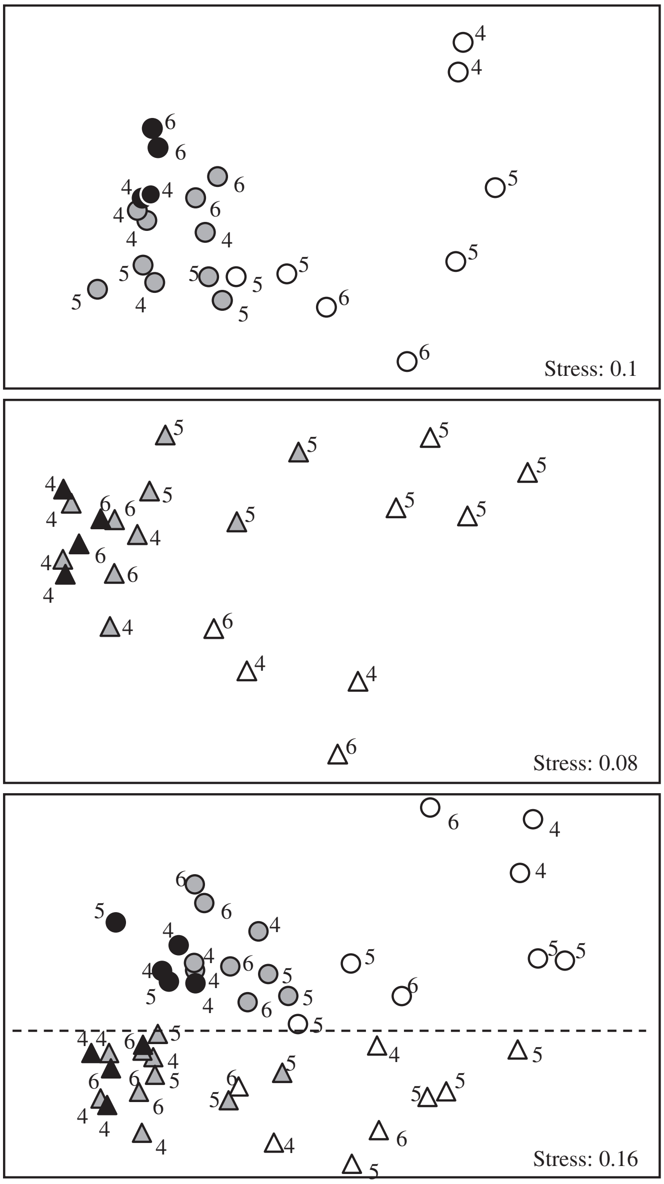

Fig. 4. Non-metric multi-dimensional scaling ordination plot of monthly average ICS (upper; circles), estuary (middle; triangles) and combined (lower) catch composition (2004–2006) from shallow and deep depth strata. Data are coded by season (empty symbols = early summer [June, July], shaded symbols = late summer [August, September], solid circles = fall [October, November]) and year (2004 = 4, 2005 = 5, 2006 = 6). Depth identifiers are not shown to preserve clarity.

stratified, monthly-averaged species composition from each year (Fig. 4, upper and middle panels).

Between habitats, the ICS and estuary juvenile fish assemblages were significantly different in all direct comparisons (Habitat as a main effect: $R = 0.19$, $p = 0.001$). The consistent, seasonal trajectories of assemblage structure from early summer to fall were conserved in the nMDS plot of the combined dataset (Fig. 4 lower panel); yet, there was a progressive increase in dissimilarity between the ICS and estuary fish assemblages from the early summer to the fall. This is evidenced by the increase in seasonal ANOSIM R-statistic value from $R = 0.08$ ($p = 0.01$) in the early summer to $R = 0.25$ ($p = 0.001$) in the late summer and $R = 0.60$ ($p = 0.001$) by the fall. This divergence was due in a large part to differences in the relative dominance of bay anchovy and weakfish over time in each habitat. During early and late summer, bay anchovy were the most abundant species in both habitats. Weakfish became progressively more abundant over time in the ICS and were the most abundant species caught by the fall; whereas bay anchovy remained numerically dominant in the estuary across seasons (Fig. 3).

Seasonal changes in biodiversity corresponded with compositional turnover and shifts in numerical abundance among species (Table 2). Significant seasonal differences occurred in species richness S (ICS: $F_{2,115} = 68.8$, $p < 0.0001$; *estuary*: $F_{2,462} = 143.8$, $p < 0.0001$), and evenness J (ICS: $F_{2,115} = 7.51$, $p = 0.0009$; *estuary*: $F_{2,462} = 68.9$, $p < 0.0001$). The year effect was significant for S in both habitats ($p < 0.0001$), but only in the ICS for J ($p = 0.03$). Seasonally, S increased c. 2–fold in the ICS and the estuary from early to late summer, corresponding with the appearance of juvenile species such as Atlantic menhaden (*Brevortia tyrannus*), black sea bass (*Centropristis striata*), smallmouth flounder, Atlantic croaker, and scup (*Stenotomus chrysops*). From late summer to fall, mean species richness per haul remained stable in the ICS but showed a statistically significant increase in the estuary despite the disappearance of 7 species and appearance of hogchoker (*Trinectes maculatus*) and lookdown (*Selene vomer*; Table 2). Total seasonal S (i.e., sum of novel species) was similar between habitats: ICS = 21, 35, and 32; and estuary = 26, 36, and 31 for early summer, late summer, and fall, respectively. Unlike S, J declined with the progression of the seasons. In both habitats, J declined from early to late summer before stabilizing and remaining relatively unchanged from late summer to fall. Increased abundance of numerically dominant species in both habitats (e.g., bay anchovy, silver perch, weakfish) corresponded with the progressive seasonal decline in J (Table 2).

3.4. Species growth and CPUE

Overall, growth rates were markedly similar between habitats for bay anchovy, weakfish, spot, summer flounder, and Atlantic butterfish. Changes in length distributions of these species over time indicated temporal progression of length modes in each habitat (Fig. 5). During the early and late summer months of June–September, relatively smaller fish accounted for a larger proportion of the total catch of weakfish and Atlantic butterfish in the estuary versus the ICS. There was evidence of halted modal progression in the size of bay anchovy from September to the later fall months within the estuary (but not the ICS) as well as increased incidence of smaller summer flounder in the ICS during late summer and fall. A cohort of small spot (44–64 mm TL) was present in the ICS during fall of 2006; there was no evidence of a similar-sized cohort in the concomitant estuarine sampling (Fig. 5). Estimates of in situ growth rate (based on the monthly progression of length modes) ranged from 0.21 to 0.59 mm day^{-1} for bay anchovy to 1.00–2.05 mm day^{-1} for summer flounder (Table 3). The rank order of growth rates between habitats varied by species – average growth of spot, summer flounder, and Atlantic butterfish was slightly higher in the ICS whereas bay anchovy, and weakfish growth rate estimates were higher in the estuary. Despite these rank order differences, direct comparisons of average growth rate between habitats were not significant for any species (paired t-test, $p \geq 0.22$).

Unlike the between-habitat similarities in growth rate we observed among species, there were significant differences in species $\text{CPUE}_{\text{Gear}}$ between habitats. Increasing seasonal trends in abundance were significant for $\text{CPUE}_{\text{Gear}}$ of bay anchovy, weakfish, and summer flounder within habitats ($p < 0.0001$) (Fig. 6). Seasonal effects also occurred for spot and Atlantic butterfish in the estuary ($p \leq 0.02$). Peak abundances of spot were observed in late summer in the estuary and although Atlantic butterfish densities showed a late summer minimum, seasonal pair-wise comparisons of Atlantic butterfish were not significant. In direct comparisons of $\text{CPUE}_{\text{Gear}}$ between habitats, bay anchovy (Kruskal–Wallis test, $\chi^2 = 25.1$, $p < 0.0001$), weakfish ($\chi^2 = 15.9$, $p < 0.0001$), summer flounder ($\chi^2 = 6.2$, $p = 0.01$) and Atlantic butterfish ($\chi^2 = 84.2$, $p < 0.0001$) abundances in late summer were significantly different between habitats. Gear-calibrated abundances of bay anchovy, weakfish and Atlantic butterfish were 8.1, 4.2 and 12.8-fold higher in the ICS (Table 4). Conversely, spot and summer flounder were 2.4 and 5.8-fold more abundant in the estuary during the late summer.

4. Discussion

The purpose of this study was to compare the seasonal assemblages of juvenile fishes that utilize temperate estuaries and the coastal ocean as nursery habitats. We observed similar species composition, schedules of species incidence, similar growth rates, and comparable biodiversity patterns in lower Chesapeake Bay and Maryland's ICS. Between habitats, there was nearly complete overlap in dominant species and a strong correspondence of assemblage changes between seasons. On the other hand, seasonal changes in dominant species differed substantially between systems as did their estimated densities. Overall, this study provides multiple lines of evidence that temperate ICS habitats are capable of serving as functional nurseries for early life history stages of many transient marine species that are both similar (e.g., seasonal residence schedules, growth conditions) to and different (e.g., species density, species rank-abundance) from estuarine nurseries.

4.1. The inner continental shelf – evidence for a nursery role

The generalized spring-summer spawning, summer residence, and fall migration life history strategy is so prevalent among temperate marine coastal species that the pulsed arrival and departure of age-0 assemblages has been assimilated in the scientific literature as a characteristic feature of temperate estuaries (e.g., Nixon and Oviatt, 1973; Odum and Copeland, 1974; Cain and Dean, 1976; Ayvazian et al., 1992). A particularly salient feature of the current study is the remarkable seasonal correspondence between an ICS and estuarine habitat in the progression of age-0 assemblage structure, temporal patterns of biodiversity, species phenologies, and growth. Taken together, this parallelism in seasonal structuring supports the conceptual model of a common age-0 species pool displaying an overall pattern of occurrence in either habitat throughout the critical summer growth period. This does not imply genetic homogeneity between habitats, but rather contemporaneous use of multiple nursery habitats by spatially disjunct cohorts.

Seasonal changes in estuarine and oceanic assemblage structure were most pronounced from early to late summer and coincided with significant increases in total species richness and abundance of several dominant species. The early-late summer transition corresponds with primary settlement and early growth stanzas for many coastal species of the MAB (Able and Fahay, 1998); therefore, rapid changes in the demersal age-0 assemblage structure would be expected as new species settle and become available to the sampling gear. Studies from other temperate estuaries and coastal ocean habitats of the MAB have noted this spring-summer assemblage dynamic coincident with recruiting age-0 cohorts (e.g., Szedlmayer and Able, 1996; Witting et al., 1999; Hagan and Able, 2003; Jung and Houde, 2003; Martino and Able, 2003; Able et al., 2006; Wingate and Secor, 2008).

The high similarity we observed between late summer and fall assemblages was unexpected given the timing of seasonal species migrations reported in previous studies of other coastal MAB habitats (e.g., Witting et al., 1999; Layman, 2000; Hagan and Able, 2003; Able et al., 2006; Murphy and Secor, 2006). Juveniles of most temperate transient species (i.e., those that

Table 2

Species richness (±SD), evenness (±SD) and total catch (unstandardized) per season for age-0 juvenile species from Maryland's inner continental shelf (ICS) and lower mainstem Chesapeake Bay (estuary). Seasons are coded as: ES (early summer – June, July), LS (late summer – August, September), and Fall (October, November). Mean seasonal biodiversity values with different alphabetical superscripts (A–C) are significantly different in within-habitat comparisons at $\alpha = 0.05$.

Biodiversity metric/Species		ICS			Estuary		
		ES	LS	Fall	ES	LS	Fall
Species richness (*S*)		5.4 (2.7)^{A}	10.9 (3.0)^{B}	12.1 (3.9)^{B}	2.2 (1.3)^{A}	5.5 (2.4)^{B}	6.7 (2.2)^{C}
Species evenness (*J*)		0.49 (0.24)^{A}	0.39 (0.18)^{B}	0.31 (0.13)^{B}	0.84 (0.22)^{A}	0.55 (0.29)^{B}	0.48 (0.30)^{B}
Alosa aestivalis	Blueback herring		9				
Alosa mediocris	Hickory shad				2		
Alosa pseudoharengus	Alewife				2		
Anchoa hepsetus	Striped anchovy	4	5536		75	1725	380
Anchoa mitchilli	Bay anchovy	1200	125,482	7751	665	61,888	49,702
Archosargus probatocephalus	Sheepshead			2			
Astroscopus guttatus	Northern star gazer				1	3	
Bairdiella chrysoura	Silver perch	5	1791	4411	2	198	219
Brevoortia tyrannus	Atlantic menhaden		61	34	2	1	1
Centropristis striata	Black sea bass			1		2	4
Chaetodipterus faber	Atlantic spadefish					31	14
Clupea harengus	Atlantic herring		5				
Conger oceanicus	American conger			1			
Cynoscion regalis	Weakfish	1720	86,779	35,229	248	4917	2103
Decapterus punctatus	Round scad	432	157				
Etropus microstomus	Smallmouth flounder		9	20	1	397	199
Etrumeus teres	Round herring	2004	1439		7		
Gobiosoma bosc	Naked goby		3		1	1	
Gobiosoma ginsburgi	Seaboard goby					6	1
Hippocampus erectus	Lined seahorse				4	12	16
Hypsoblennius hentz	Feather blenny				1	3	
Larimus fasciatus	Banded drum	1	11	8		104	30
Leiostomus xanthurus	Spot	290	1228	30	429	1687	2
Menidia menidia	Atlantic silverside			14			
Menticirrhus spp.	Kingfish	80	3191	838	101	2374	661
Merluccius bilinearis	Silver hake			15			
Micropogonias undulatus	Atlantic croaker			80		547	1874
Mustelus canis	Smooth dogfish	110	569	307	2	3	
Ophidion marginatum	Striped cusk-eel		2				
Opisthonema oglinum	Threadfin shad		11	3		177	3
Opsanus tau	Oyster toadfish					7	2
Orthopristis chrysoptera	Scup		39	7		2	1
Paralichthys dentatus	Summer flounder	29	85	176	112	292	149
Peprilus alepidotus	North Atlantic harvestfish					163	60
Peprilus triacanthus	Atlantic butterfish	8056	16,452	274	189	126	82
Pogonias cromis	Black drum		130	7			
Pomatomus saltatrix	Bluefish	1191	5852	200	7	3	28
Prionotus carolinus	Northern searobin					6	10
Prionotus evolans	Striped searobin		3	6	1	9	6
Raja eglanteria	Clearnose skate	6	34	2		2	
Scomberomorus maculatus	Spanish mackerel					4	
Scophthalmus aquosus	Windowpane flounder	184	594	69	55	31	5
Selar crumenophthalmus	Bigeye scad		9				
Selene setapinnis	Atlantic moonfish	46	1500	235		2	17
Selene vomer	Lookdown		21				4
Sphoeroides maculatus	Northern puffer	92	123	51	3	37	23
Sphyraena borealis	Northern sennet	9	18	4			
Stenotomus chrysops	Scup	71	327	16	19	193	33
Syngnathus fuscus	Chain pipefish		3	1	6	21	40
Synodus foetens	Inshore lizard fish		15	1	16	111	30
Trachurus lathami	Rough scad	34	762				
Trinectes maculatus	Hogchoker						1
Urophycis chuss	Red hake			2			
Urophycis regia	Spotted hake	4046	1969	6	63	11	

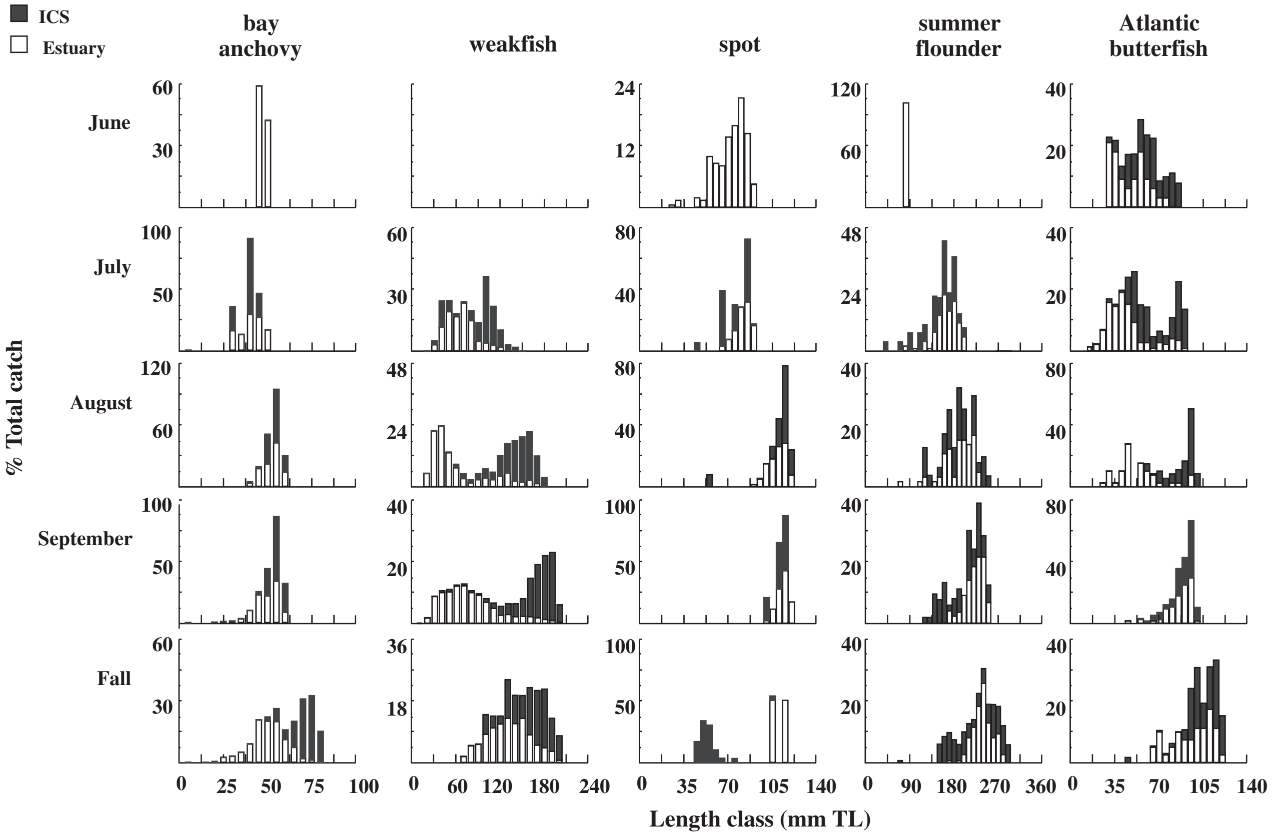

Fig. 5. Monthly (October and November data are combined in Fall panel) age-0 length distribution (total length [TL] mm) for five abundant species from Maryland's inner continental shelf (ICS, solid bars) and lower Chesapeake Bay (Estuary, empty bars). Catches are plotted as percent total catch per length class from each habitat (% Total catch).

Table 3
Habitat-specific mean growth rates in mm day^{-1} (G [±SD]) and coefficient of variation (%) of five juvenile-stage species from this study and previous studies of regional estuarine environments.

Species	G (±SD)	CV	Habitat	Ecosystem	Study
Bay anchovy	0.39 (0.08)	21	ICS	Maryland ocean	This study
	0.42 (0.12)	29	Estuary	Chesapeake Bay	This study
	0.2		Estuary	MAB (composite)	Able and Fahay, 1998
	0.53–0.56		Estuary	Great South Bay (NJ)	Castro and Cowen, 1991
	0.48–0.55		Estuary	Hudson River (NY)	Jordan et al., 2000 [*]
	0.15		Estuary	Narragansett Bay (RI)	Lapolla, 2001
	0.36–0.61		Estuary	Chesapeake Bay	Zastrow et al., 1991
	0.41		Estuary	Chesapeake Bay	Newberger and Houde, 1995
Weakfish	0.99 (0.04)	4.0	ICS	Maryland ocean	This study
	1.14 (0.25)	21.9	Estuary	Chesapeake Bay	This study
	1.0		Estuary	MAB (composite)	Able and Fahay, 1998
	0.29–1.49		Estuary	Delaware Bay	Lankford and Targett, 1994
	0.69–0.97		Estuary	Delaware Bay	Paperno et al., 2000
Spot	0.86 (0.11)	12.8	ICS	Maryland ocean	This study
	0.71 (0.19)	44.2	Estuary	Chesapeake Bay	This study
	0.7		Estuary	MAB (composite)	Able and Fahay, 1998
	0.56		Estuary	Chesapeake Bay	McCambridge and Alden, 1984 [†]
Summer flounder	1.54 (0.42)	27	ICS	Maryland ocean	This study
	1.42 (0.41)	29	Estuary	Chesapeake Bay	This study
	1.5–1.9		Estuary	MAB (composite)	Able and Fahay, 1998
	0.11–0.27		Estuary	Masonboro Is., (NC)	Necaise et al., 2005 [‡]
	1.3–1.4		Estuary	Duplin River (GA)	Reichert and Vanderveer, 1991 [§]
Atlantic butterfish	0.51 (0.01)	2.0	ICS	Maryland ocean	This study
	0.47 (0.21)	44.7	Estuary	Chesapeake Bay	This study
	0.4		Estuary	MAB (composite)	Able and Fahay, 1998

[*] Median summer growth rates of larval stage bay anchovy.
[†] Late summer growth rates from Table 1, p. 483 of McCambridge and Alden (1984).
[‡] Field enclosure experiment using juveniles transplanted from NH culture facility.
[§] Laboratory study using juveniles (28–46 mm) collected from Duplin River (held at 23.7–24.8 °C).

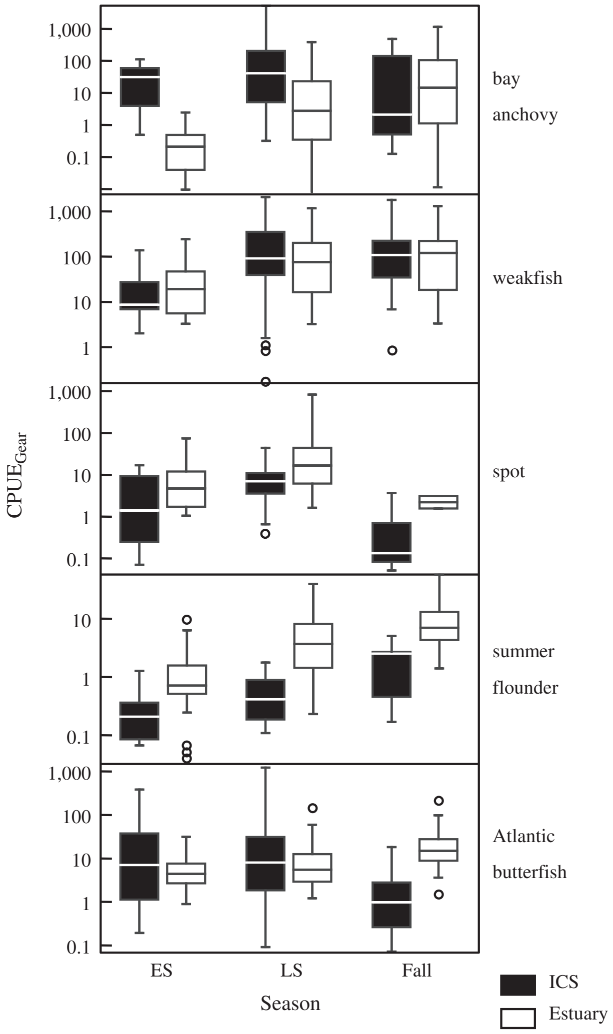

Fig. 6. Age-0 gear-calibrated catch-per-unit-effort (CPUE$_{Gear}$ = catch ha^{-1}) for five species from Maryland's inner continental shelf (ICS, solid boxes) and lower Chesapeake Bay (Estuary, empty boxes). Seasons: early summer (June, July – ES), late summer (August, September – LS) and fall (October, November); depth strata: shallow (<10 m), deep (>10 m). Box edges mark the 1st and 3rd quartiles (interior line = median), whiskers mark 1.5× the interquartile range beyond the edges and circles are values between 1.5× and 3× the interquartile range beyond the edges.

Table 4
Sample size (n – sites with positive catch, [Total late summer sample size – N_{ICS} = 58, $n_{estuary}$ = 228]) and geometric mean late summer catch ha^{-1} ± 1SE (CPUE$_{Gear}$) for five abundant juvenile-stage species in Maryland's inner continental shelf (ICS) and lower mainstem Chesapeake Bay (estuary).

Species	ICS		Estuary	
	n	CPUE$_{Gear}$	n	CPUE$_{Gear}$
Bay anchovy*	48	27.3 (19.4, 38.2)	162	3.4 (2.9, 3.9)
Weakfish*	52	61.6 (45.6, 83.2)	149	14.8 (12.5, 17.5)
Spot	13	0.7 (0.4, 0.9)	67	1.6 (1.3, 1.9)
Summer flounder*	21	0.2 (0.1, 0.2)	96	1.1 (1.0, 1.3)
Atlantic butterfish*	47	6.5 (4.9, 8.4)	41	0.5 (0.4, 0.6)

* All species CPUE$_{Gear}$ distributions were significantly different between habitats (Kruskal–Wallis test, $\alpha = 0.05$).

engage in seasonal migrations) migrate to southern or offshore shelf (or both) overwintering habitats although individuals of some species such as Atlantic croaker (Miller et al., 2003), hogchoker (Szedlmayer and Able, 1996) and summer flounder (Packer et al., 1999) will overwinter within the estuary. Indeed, a substantial faunal turnover was observed during this period – nine species (temperate transients and expatriate subtropicals; Able and Fahay, 1998; Able, 2005; Wood et al., 2009) that were present during late summer were absent in the fall, including seven from the ICS (hickory shad *Alosa aestivalis*, Atlantic herring *Clupea harengus*, round scad, round herring *Etrumeus teres*, striped cusk-eel *Ophidion marginatum*, bigeye scad *Selar crumenophthalmus*, rough scad) and two from the estuary (northern stargazer *Astroscopus guttatus*, Spanish mackerel *Scomberomorus maculatus*). At the same time, hogchoker appeared in the lower estuary whereas five species were observed in the ICS only during fall sampling (sheepshead *Archosargus probatocephalus*, American conger *Conger oceanicus*, Atlantic silverside *Menidia menidia*, silver hake *Merluccius bilinearis*, red hake *Urophycis chuss*). The timing of these occurrences is consistent with the described life history of these species (i.e., shelf overwintering of Atlantic silverside, American conger, red hake: Conover and Murawski, 1982; Able and Fahay, 1998; Steimle et al., 1999; fall settlement of silver hake: Steves and Cowen, 2000) and suggests a seasonal turnover in assemblage structure within the study area. Still, the overall similarity of the late summer and fall assemblages as a whole indicates that sampling ended too early to fully capture the transition to a winter assemblage in either habitat.

The use of area-swept catch standardization of survey data instead of the more rigorous gear calibration during assemblage analyses is a potential source of bias in this study. If species catches from each survey do not scale equivalently to area swept or if the rank order of species vulnerability to the gear varies consistently, comparisons of assemblage structure will not be reliable. The available evidence suggests that such biases are not likely at the species-level (e.g., Fig. 2); yet, the better fit of length-dependent vs. length-independent gear-calibration models indicates that relative vulnerability to the gears varies among certain length-classes for most species. The length-dependent relative vulnerability of these species to the two trawls should be considered when interpreting the multispecies results (assemblage analysis) at the species-level.

4.2. Productivity

Beck et al. (2001) propose four factors that may be used to define and identify nursery habitat at the species-level: growth, density, survival and realized production (i.e., contribution to adult stock). Here, our estimates of species growth rates did not differ between habitats and were within the range and magnitude of previous estimates from estuaries and coastal systems of the MAB (Table 3). This suggests that these species are experiencing similar growth trajectories despite observed differences in ambient physicochemical conditions. For example, other factors being constant, the cooler water temperatures in the ICS would be expected to reduce metabolic rates in the marine habitat, resulting in slower growth rates. The absence of this temperature–growth relationship might indicate that estuarine conditions exceeded thermal optima during part of the summer nursery period or that the effect of temperature on growth in the ICS was offset by environmental variables or improved foraging conditions. The consistency of in situ modal length progression for each of the five diagnostic species provides general support for the broad assumption that juveniles are predominantly residing within a particular habitat following recruitment. Size-dependent movements between habitats in response to ontogenetic or environmental cues would be expected to obscure or skew length progression within habitats. Such a pattern may have occurred for bay anchovy and weakfish in the estuary from late summer to fall (Fig. 5), associated with larger juveniles migrating into ICS waters ahead of smaller conspecifics (Vouglitois et al., 1987; Able and Fahay, 1998).

Between habitats, there was a strong correspondence in the identity of the numerically dominant species contributing to the observed assemblage structure. Three of the most abundant species in both habitats, bay anchovy, weakfish and Atlantic butterfish, are known to spawn on either side of the marine-estuarine boundary; all early life stages (i.e., egg to post-transition juvenile) of these species have been documented in coastal ocean and estuarine habitats of the MAB (Able and Fahay, 1998). Flexibility in spawning location coupled with a relatively short incubation period at summer temperatures (e.g., bay anchovy ~ 24 h, weakfish ~ 50 h; Able and Fahay, 1998) suggests local recruitment processes might be partially responsible for the numerical dominance of these species in both habitats. In a study of fish assemblage structure along the Mullica River-New Jersey inner continental shelf ecocline, Martino and Able (2003) found bay anchovy, weakfish, and Atlantic butterfish to be three of the most abundant species co-occurring in polyhaline and euhaline habitats.

Although we did not attempt to estimate survival or production rates, the density and growth rates of age-0 individuals observed in the ICS emphasizes the potential productivity of this spatially extensive habitat as a nursery. If the values observed in the Maryland ICS sampling area are representative of relative densities along the 211-km length of the Delmarva Peninsula (southern terminus of Delaware Bay, DE to the northern terminus of Chesapeake Bay, VA) and assuming an approximate 26-km offshore boundary of the 20-m isobath (c. 551,540 ha), estimated age-0 densities indicate trawlable relative abundances of 1.50×10^7 bay anchovy, 3.40×10^7 weakfish, 3.65×10^5 spot, 1.06×10^5 summer flounder, and 3.57×10^6 Atlantic butterfish during August and September. In lower Chesapeake Bay (c. 1,000,526 ha within the potential sampling polygon), estimated estuarine relative densities ($\text{CPUE}_{\text{Gear}}$) scale to 3.37×10^6 bay anchovy, 1.48×10^7 weakfish, 1.60×10^6 spot, 1.10×10^6 summer flounder, and 5.04×10^5 Atlantic butterfish. These calculations suggest that the shallow ICS habitat of the Delmarva Peninsula may support 446% (bay anchovy), 229% (weakfish), 23% (spot), 10% (summer flounder) and 708% (Atlantic butterfish) of the species-specific abundances present in lower Chesapeake Bay during the late summer. Current management plans for most commercially and recreationally targeted marine finfish species are based on population models informed by estuarine and (or) offshore continental shelf surveys; yet, as the above exercise suggests, a substantial fraction of juvenile production for many species is likely contributed by ICS habitats. If true, focused surveys of the Mid-Atlantic Bight ICS (e.g., NEMAP program, Bonzek et al., 2009) would aid management efforts by providing increased resolution of annual year-class strength and variability.

It is worth noting that estimates of trawlable abundance for several species from the lower main stem Chesapeake Bay were substantially higher than those presented in an earlier study using a mid-water trawl (Jung and Houde, 2003). A recalculation of ICS and estuary species densities (from this study) based on arithmetic means instead of geometric means showed that when treated similarly, estimates from the current study indicated higher abundances of demersal species (1–2 orders of magnitude) if scaled to a common area. Conversely, bay anchovy estimates were nearly 100-fold higher in the Jung and Houde (2003) study, indicating that the bottom trawl used in the current analysis was substantially less efficient in sampling this predominantly pelagic species than the mid-water trawl used in the earlier study. Ultimately, the goal of the current analysis was a robust comparison of relative abundance between ICS and estuary habitats. Therefore, while the relative abundances reported in Table 4 and absolute abundances coarsely estimated above are not fully reflective of the true abundance of these species (especially pelagic spp.), these values provide calibrated estimates of abundance suitable for direct comparisons between habitats.

Identifying the prevalence and vital rates of juvenile fishes is a necessary initial step in identifying nursery habitats; yet these metrics alone are not sufficient evidence of functional nursery value (Beck et al., 2001; Kraus and Secor, 2004; Dahlgren et al., 2006). One of the most difficult tasks for assessing nursery function is quantifying the realized contribution of recruits to the adult stock on a 'per habitat' basis (Beck et al., 2001; Gillanders et al., 2003). This requires interpretations of population linkages across multiple spatial and temporal scales that are complicated by early life history dynamics such as cohort-specific patterns in nursery habitat use (McBride and Conover, 1991; Neuman and Able, 2003) and source-sink dynamics (e.g., McBride and Able, 1998; McBride and McKown, 2000). Such an analysis was beyond the scope of this study.

4.3. *Conclusions*

Our findings contribute to the growing conceptual model of neritic inner continental shelf areas as productive nursery habitats for a diverse assemblage of juvenile finfish in addition to the recognized role of the ICS as a latitudinal and longitudinal movement corridor. We identified similarities in juvenile biodiversity, assemblage composition, species occurrence phenologies, and individual growth rates in lower Chesapeake Bay and Maryland's ICS. In conjunction with the evidence of comparable juvenile densities between habitats, these results provide compelling evidence that the ICS habitat plays an important role in the interannual recruitment dynamics for many of these species.

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Appendix A

Total catch (N), geometric mean density ($\text{CPUE}_\text{A} = \text{Catch ha}^{-1}$) and frequency of occurrence (%FO) for the 54 juvenile-phase species from trawl surveys of the Maryland, USA, inner continental shelf (ICS) and lower polyhaline main stem of Chesapeake Bay (Estuary). Ecomorphological traits used to determine species groups for gear calibration models: morphology, swimming type,* habitat, behavior and maximum length† (mm TL). Abbreviations: Morphology – fusiform (Fu), horizontally compressed (Hc), flat (Fl); Swimming type – carangiform (Ca), subcarangiform (Su), anguilliform (An); Habitat – pelagic (P), demersal (D), structural (S), benthic/epibenthic (B); Behavior – schooling (Sc), shoaling (Sh), solitary (So).

Family	Species	Ocean			Estuary			Ecomorphological traits
		N	CPUE_A	%FO	N	CPUE_A	%FO	
Achiridae	*Trinectes maculatus*	–	–	–	1	<0.01	<1%	–
Atherinopsidae	*Menidia menidia*	14	<0.01	1%	–	–	–	–
Batrachoididae	*Opsanus tau*	–	–	–	9	0.01	1%	–
Blenniidae	*Hypsoblennius hentzi*	–	–	–	4	<0.01	1%	–
Carangidae	*Decapterus punctatus*	589	0.04	9%	–	–	–	–
	Selar crumenophthalmus	9	<0.01	2%	–	–	–	–
	Selene setapinnis	1781	0.13	49%	19	0.01	1%	–
	Selene vomer	21	<0.01	2%	4	<0.01	<1%	–
	Trachurus lathami	796	0.04	10%	–	–	–	–
Clupeidae	*Alosa aestivalis*	9	<0.01	3%	–	–	–	–
	Alosa mediocris	–	–	–	2	<0.01	<1%	–
	Alosa pseudoharengus	–	–	–	2	<0.01	<1%	–
	Brevoortia tyrannus	95	0.04	18%	4	<0.01	1%	–
	Clupea harengus	5	<0.01	2%	–	–	–	–
	Etrumeus teres	3443	0.08	11%	7	<0.01	1%	–
	Opisthonema oglinum	14	<0.01	4%	180	0.10	6%	–
Congridae	*Conger oceanicus*	1	<0.01	1%	–	–	–	–
Engraulidae	*Anchoa hepsetus*	5540	0.35	21%	2179	0.44	31%	Fu, Ca, P/D, Sc, 90
	Anchoa mitchilli	134,434	1.35	54%	112,255	1.53	55%	Fu, Ca, P/D, Sc, 70
Ephippidae	*Chaetodipterus faber*	–	–	–	45	0.08	6%	–
Gobiidae	*Gobiosoma bosci*	3	<0.01	2%	2	<0.01	<1%	–
	Gobiosoma ginsburgi	–	–	–	7	0.01	1%	–
Haemulidae	*Orthopristis chrysoptera*	46	0.01	4%	3	<0.01	1%	–
Merlucciidae	*Merluccius bilinearis*	15	<0.01	3%	–	–	–	–
Ophidiidae	*Ophidion marginatum*	2	<0.01	2%	–	–	–	–
Paralichthyidae	*Etropus microstomus*	30	0.01	5%	597	0.30	24%	Fl, An, B, So, 100
	Paralichthys dentatus	290	0.07	40%	553	0.48	38%	Fl, An, B, So, 270
Phycidae	*Urophycis chuss*	2	<0.01	1%	–	–	–	–
	Urophycis regia	6022	0.27	70%	74	0.05	4%	–
Pomatomidae	*Pomatomus saltatrix*	7244	0.19	76%	38	0.05	4%	Fu, Ca, P, Sc, 270
Rajidae	*Raja eglanteria*	42	0.05	13%	2	<0.01	<1%	–
Sciaenidae	*Bairdiella chrysoura*	6207	0.24	37%	419	0.16	13%	Hc, Su, D, Sh, 150
	Cynoscion regalis	123,728	1.24	66%	7268	0.63	45%	Fu, Su, D, Sh, 185
	Larimus fasciatus	20	0.01	8%	134	0.11	8%	–
	Leiostomus xanthurus	1548	0.28	20%	2118	0.36	23%	Hc, Su, D, Sh, 120
	Menticirrhus spp.	4109	0.19	49%	3136	0.71	50%	Fu, Su, D, Sh, 220
	Micropogonias undulatus	80	<0.01	3%	2421	0.32	21%	–
	Pogonias cromis	137	0.02	11%	–	–	–	–
Scombridae	*Scomberomorus maculatus*	–	–	–	4	<0.01	<1%	–
Scophthalmidae	*Scophthalmus aquosus*	846	0.13	69%	91	0.14	11%	Fl, An, B, So, 205
Serranidae	*Centropristis striata*	1	<0.01	1%	6	<0.01	1%	–
Sparidae	*Archosargus probatocephalus*	2	<0.01	1%	–	–	–	–
	Stenotomus chrysops	415	0.09	15%	245	0.17	14%	Hc, Su, D/S, Sh, 100
Sphyraenidae	*Sphyraena borealis*	31	0.02	14%	–	–	–	–
Stromateidae	*Peprilus alepidotus*	–	–	–	223	0.14	11%	–
	Peprilus triacanthus	24,782	0.81	73%	397	0.29	23%	Hc, Ca, P, Sc, 90
Syngnathidae	*Hippocampus erectus*	–	–	–	32	0.05	4%	–
	Syngnathus fuscus	4	<0.01	3%	67	0.08	7%	–
Synodontidae	*Synodus foetens*	16	<0.01	6%	157	0.18	14%	–
Tetraodontidae	*Sphoeroides maculatus*	266	0.07	36%	63	0.09	7%	–
Triakidae	*Mustelus canis*	986	0.15	78%	5	0.01	1%	–
Triglidae	*Prionotus carolinus*	–	–	–	16	0.03	3%	–
	Prionotus evolans	9	<0.01	3%	16	0.03	3%	–
Uranoscopidae	*Astroscopus guttatus*	–	–	–	4	0.01	1%	–

[*] Swimming type designations based on characteristics outlined in Helfman et al. (1997).

[†] Only maximum shown; length cut-offs were lower during some seasons and years. Determinations were informed by

[1]published autumnal age-0 length (Able and Fahay, 1998)

[2]modal analysis of year-specific historical age-0 length data from Bluecoast survey data (2004–2008).

Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecss.2011.12.019.

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