ABSTRACT

Title of Document: INVESTIGATING THE ROLE OF THE MID-
                                 ATLANTIC INNER CONTINENTAL SHELF
                                 AS A MARINE FINFISH NURSERY

                                 Ryan Jordan Woodland, Doctor of Philosophy,
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Directed By: Professor Dr. David H. Secor, University of
                                 Maryland Center for Environmental Science
                                 Chesapeake Biological Laboratory

The paradigm of estuarine-dependence in marine fishes has been challenged by

evidence of facultative recruitment by juveniles to both estuarine and inner

continental shelf (ICS) nursery habitats. This ecological flexibility suggests that the

potential nursery area for marine fishes may be more expansive than previously

considered. Two lines of investigation were undertaken to evaluate the overarching

hypothesis that ICS habitats serve a nursery function for finfish that also use estuarine

nurseries: 1) a direct comparison of seasonal, annual and compositional assemblage

structure between an ICS habitat of the Middle Atlantic Bight (Delmarva Peninsula)

and an adjacent estuary (lower Chesapeake Bay); and 2) an investigation of trophic

structuring within an ICS demersal finfish assemblage with an emphasis on

ontogenetic niche. In comparisons between nursery types, there was a strong

seasonal similarity in assemblage structure between the estuary and ICS despite

significant differences in abundance estimates at the species level. Juvenile trophic niche of two indicator species, bluefish and bay anchovy, was wider and more diverse in the estuary yet physiological condition was similar or higher in the ICS. In focused studies on the ICS food web, diet overlap was common among consumers, yet stable isotope evidence indicated prey resources were partitioned along vertical (trophic position) and horizontal (pelagic–benthic pathway) trophic axes. Benthic and pelagic food webs were tightly coupled in most juvenile phase finfish; yet, this relationship showed signs of decoupling in older age classes, suggesting an increased reliance on benthic trophic pathways with age and size. Several prey species that link pelagic and benthic food webs were shown to be important in the diets of demersal finfish, particularly mysid shrimp. Comparative assemblage and food web studies demonstrated that the ICS functions as summer nursery habitat for a wide variety of temperate marine finfish that also use proximal estuarine nurseries. The contribution of ICS nurseries to annual juvenile production represents a critical, but unknown component of population demographics for many marine species and must be considered to conserve essential fish habitats and account for recruitment variability in fisheries stock assessments.

INVESTIGATING THE ROLE OF THE MID-ATLANTIC INNER
CONTINENTAL SHELF AS A MARINE FINFISH NURSERY: A
COMPARATIVE APPROACH

By

Ryan Jordan Woodland

Dissertation submitted to the Faculty of the Graduate School of the
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of the requirements for the degree of
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Advisory Committee:
Professor Dr. David H. Secor, Chair
Professor Dr. Raleigh R. Hood
Professor Dr. Edward D. Houde
Professor Dr. Margaret A. Palmer
Professor Dr. Michael J. Wilberg

Dedication

This dissertation is dedicated to my family – my eternally patient wife, chronically

impatient kids, long suffering parents, and refreshingly candid brother.

Acknowledgements

I'd like to extend my heartfelt thanks to my advisor, Dave Secor. In addition to being an excellent graduate mentor, Dave has supported me in all aspects of my professional and personal life. He'll remain a lifelong friend and colleague after I have left CBL. I also had the pleasure to work with an excellent dissertation committee that included Ed Houde, Mike Wilberg, Raleigh Hood and Marget Palmer. I was always assured a rapid response to queries, quick manuscript reviews, and a collegial 'open door' policy whenever I had a question (which was often).

It would be impossible for me to sufficiently thank all my friends at CBL for their contribution to my mental stability over the years. I'm firmly convinced that the successful completion of a PhD requires maintaining some semblance of life removed from the pursuit of the degree. Fortunately, CBL is rife with students, faculty, and researchers who are more than happy to pick up a volley ball, haul a kayak, or call a happy hour. Without the various pick-up sports, impromptu outings, and lively social events, I'm farily certain I wouldn't be writing this Acknowledgements section right now.

Finally, my family has been my primary source of inspiration and motivation during my graduate career. Constant support from my wife and general (albeit rather rambunctious) enthusiasm from our kids has kept me going despite the obstacles, challenges, and hurdles that accompany graduate school and family life. To my parents and brother: thank you for giving me the confidence to start this journey.

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Chapter 1: Overview

Introduction

Nominally, any habitat used by a juvenile fish during ontogeny, including movement corridors, feeding areas, or refugia can be considered juvenile habitat. The designation of an area as a 'nursery' implies that the habitat possesses a unique set of biotic, abiotic, or geographical attributes that yield a component of juvenile production that is ecologically significant to the population dynamics of that species. Within the last decade, a body of scientific literature has attempted to operationally define nursery habitat; these efforts have appreciably refined the concept, providing benchmark metrics and functions that can be assessed in a quantitative manner. These metrics typically include habitat-specific densities, growth and survival rates, and realized juvenile production, but can also include population-level functions such as maintaining genetic diversity, reducing annual recruitment variability, or contributing to meta-population resilience.

In parallel with the nursery concept, there has been a growing acknowledgment of the potential importance of coastal ocean habitats to the juvenile production of many species, which are considered dependent on estuaries during early life stages. Faunal similarities between coastal ocean and estuarine habitats have long been recognized, particularly associated with low salinity estuarine plumes or coastal water masses (e.g., McHugh 1967); yet, until recently, the nursery function of this expansive, estuary-like habitat was generally overlooked beyond its role as a migration corridor between oceanic and estuarine zones. Studies verifying the

seasonal persistence of juvenile conspecifics in proximal coastal ocean and estuarine

habitats provided an observational foundation for the conceptual 'coastal continuum'

models of Ray (Ray 1991; Ray 2005) and his contemporaries (e.g., Dame and Allen

1996; Able 2005; Sheaves et al. 2006). These conceptual models emphasize the

spatial, biotic, and abiotic connectivity of coastal ecosystems, extending from the sub-

tributaries of large estuaries to the continental shelf with habitats of various scales

nested hierarchically within a series of overlapping physical and physicochemical

gradients.

Efforts to integrate the nursery and coastal continuum concepts are appearing

more frequently, particularly for economically important species such as bluefish

Pomatomus saltatrix on the US Atlantic coast (Mcbride et al. 1993; Able et al. 2003;

Callihan et al. 2008) and California halibut *Paralichthys californicus* on the US

Pacific coast (Fodrie and Mendoza 2006; Fodrie et al. 2009). Still, the role of coastal

habitats remains largely unknown during the juvenile life-stages of marine finfish that

have historically been studied in estuarine habitats. Our incomplete knowledge of

juvenile habitat use in shallow coastal ocean environments is symptomatic of a

general lack of information on the community dynamics that drive species

interactions and ultimately influence juvenile production in these areas. Here, I have

broadly structured my dissertation around two complementary lines of investigation

that address the general hypothesis that coastal ocean habitats serve an important

nursery function for many finfish that also use estuarine nurseries. The first section

includes three chapters that focus on a direct comparison of assemblage structure and

single species growth, abundance, and trophic ecology between a temperate inner continental shelf habitat (ICS) of the Middle Atlantic Bight (Delmarva Peninsula) and an adjacent estuary habitat (lower mainstem Chesapeake Bay, VA). The second section is composed of two chapters that investigate the trophic structuring of a demersal finfish assemblage within the ICS habitat.

Direct comparisons of survey data collected with different sampling platforms are, almost always, subject to bias because the relative vulnerability of a given species or size class is highly dependent on gear-type or dimensions. One of the major hurdles facing multi-survey comparisons of nursery function or assemblage structure is resolving gear-specific differences in observed catch – the absence of a gear-calibration component severely limits any inferences that may be drawn when comparing historical data collected by dissimilar survey gears. In Chapter 2, I use data from a paired-haul gear calibration experiment to model size-dependent differences in relative catchability of juvenile fish species for two bottom trawls of dissimilar dimensions. The paired-haul experiment was conducted jointly with researchers from the Virginia Institute of Marine Science to allow direct comparisons of historical survey data collected from the ICS and lower Chesapeake Bay with each trawl type. I fitted mathematical models to catch-at-size for ecomorphologically similar groups of species, with groups objectively defined by a multivariate analysis of morphology, size, location within the water column, and social behavior.

In estuaries and ICS habitats of the temperate Middle Atlantic Bight, 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. In Chapter 3, I used the models derived in Chapter 2 to calibrate historical survey datasets from the ICS and estuary. This allowed me to compare spatial, temporal, and compositional trends within and between the ICS and estuary. I used a combination of multivariate and univariate methods to compare juvenile phenologies and temporal assemblage structuring, and to estimate growth and abundances for five dominant species: bay anchovy *Anchoa mitchilli*, weakfish *Cynoscion regalis*, spot *Leiostomus xanthurus*, summer flounder *Paralichthys dentatus*, Atlantic butterfish *Peprilus triacanthus*. By scaling observed densities to habitat area, I extrapolated relative juvenile abundances for the entire Delmarva ICS and lower Chesapeake Bay.

Beyond broad patterns of assemblage structure, comparison of nursery function should also evaluate ecological mechanisms that underlay juvenile production dynamics for species that use both nurseries. One critical component of juvenile habitat quality is the availability of an accessible forage base that supports positive somatic growth and energy storage. In the fourth chapter, I investigated the ecological consequence of nursery habitat 'selection' by juveniles of two species (bay anchovy and bluefish) by comparing realized trophic niche of cohorts from each habitat. I used both stomach contents and stable isotope approaches to estimate and compare niche width, niche variability and vertical trophic position for these species in the ICS and estuary. I also calculated and compared two metrics of physiological

condition to examine the relationship between trophic niche characteristics and juvenile condition between habitats.

A diverse group of small-bodied elasmobranch species use ICS habitats as both nurseries and adult foraging areas (Castro 1993; Musick et al. 1993). These small predators mediate the vertical structure of demersal food webs by feeding at multiple trophic levels (i.e., top-down) while simultaneously serving as an important prey item for larger coastal and pelagic shark species (i.e., bottom-up). Although small elasmobranchs occupy a potentially influential position within ICS food webs, quantitative diet information is incomplete for this ecological group, particularly for non-shark species or juvenile life stages. In Chapter 5, I examined the trophic niche of three small elasmobranch species (smooth dogfish *Mustelus canis*, clearnose skate *Raja eglanteria*, and bullnose ray *Myliobatis freminvillii*) to evaluate their potential role as predators of juvenile teleosts and competitors with older and larger teleosts. Both stable isotope and stomach contents data were used to test the importance of piscivory as a primary feeding strategy for the elasmobranchs relative to sympatric teleosts known to be piscivorous. Evidence of niche overlap, particularly between clearnose skate and southern kingfish *Menticirrhus americanus*, was further evaluated based on initial similarities in diet composition. This species pair was examined for concordance in spatial and temporal catch patterns, diel patterns in stomach fullness, and shared similarities between catch patterns and environmental conditions.

In continental shelf ecosystems, demersal food webs integrate pelagic and benthic food sources delivered via vertical flux of photosynthesis-driven production from the surface mixed layer (pelagic pathway) or *in situ* detrital-based production

(benthic pathway). This trophic cycling has been well-studied in macrobenthic and planktonic communities, yet the importance of each trophic pathway to the demersal finfish community is unknown. This is especially true of juvenile stages or small-bodied species that face physical constraints on forage availability (e.g., gape limits). In the sixth chapter, I bring together a large trophic dataset to analyze the relative importance of pelagic versus benthic food webs to a demersal finfish assemblage from the ICS. Isotopic mixing models and stomach contents data were used to estimate the ratio of benthic:pelagic carbon or prey biomass for individual species. The proportional contribution of each trophic pathway was then compared between age classes, among species, and across functional groups as defined by vertical habitat in the water column. Feasible contributions of representative pelagic and benthic prey categories were modeled for one finfish species each from three functional groups (bay anchovy, weakfish, summer flounder) based on the stable isotope signatures of prey and consumers. Finally, I examined evidence for size-structuring within the ICS food web; propose a potential role of mysid shrimp as a direct conduit between pelagic production sources and demersal finfish; and discuss the potential for spatial trends in the strength of benthic-pelagic coupling across the continental shelf.

Following Chapter 6, I have provided a synthesis of some of the primary findings of my dissertation research. For several select findings, I have also presented management implications and suggestions for future research. Two potential future studies are presented in greater detail in a separate subsection of the

synthesis. These analyses are natural extensions of the research themes developed in

Chapters 2-6 yet require additional data from external sources prior to initiation.

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Chapter 2: Modeling Relative Catchability of Juvenile Marine Fish in a Paired-trawl Experiment

Abstract

With the shift toward ecosystem-based management, there is a growing need to inter-calibrate established monitoring surveys to provide best-estimates of spatial patterns in productivity and species density. Relative catchability (q_r) between trawl surveys for fish species is typically estimated as a single "bulk" conversion coefficient; yet for multi-species surveys there is increased interest in modeling q_r as a size-variable function. The suitability of bulk estimates of q_r versus a size-specific logistic model for 13 species of age 0 marine fish and one marine invertebrate were compared using the SELECT method (Millar 1992). Each model was fitted to catch data from six groups of similar species collected during a paired-trawl experiment in nearshore waters of the US Mid-Atlantic Bight. Species groupings were determined based on cluster analysis of a suite of eco-morphological characteristics selected to maximize the likelihood of similar gear vulnerability. The logistic model provided the best fit for five of the six species groups, indicating length-specific estimates of q_r were preferable to bulk estimates for these species groups. In addition, the SELECT method, in conjunction with information-theory (i.e., QAICc), provides a simple method of assessing the support for bulk versus length-based models given the often data-sparse conditions arising from small scale inter-calibration experiments.

1. Introduction

Sampling across numerous habitats and disjunct spatial areas is often required to adequately describe annual juvenile production and identify critical nurseries of marine fishes (Beck et al. 2001; Able 2005). Typically, different scientific surveys use dissimilar gear types or sizes to target particular sets of species across the range of juvenile habitat, resulting in datasets that are not directly comparable due to differences in the relative catchability q_r of each gear for a particular species or size class (Gunderson 1993; Pelletier 1998). The lack of comparability among surveys is viewed as a principal hindrance to a range of fisheries concerns, from stock assessment (e.g., Pelletier 1998; Kingsley et al. 2008) to determining community structure (e.g., Stokesbury et al. 1999) to parameterizing ecotrophic models (e.g., Sparholt 1990; Fraser et al. 2007).

Calibration of q_r between gears requires a study using standardized deployments to estimate gear-specific conversion coefficients. These conversion coefficients are generally applied as a case-specific modifier of catch (or equivalently effort) and have been shown to vary among taxa, size classes, gear-types, sampling methods, geographic areas and over time (Pelletier 1998; Millar and Fryer 1999; Özbilgin et al. 2006; Powell et al. 2006; Wells et al. 2008). A common approach to analyzing q_r between trawls is a side-by-side paired-trawl experiment in which the two trawls are deployed simultaneously by two vessels sampling adjacent areas (Pelletier 1998). Logistical constraints during such experiments can often limit the number of comparable gear deployments, resulting in relatively low sample sizes.

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This in turn can increase the variance of q_r estimates (Millar and Fryer 1999) and lead to a high incidence of null catches (Powell 2006): situations in which one (single null) or both (double null) gears fail to catch a species or size class of interest. As an example, a recent gear comparison study conducted in Mid-Atlantic Bight waters resulted in 56% single null catch pairs for summer flounder (*Paralichthys dentatus*).

Here, a trawl calibration test was conducted by grouping species into eco-morphological groups based on considerations of body-shape, habitat preference, and behavior. Morphological and ecological species groupings have previously been used to increase the generality of catchability estimates across species (Harley and Myers 2001) and to extend catchability estimates from species with formal stock assessments to similarly shaped species for which detailed assessments are lacking (Sparholt 1990; Fraser et al. 2007). In addition, aggregating species data into groups should increase the number of paired catch observations while reducing the variability associated with limited sampling schedules.

Often, single or "bulk" (sensu Harley and Meyers 2001) q_r conversion coefficients are calculated for a particular species (e.g., Pelletier 1998; NEFSC 2002), age class (e.g., Tyson et al. 2006; Wells et al. 2008) or broadly defined size class (e.g., Powell 2006; Kingsley et al. 2008). Species vulnerability is known to be highly size-dependent (Gunderson 1993); therefore, applying a bulk estimate of q_r across all size classes of a species likely introduces bias into estimates of relative abundance. To allow for potential size-related patterns in catchability, mathematical

models can be fitted to relative catch-at-size data (e.g., Warren 1997; Fryer et al. 2003; Holst and Revill 2009). Whereas many methods for analyzing gear comparison data have been described, the SELECT method (Millar 1992) provides an established, adaptive approach that is applicable to paired-trawl studies (Cadigan and Millar 1992; Millar and Fryer 1999; Herrmann et al. 2007).

Specific to this study, rapid growth during the first year of life for juvenile marine fishes and invertebrates and concomitant changes in relative vulnerability support the evaluation of size-dependent functional approaches to estimating q_r coefficients. Information-theoretic model selection methods (Johnson and Omland 2004) were used to statistically compare bulk and functional q_r estimates from a paired-trawl experiment. Relative gear selectivity was evaluated for age 0 fish and squid of a nearshore US Mid-Atlantic fish assemblage from a side-by-side paired-trawl experiment using two models to describe variation in relative catchability with size using the SELECT method. Prior to the modeling component of the study, individual species were grouped into eco-morphological groups as a means of 1) compensating for prevalent intra-species single null catch observations, 2) increasing the generality of estimates across similar species and 3) overcoming statistical issues related to small sample sizes due to the limited number of paired tows.

2.1 Field collections

The paired-trawl experiment was conducted on August 9-10 2008 in Maryland's

shallow coastal zone. The two vessels included in the study were the R/V *Fish Hawk*

(Virginia Institute of Marine Science [VIMS]; Gloucester, VA) and the R/V *Seawolf*

(State University of New York Stony Brook; Stony Brook, NY). The 29' R/V *Fish*

Hawk is the sampling vessel used in a long-term survey of juvenile finfish abundance

conducted in the Virginia portion of Chesapeake Bay (Fabrizio and Montane 2007,

VIMS survey); whereas the 80' R/V *Seawolf* has been the primary sampling vessel of

a multi-year survey of juvenile finfish in shallow coastal waters of Maryland

(Callihan et al. 2008; MD survey). The two trawls used in the paired-trawling

experiment were those deployed by each vessel in their respective surveys and

consisted of a 9.14-m footrope semi-balloon demersal otter trawl deployed for 5

minutes (VIMS survey) and a 28.5-m footrope Yankee demersal otter trawl deployed

for 20 min (MD survey). Both trawls had cod-end liners of 6.35-mm stretch mesh

(see Appendix A for generalized otter trawl schematic).

Paired tows were organized to maximize the spatial and temporal proximity of

gear deployments. Eight stations along the coast of Assateague Island (MD) ranging

from 5-20 m depth were pre-selected to ensure an adequate range of depths sampled

(Fig 1). All tows were conducted parallel to shore along north-to-south transects with

inshore versus offshore vessel positioning alternated among sites to avoid biases in

catch arising from consistent differences in depth sampled or proximity to shore. For

six of the eight sites the R/V *Seawolf* initially deployed its trawl along the sampling path. Once the larger vessel set its gear, the R/V *Fish Hawk* deployed its trawl approximately 0.5 km distant while maintaining a parallel heading for the duration of its tow. Due to longer catch processing time associated with substantially larger catches by the R/V *Seawolf*, two sites sampled by the R/V *Fishhawk* on August 9 were not sampled by the R/V *Seawolf* until the following day. Other than this discrepancy, spatial considerations of the paired-trawl design (e.g., parallel orientation, distance between transects, directionality) were maintained for sites sampled on different days. Vessel speed of the R/V *Seawolf* was maintained at approximately 3 knots while the R/V *Fish Hawk* averaged 2.6 knots resulting in sampling transects of 1.85 km (R/V *Seawolf*) and 0.4 km (R/V *Fish Hawk*).

Once onboard, the catch was sorted by species and sub-divided into age 0 or age 1 and older cohorts based on published length cutoff values (e.g., Able and Fahay 1998) and modal analysis of species length data during previous years (Woodland and Secor *unpublished data*). A subsample (n=30) of each species and cohort combination was measured for total length (TL) and weighed while the remainder was counted. In cases of extremely large catches, the entire catch for a given species or size class was weighed and the subsample used to gravimetrically estimate total catch in numbers.

2.2 Data analysis

Catch data from each vessel were used to investigate overall and size-specific patterns in q_r for juveniles of thirteen species of fish and one invertebrate (Table 1). These species were selected for analysis because of their common presence in the historical datasets of both the MD nearshore and VA Chesapeake Bay surveys. Catch for each species was aggregated into 5-mm length bins and then truncated to retain only those length-classes conforming to the age 0 cohort (Fig 2).

Bray-Curtis similarities were calculated for the species of interest based on a suite of five eco-morphological characteristics (Table 1) that are potentially important determinants of a species' susceptibility to trawls: age 0 size, morphology, locomotion, location in the water column and schooling tendency. Juvenile size and morphology can influence vulnerability to the gear (*available-selection curve*, Millar and Fryer 1999) as well as physical retention based on size-selectivity of the trawl body and cod-end mesh dimensions (*contact-selection curve*, Millar and Fryer 1999). Swimming mode (i.e., locomotion) and demersal orientation have been shown to influence escape velocity and relative gear vulnerability (Breen et al. 2004; Winger et al. 2004; Hannah et al. 2005; Ryer 2008). Evidence of species-specific behavioral (e.g., Suuronen et al. 1997; Winger et al. 2008; King et al. 2004) or density-mediated effects (e.g., Powell et al. 2006; Kingsley et al. 2008) on species vulnerability suggests schooling behavior, which increases cohesive aggregate movement and spatial patchiness (Helfman et al. 1997), may be a factor in differential vulnerability to gears. Here, habitat preferences and schooling behavior (Table 1) were based on

Fig 1 Study area near Assateague Island, MD with individual trawl locations (filled circles) indicated. Inset map shows the location of the study area relative to Chesapeake Bay.
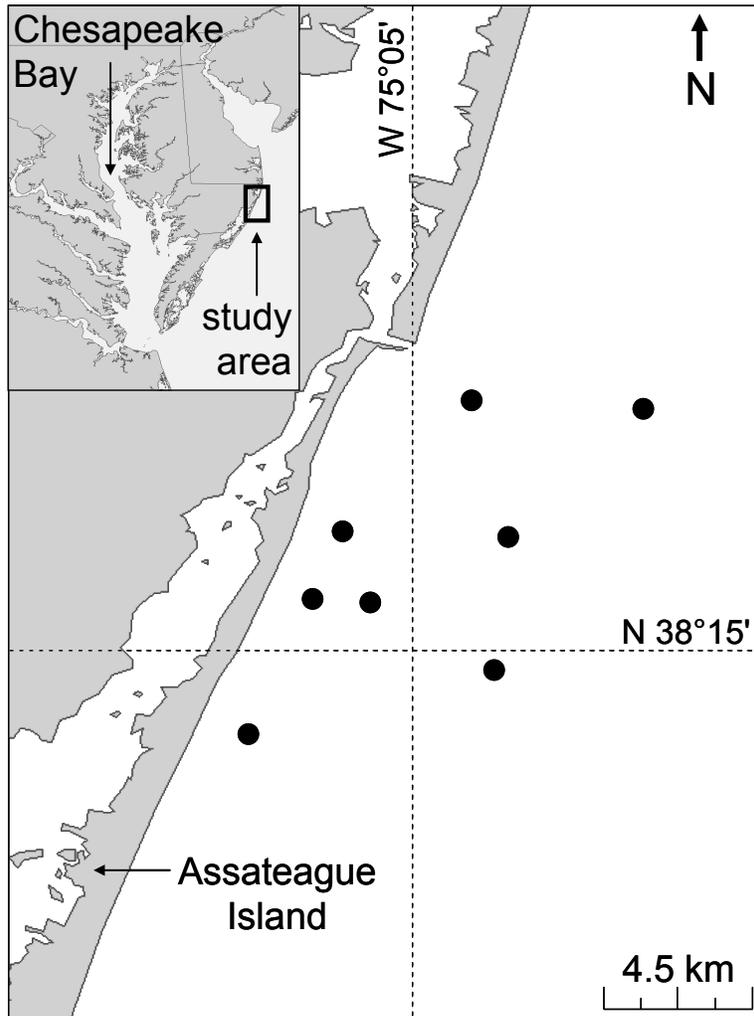
Table 1 Eco-morphological traits of species of interest used in cluster analysis to determine group membership. Maximum length (age 0) rankings based on published size-at-age (see Fig 2 for lengths included in analysis).

Group	Species	Morphology, swimming type [a]	Habitat, behavior [b 1,2]	Maximum length [c]
Anchoa	*Anchoa hepsetus*	fusiform, carangiform	pelagic/demersal, schooling	90 [3]
	A. mitchilli	fusiform, carangiform	pelagic/demersal, schooling	70 [3]
Deep-bodied	*Leiostomus xanthurus*	horizontally compressed, subcarangiform	demersal, shoaling	120 [3]
	Bairdiella chrysoura	horizontally compressed, subcarangiform	demersal, shoaling	150 [3]
	Stenotomus chrysops	horizontally compressed, subcarangiform	demersal/structural, shoaling	100 [3]
Flatfish	*Paralichthys dentatus*	flat, anguilliform	benthic/suprabenthic, solitary	270 [3]
	Raja eglanteria	flat, rajiform	benthic/suprabenthic, solitary	230 [4,5]
	Etropus microstomus	flat, anguilliform	benthic/suprabenthic, solitary	100 [3]
	Scophthalmus aquosus	flat, anguilliform	benthic/suprabenthic, solitary	205 [3,4]
Fusiform	*Menticirrhus* spp.	fusiform, subcarangiform	demersal, shoaling	220 [3]
	Cynoscion regalis	fusiform, subcarangiform	demersal, shoaling	185 [3,4]
Pelagic	*Pomatomus saltatrix*	fusiform, carangiform	pelagic, schooling	290 [3]
	Peprilus triacanthus	horizontally compressed, carangiform	pelagic, schooling	90 [3]
Loligo	*Loligo* spp.	fusiform, jet propulsion	pelagic/demersal, schooling	100 [6]

[a] Swimming type designations were based on characteristics outlined in Helfman et al. 1997

[b] Habitat preference and schooling behavior designations were derived from:

[1] regional species descriptions (general - Murdy et al. 1997, age 0 - Able and Fahay 1998)

[2] agency species reports (United States Geological Survey Species Profiles: Life histories and environmental requirements of coastal fishes and invertebrates, www.nwrc.usgs.gov; National Oceanic and Atmospheric Administration Essential Fish Habitat source documents: Life history and habitat characteristics, www.nefsc.noaa.gov)

[c] Maximum length cut-off determinations were informed by:

[3] published autumnal age 0 length (Able and Fahay 1998)

[4] modal analyses of historical age 0 length data from the MD survey (2004-2008)

[5] Packer et al. 2003

[6] Jacobson 2005

published accounts on juvenile spatial ecology, particularly: Murdy et al. (1997),

Able and Fahay (1998), species profiles for coastal fishes and invertebrates published

by the United States Geological Survey (www.nwrc.usgs.gov) and the National

Oceanic and Atmospheric Administration's Essential Fish Habitat source documents

on life history and habitat characteristics of select marine fish species

(www.nefsc.noaa.gov).

Categories within each eco-morphological characteristic were sequentially

ordered according to functional similarity, then replaced with an integer value (e.g.,

swimming type: rajiform = 1, anguilliform = 2, subcarangiform = 3, carangiform = 4,

jet-propulsion = 5). In the case of maximum age 0 length, lengths were ranked from

smallest to largest with ties given identical integer values (e.g., *Anchoa mitchilli* = 1,

A. hepsetus = 2, *Peprilus triacanthus* = 2). Bray-Curtis similarities were calculated

from the eco-morphological characteristic values (4th root-transformed) and used in

an agglomerative hierarchical cluster analysis based on unweighted average linkage

using group means (Quinn and Keough 2003) to determine optimal species groupings

for subsequent analysis of relative catchability.

2.3 Modeling catchability

When comparing multiple gears, deriving an index of abundance requires

standardizing the observed catch to account for differences in the vulnerability of

species groups to each gear by calculating a relative catchability conversion

coefficient. The SELECT method (Millar 1992) was applied to model changes in q_r

Fig 2 Length-specific catch for thirteen marine fish species and one marine invertebrate from a paired-trawl experiment between a 10m (open histograms) and 30m (filled histograms) demersal trawl. Length cut-offs for the juvenile phase of each species are denoted by a dotted line. All length classes for species marked with an asterisk were considered juveniles.
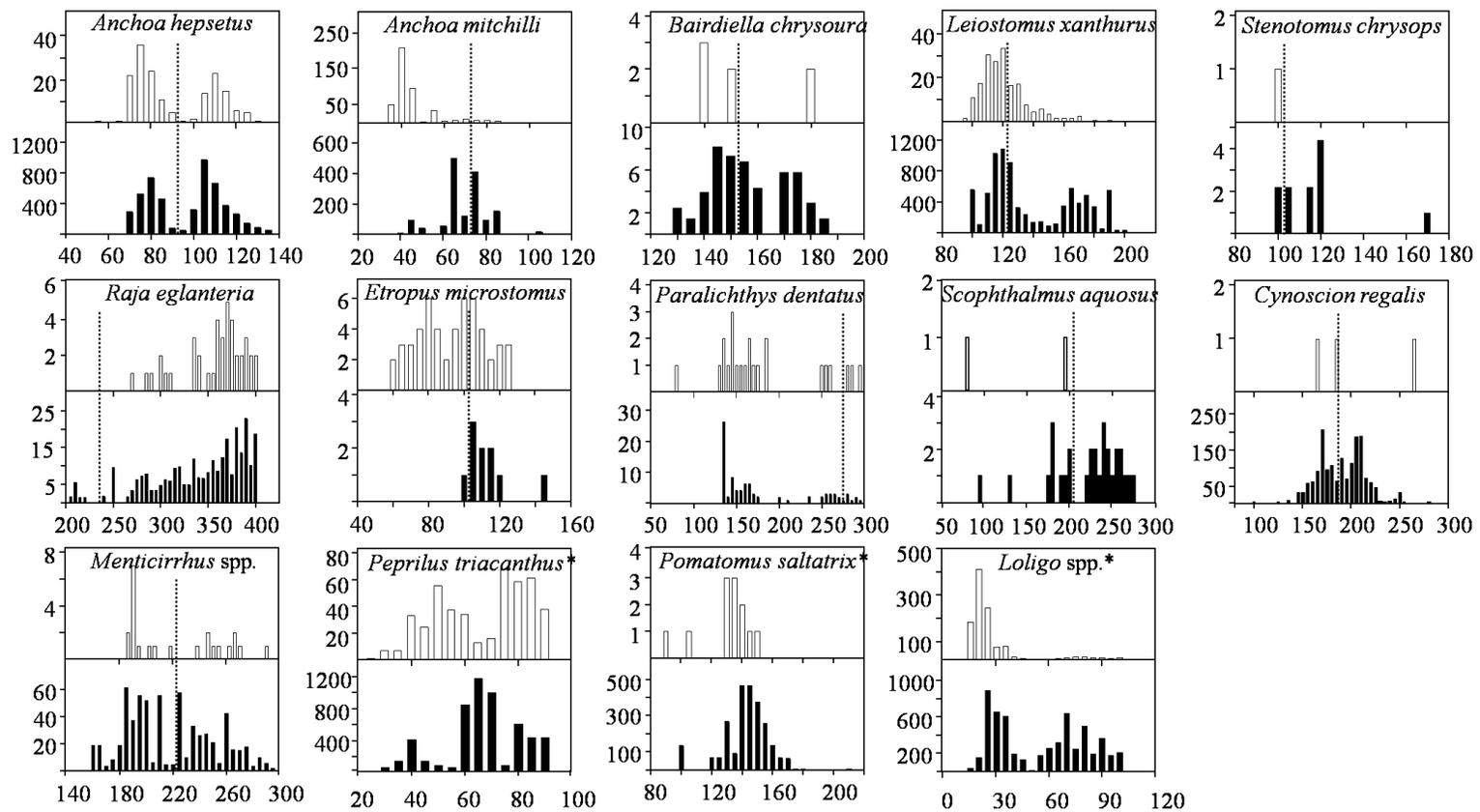
across length-classes l for each species group. The SELECT method involves fitting a model to the proportion of the total catch (summed between gears) of each length class that was captured by one of the two gears of interest. The theory behind this approach is well developed (e.g., Millar 1992; Millar and Walsh 1992; Fryer and Millar 1999; Millar et al. 2004) and will not be reviewed in detail here. Briefly, the subsampled catch per haul h for each species group length-class was scaled up across trawl types (small trawl=10m; large trawl=30 m) to total catch at size $N_{l,total}^h$ (i.e., $N_{l,total}^h = N_{l,10m}^h + N_{l,30m}^h$) by gravimetric conversion of subsample weight per length-class to total catch-at-size numbers. A logistic relative catchability model

$$\hat{q}_r(l) = \frac{e^{(\alpha+\beta l)}}{1+e^{(\alpha+\beta l)}}$$

was then fitted to the observed proportions of the total catch per length-class contributed by the 30-m trawl, $\phi_{l,30m}$, summed across all eight paired tows. Scaling the observed proportions to the total catch allows the catch from the 30-m trawl to be treated as a sample from a binomial distribution, $N_{l,30m}^h \sim Binomial\left(N_{l,total}^h, \phi(l)\right)$, where the probability of capture in the larger trawl is

$$\phi_{l,30m} = \frac{p\hat{q}_r(l)}{(1-p)+p\hat{q}_r(l)},$$

and p represents the probability that an individual fish is observed in the catch of one trawl given that it is caught by either trawl (Millar 1992).

The conditional probability, p, can vary across hauls despite efforts to precisely replicate gear deployments (Fryer 1991; Millar et al. 2004). Due to the

limited number of paired-trawls in this experiment and between-haul variability in the occurrence of individual length-classes in the catch, the data lacked the degrees of freedom necessary to directly model haul-specific estimates of p. However, a useful approach to understanding the true variation between hauls is to evaluate the degree of overdispersion in the catch data. The replication estimate of dispersion (REP), was calculated as

$$REP = \frac{Q}{df},$$

where Q is the Pearson chi-square statistic for model goodness-of-fit and df is the appropriate degrees of freedom (Millar et al. 2004). For those species groups that displayed significant overdispersion of catch at length between hauls (H_0: $Q \sim \chi^2_{df}$, α = 0.05), standard error estimates of the model parameters were multiplied by the square root of the REP. Terms included in the calculation of the REP were limited to those length-classes for which predicted catches of both gears were > 1 and the calculation of the degrees of freedom followed Millar et al. (2004).

I also fitted an invariant (bulk) model to the observed $\phi_{l,30m}$ values to determine if a simpler one-parameter model was more appropriate than the two-parameter length-specific model. The bulk conversion coefficient was estimated as a single-parameter model,

$$\phi_{l,30m} = \beta,$$

with β providing a size-independent estimate of $\hat{q}_r$.

All models were fitted by maximizing the log-likelihood function

$$\sum \left(N_{l,30m} \log \phi(l) + N_{l,10m} \log(1 - \phi(l)) \right)$$ across length-classes (Millar and Walsh

1992) using MS Excel Solver ®. By pooling catch data across hauls during model-fitting the implicit assumption is that the trawls sampled from the same population of fish at each site (Wells et al. 2008). This approach yields a combined haul estimate of the mean model parameter values and is amenable to data-limited situations that lack the degrees of freedom required for more rigorous methods (e.g., mixed-models; Fryer et al. 2003). Models were compared using quasi-Akaike's Information Criterion corrected for overdispersion and small sample size (QAICc); information criterion differences Δ_i and Akaike weights w_i (Burnham and Anderson 2002; Johnson and Omland 2004) were calculated using the log-likelihoods from the size-specific and bulk models and used to inform model selection.

3. Results

Overall, 70% of all observed species were present in the catches of both trawls (Appendix B). Despite the small number of paired hauls, catches-at-size within ecomorphological groups were sufficient to support an information theoretic approach to model selection. Within one exception, q_r of ecomorphological species groups was best described by the logistic (i.e., size-dependent) model.

Cluster analysis supported five groups at $\geq 95\%$ within-group similarity, one of which was composed of a single species (bluefish *Pomatomus saltatrix*). However, bluefish was grouped with butterfish *Peprilus triacanthus* (93% similarity)

to retain the multi-species group focus of the analysis. Finally, a single cluster of five species (96.5% similarity) was separated into two groups (deep-bodied and fusiform) based on high similarity patterns within the original cluster (Fig 3). This resulted in six species groups that ranged in membership from two to four species with a mean group similarity of c. 97%. Multi-species groups composed of taxonomically similar species (e.g., genera - *Anchoa* group, family – fusiform group [Sciaenidae]) displayed the highest group similarities.

Realized site-specific trawl distances varied from 368-455 m for the *R/V Fish Hawk* (10m trawl, VA survey) and 1.79-1.87km for the *R/V Seawolf* (30m trawl, MD survey). As expected, total catch (N = 107,128) received much higher contributions from the 30-m trawl (n = 102,612, 96%) in nearly all length classes (Fig 2). Despite the large differences in total catch between the trawl types, there was concordance in the presence and location of species length modes.

Among species groups, the proportion of the total catch caught by the 30-m trawl generally increased with length (Fig 4), even among those groups with the narrowest length intervals (e.g., *Anchoa* group – 50 mm, deep-bodied group – 55 mm). All relative catchability models successfully converged to stable parameter estimates, although patterns in the deviance residuals (Fig 4) indicate over- and under-estimation of q_r for some length-classes within species groups. Because catch proportions among hauls were overdispersed for all species groups, parameter standard error estimates were accordingly corrected (Table 2). The logistic model

Fig 3 Hierarchical cluster analysis of species eco-morphological characters based on Bray Curtis similarities. Group membership is indicated by the dotted rectangles and group identifiers (with similarity level) are presented within the dendrogram.
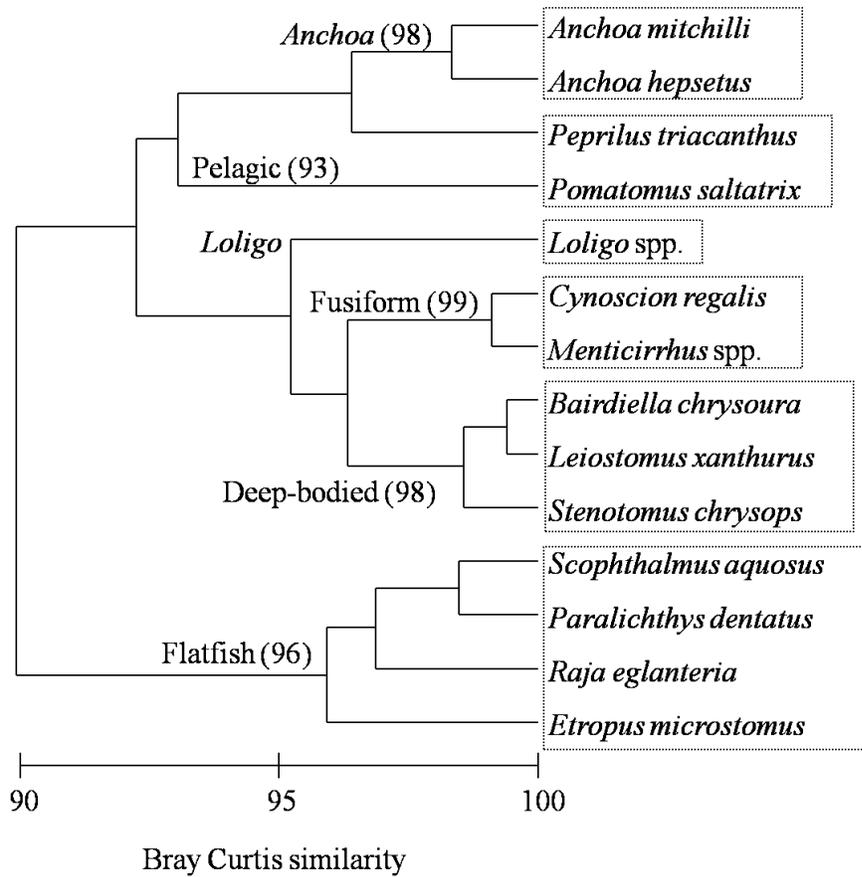
Fig 4 Maximum likelihood estimates for logistic (solid line) and linear (dotted line) relative catchability models fitted to the proportion of the total catch of each species group caught by the 30m trawl. Deviance residuals from the best fit model for each species group (logistic for all groups except fusiform group) are shown in panels on the right.
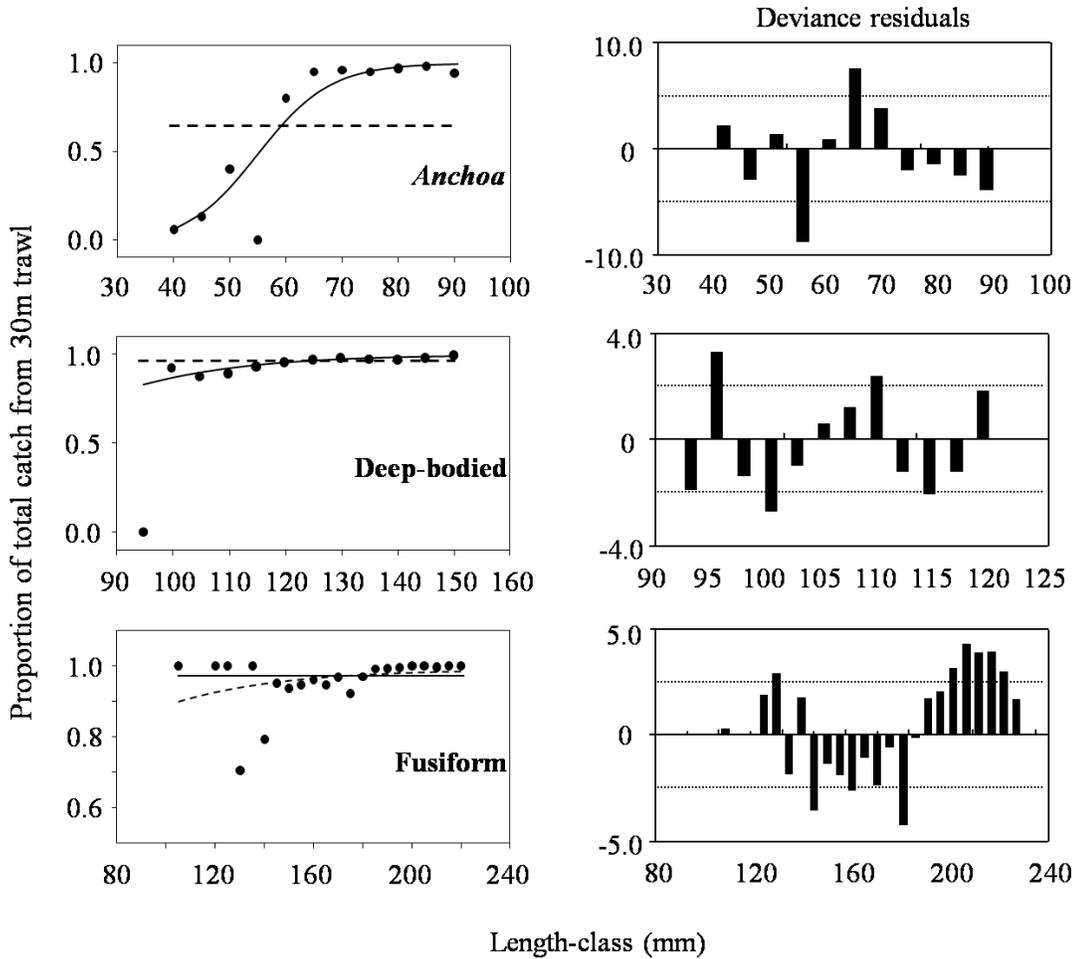
Fig 4 *continued*
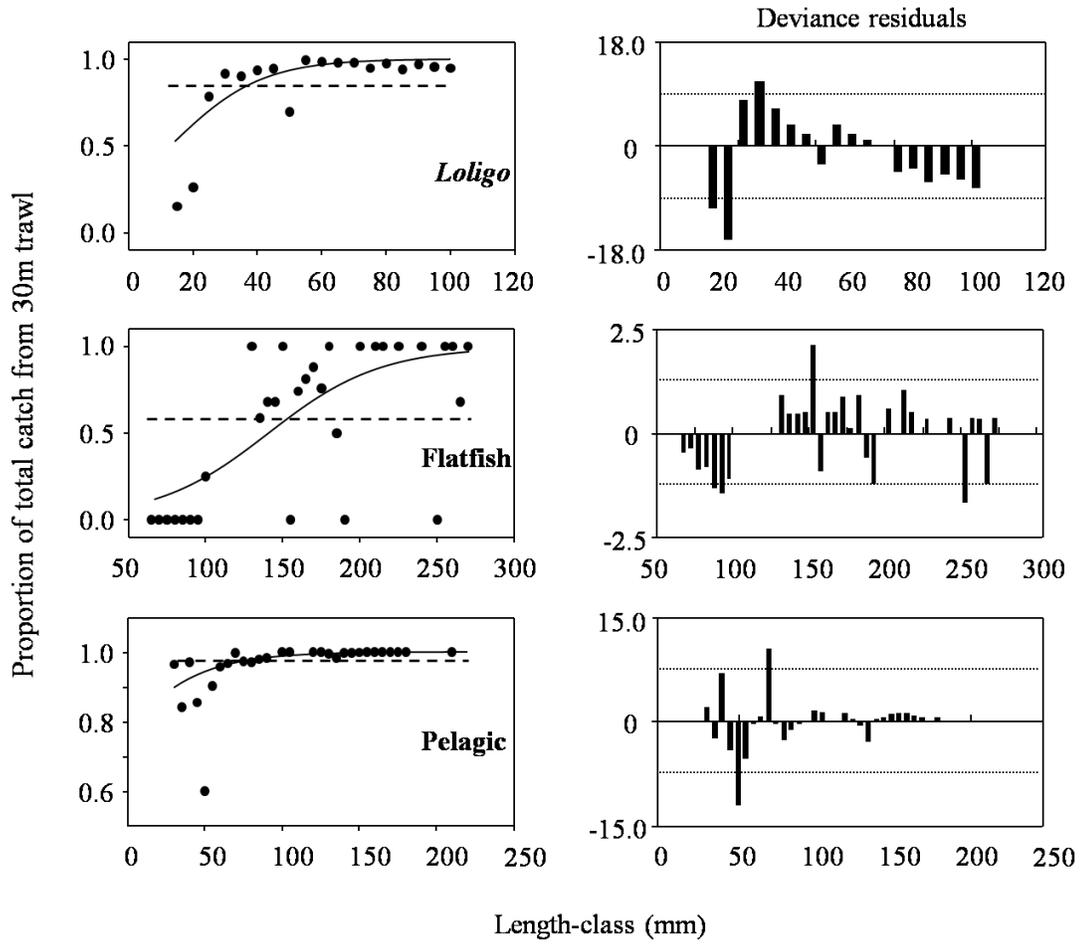
Table 2 Model comparison of bulk and length-specific relative catchability models. Included are the number of observed paired-catches at length n (the number of hauls with positive catch for each species group is given in parentheses), the maximum likelihood parameter estimates for each model (± SE corrected for overdispersion), Quasi-Akaike's Information Criterion corrected for small sample size QAICc, difference among QAICc values Δ_i, and Akaike weights for each model w_i. The most probable model based on QAICc is bolded.

| Group | n | Model | Model parameters | | QAICc | Δ_i | w_i |
			α	β			
Anchoa	45 (7)	**logistic**	**-8.41 ± 2.89**	**0.15 ± 0.05**	**6.87**	**0.00**	**1.000**
		bulk		0.71 ± 6.09	49.31	42.44	0.000
Deep-bodied	67 (8)	**logistic**	**-2.69 ± 2.55**	**0.05 ± 0.02**	**8.70**	**0.00**	**0.735**
		bulk		0.95 ± 1.53	10.74	2.04	0.265
Flatfish	107 (8)	**logistic**	**-3.83 ± 2.50**	**0.03 ± 0.02**	**11.69**	**0.00**	**0.738**
		bulk		0.61 ± 0.14	13.76	2.07	0.262
Fusiform	75 (8)	logistic	2.89 ± 15.98	0.001 ± 0.10	5.27	2.45	0.227
		bulk		**0.97 ± 0.04**	**2.82**	**0.00**	**0.773**
Pelagic	121 (8)	**logistic**	**1.21 ± 1.00**	**0.03 ± 0.01**	**15.69**	**0.00**	**0.907**
		bulk		0.98 ± 0.13	20.25	4.56	0.093
Loligo	103 (8)	**logistic**	**-1.07 ± 0.93**	**0.07 ± 0.03**	**14.38**	**0.00**	**1.000**
		bulk		0.85 ± 0.24	30.42	16.04	0.000

yielded the best (lowest) $QAIC_C$ scores for five of the six species groups (Table 2).

For the deep-bodied and flatfish species groups, the bulk model yielded a difference

in QAICc scores, Δ_i of about 2 when compared to the logistic model, arguably

providing a reasonable alternative (Burnham and Anderson 2002). Despite this,

Akaike weights supported the selection of the logistic over the bulk model as the best

model for the *Anchoa*, deep-bodied, flatfish, *Loligo* and pelagic groups ($w_i \geq 0.74$),

while the bulk model provided the best fit to the fusiform group data ($w_i > 0.77$).

To verify that the eco-morphological groups were yielding similar results to

what might be expected using individual species data, the logistic q_r model was fit to

the bay and striped anchovy catch data (overlapping size range 55-90 mm) for each

species and visually compared the resultant q_r models to the *Anchoa* group model:

bay anchovy $\alpha = -4.91 \pm 2.19$ ($\pm$ SE corrected for overdispersion), $\beta = 0.11 \pm 0.03$;

striped anchovy $\alpha = -3.20 \pm 0.81$, $\beta = 0.08 \pm 0.01$; *Anchoa* group $\alpha = -4.73 \pm 2.89$, $\beta =$

0.11 ± 0.05. These results indicate that the *Anchoa* group model parameters were

similar in value and slightly more variable than parameters estimated for individual

anchovy species.

4. Discussion

In this study, two models of relative catchability were compared for six species

groups encompassing two age 0 squid and thirteen age 0 fish species commonly

sampled by trawl surveys in shallow marine and estuarine nursery habitats of the

Middle Atlantic Bight (Able and Fahay 1998). This analysis specifically focused on

the type of data-limited situations likely to arise from small scale gear comparison experiments between disparate surveys and evaluated the suitability of bulk versus length-based models of q_r. Results indicated that q_r was size-dependent and varied substantially between a 30-m bottom trawl used in a survey of nearshore coastal waters and a 10-m bottom trawl deployed in a juvenile finfish survey of Chesapeake Bay.

Aggregating species by eco-morphological characters is predicated on the assumption that similarity in morphological, spatial and behavioral traits among species contributes to similar probabilities of gear encounter, avoidance and retention. In a meta-analysis of long-term research trawl datasets, Harley and Myers (2001) modeled size-specific catchability for several species groups based on habitat and body shape (e.g., pelagic gadoids versus demersal gadoids). A comparable approach was used by Fraser et al. (2007) to approximate size-specific catchability for a suite of demersal fishes lacking stock assessments by assuming equivalence to similarly shaped, formally assessed species for which estimates of catchability were available (e.g., Atlantic cod *Gadus morhua*). Here, group membership was based upon a suite of eco-morphological characteristics that have been shown to influence the vulnerability of species in previous studies. In the absence of direct information on the behavioral responses of species to trawling (e.g., Winger et al. 2004; Handegard and Tjøstheim 2005), evaluation of these characteristics should provide a relatively impartial method of grouping species so as to maximize the likelihood of similar gear vulnerability within groups.

Pooling across species increased the number of observations for model fitting purposes and expanded the range of length-classes available beyond those observed for individual species during the paired-trawl experiment. In particular, several species that are typically common to both the VIMS and MD surveys during August were captured only in small numbers during this study. For example, in this study catch per unit effort of bay anchovy *Anchoa mitchilli* and striped anchovy *A. hepsetu*s was 4% and 34% respectively of the late summer average for each species (MD survey, 2004-2007) in the study area. After combining these two species into a single group, the number of paired 5-mm size-bin observations (n) increased about 50% from n = 29 (bay anchovy) and n = 22 (striped anchovy) to n = 45 (*Anchoa* group). Similar instances of low observed catch during the paired-trawl experiment of species typically sampled in high abundance by both gears (e.g., weakfish *Cynoscion regalis*) were at least partially offset by the adoption of species groups. While it would be preferable to ground-truth the species grouping composition by comparing parameter estimates from models fitted to the groups and each of their respective component species, the lack of sufficient paired catch-at-size data precluded such an analysis and was the initial impetus for investigating the eco-morphological group concept. In the example provided, a comparison of the parameter estimates among models fit to the bay anchovy, striped anchovy and combined catch data lends support to the eco-morphological approach to species aggregation used in this analysis.

The differences in observed q_r at size across species groups (Fig 4) probably resulted from a combination of spatial, behavioral and physiological factors. For example, there was a relatively high incidence of single null catches among flatfish length classes, resulting in $\phi_{l,30m}$ values of 0 or 1 across the range of length-classes considered (Fig 4). This is likely linked to spatial ecology. Excluding reproductive and migration aggregations, flatfishes do not display the strong schooling or shoaling behaviors exhibited by species such as bay anchovy, bluefish and weakfish. A relatively even dispersion of individuals would explain the low catch per unit effort (18 ± 24 SD) and reduced variability (coefficient of variation = 130%) observed in catches of flatfish relative to the other species groups (e.g., fusiform: 315 ± 474 SD, coefficient of variation = 150%). Interestingly, Winger et al. (2004) demonstrated that American plaice (*Hippoglossoides platessoides*) < 30 cm avoid capture through a kick-swim-settle swimming behavior ahead of an approaching trawl - an escape response that favors gear avoidance by individuals with greater energy reserves, which is likely an increasing function of size. The shallow slope observed in the flatfish q_r at length model (Fig 5) is consistent with a gradually increasing ability to evade the trawl with increased size and energy reserves.

Among the other groups, q_r increased rapidly with length (*Anchoa*, *Loligo* and deep-bodied groups) or displayed a high initial q_r at the minimum length-class modeled (pelagic and fusiform groups) (Fig 5). Morphology (e.g., body aspect ratio) and swimming mode of these species suggests higher burst and cruising speeds than comparably sized flatfishes (Helfmann et al. 1997). The reaction of fish to trawls can

be both species and size dependent yet individuals of a given size range within species or taxonomically similar species often display similar avoidance behaviors (King et al. 2004; Winger et al. 2004; Catchpole and Revill 2008). Species included in the *Anchoa*, *Loligo*, pelagic and fusiform groups utilize demersal and (or) pelagic habitats and may be more likely to display oblique patterns of gear avoidance such as vertical escape trajectories. For example, haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) react to approaching trawls by swimming upward in the water column whereas the more demersally oriented cod remain near the bottom (Catchpole and Revill 2008). Similarly, modified low-rise trawls with cut-back headropes have been proposed to reduce the bycatch of sympatric roundfish (e.g., gadoids, *Sebastes* spp.) in targeted demersal fisheries (Hannah et al. 2005; Catchpole and Revill 2008). This type of avoidance behavior may be particularly important to the results of this study given the substantial difference in vertical gape between trawls: VIMS survey trawl = 1.5 m (maximum potential gape based on manufactured net dimensions; Hata 1997) versus MD survey trawl = 3.0-3.5 m (realized gape from trawl mensuration study under similar fishing conditions, Callihan et al. 2008). In addition to behavioral avoidance, the sharply increasing q_r at length for the *Anchoa* and *Loligo* groups is likely influenced by the continued ontogenetic development of sensory (e.g., auditory, visual) and locomotary (e.g., swimming speed, endurance) attributes used by fish to recognize and avoid the disturbance of an approaching trawl (Kim and Wardle 2003). Development of these capabilities during ontogeny should decrease the relative vulnerability of larger individuals (Gunderson 1993) to gears with smaller gape dimensions and shorter tow durations. Finally, seasonal changes

in water temperature are likely to influence q_r by affecting reaction rates, movement speeds and energetic reserves of poikilothermic fishes. Thus, the application of gear-calibration models to historical datasets should be restricted to the same seasons in which the gear comparison experiments were conducted.

The objective of a gear comparison experiment and the resulting analysis should ultimately determine the acceptable degree of model variance. Acceptable levels of variance are situational and depend on the risks posed by increased variance estimates of gear conversion estimators compared to the cost of collecting additional data. For example, many of the published gear comparison studies are directed at evaluating the effects of gear changes on the long-term viability of regional fisheries or reconciling historical catch patterns with those generated using a new gear configuration (e.g., Pelletier 1998; Wilderbruer et al. 1998; King et al. 2004; Kingsley et al. 2008). In these cases, experimental design should reflect the need for precise gear conversion estimators given the potential risk of fishery mismanagement and historical investment in long-term surveys. Indeed, these types of studies are generally composed of >50 replicate hauls (Pelletier 1998). In other situations, agencies, individuals or small teams of researchers may be focused on comparing aspects of species catch between sampling surveys that use different gear types or deployment strategies (e.g., Walsh 1984; Stokesbury et al. 1999; Powell et al. 2006; Tyson et al. 2006). In these instances, there is often little dedicated support for gear comparison experiments (but see Tyson et al. 2006); yet meaningful incorporation of catch data from multiple extant surveys is a necessary component of a variety of

critical research areas (e.g., defining nursery habitat, deriving habitat suitability indices, investigating effects of climate change, evaluating pollution-mediated effects). To this end, limited-scope gear comparisons can yield information on spatial or temporal catch patterns that are vital to formulating topical ecological hypotheses despite levels of model variance that may be inadequate in other scientific or management settings (Millar and Fryer 1999). Based on the results of this study, even small-scale gear comparisons can yield sufficient information to support length-specific relative catchability models over bulk conversion coefficients.

As applied in this study, the SELECT method correctly accounted for subsampling of the catch and maximized the amount of data included in the analysis while minimizing potential sources of bias that may arise using other analytical approaches by combining catch-at-length data across hauls. The primary drawback to combining data across hauls is the loss of information on inter-haul variability, a known source of sampling error in trawl studies (Fryer 1991) that can artificially deflate parameter standard error estimates and invalidate model comparisons (Millar and Fryer 1999). Correcting the standard errors of the parameter estimates and the information criterion used in model selection by calculating the replication estimate of dispersion provided a more accurate estimate of model precision and adjusted inferences to best reflect the structure of the data on hand.

Fig 5 Best fitted relative catchability models for the six species groups based on the proportion of the total catch predicted to be caught by the 30m trawl.
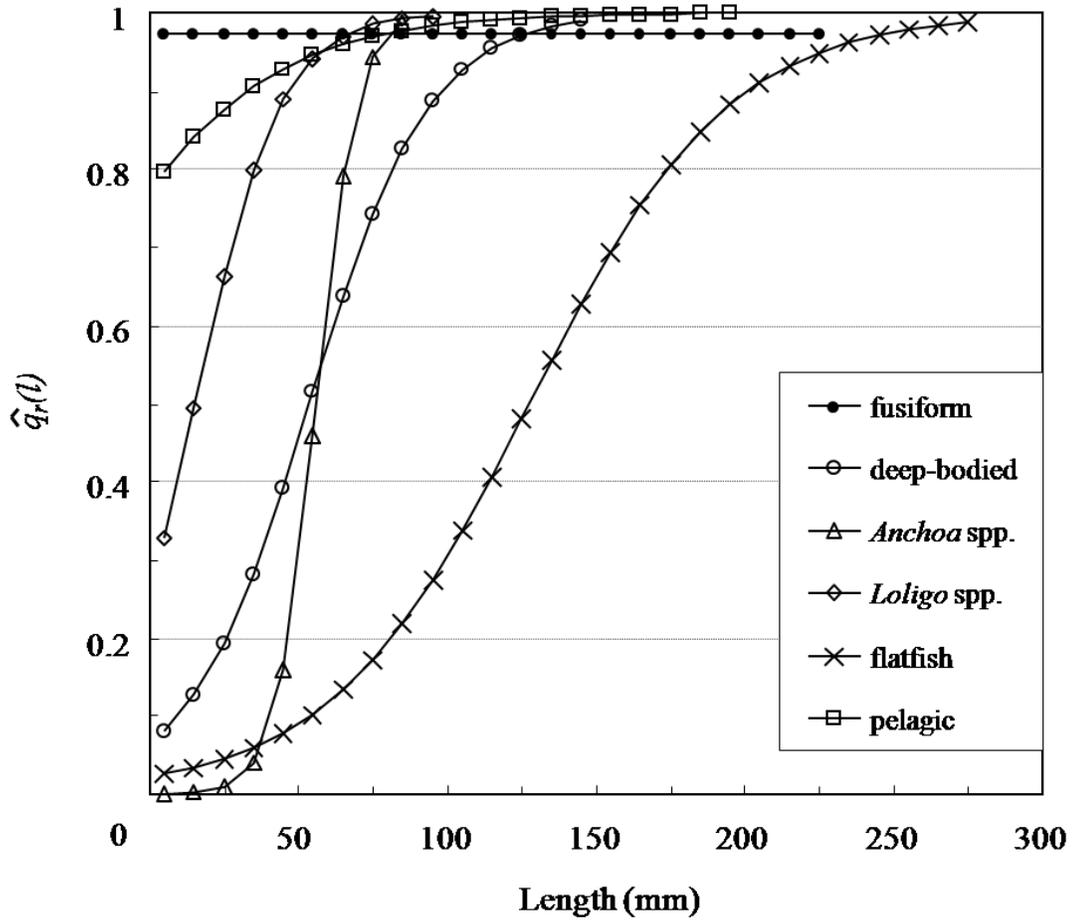
5. Conclusions

As interest in ecosystem-based management increases, there is a growing need to develop statistical methods that permit robust comparisons of juvenile abundance data gathered from disparate surveys. The consistent pattern of increased q_r at length across species groups observed during this study supports consideration of length-specific conversion factors during the first year of life for marine fishes, a life stage characterized by dynamic growth, increasing sensory acuity and rapid physiological development. This study demonstrates that the SELECT method offers a viable means of analyzing q_r from a small-scale gear comparison when combined with an information theoretic approach to model selection. Understanding and modeling the differences in catchability between these sampling gears could permit robust comparisons of juvenile density and abundance between two apparent nursery habitats.

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Appendix A Schematic of bottom trawl with a focus on trawl structures referenced in Chapter 2. The footrope extends across the mouth of the trawl and is in contact with the bottom. The catch is collected in the codend (back of the trawl), both the inner continental shelf (ICS) and lower Chesapeake Bay (Estuary) surveys use a fine mesh codend liner of 6.35 mm.
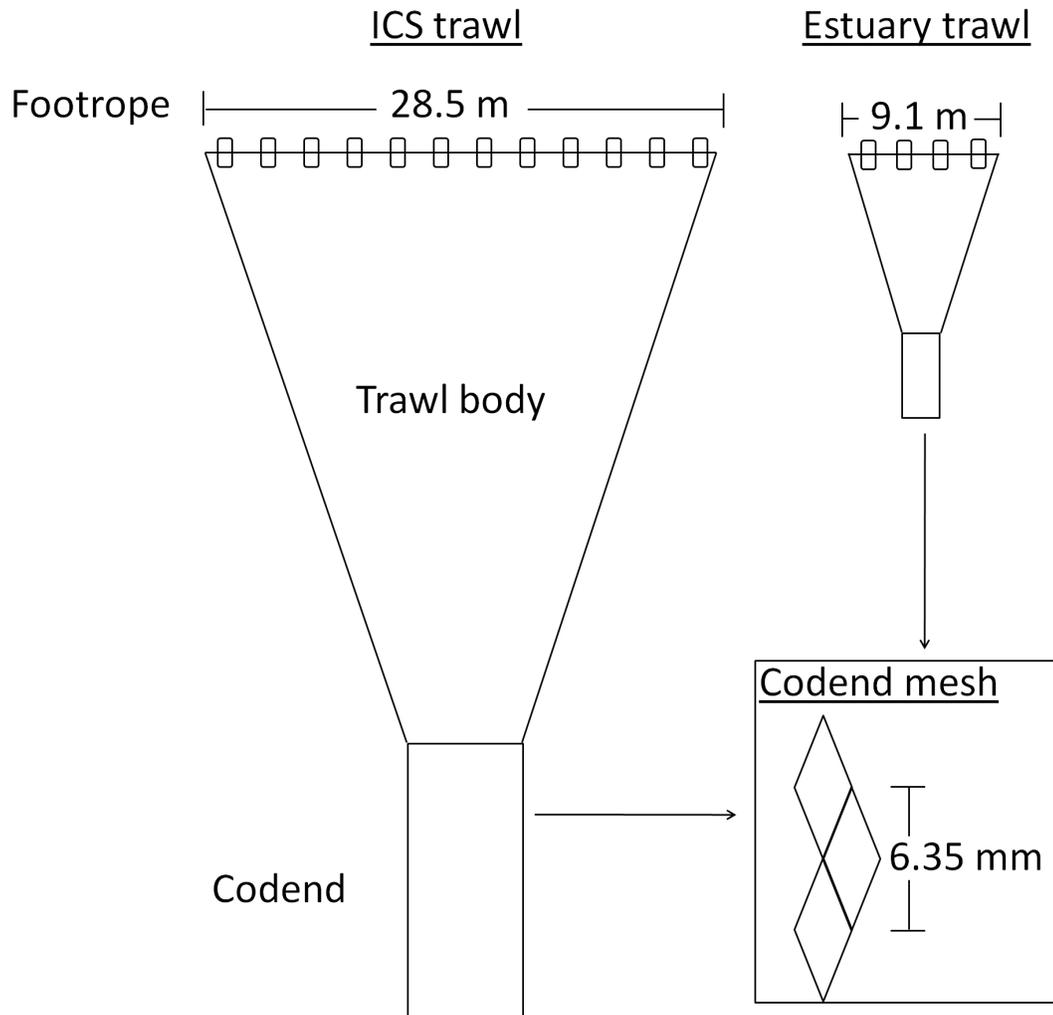
Appendix B Broad organism type, taxonomic information, total catch (N), length characteristics: min-max (mean) in mm Total length, and % frequency of occurrence (%FO) for the 36 species captured during a gear-calibration experiment on Maryland's inner continental shelf between a 30-m trawl and 10-m demersal trawl. Ecomorphological traits used to determine species groups for gear calibration models: morphology, swimming type[a], habitat, behavior and maximum length[b] (mm TL). Abbreviations: Morphology – fusiform (Fu), horizontally compressed (Hc), flat (Fl); Swimming type – carangiform (Ca), subcarangiform (Su), anguilliform (An), rajiform (Ra), jet propulsion (Je); Habitat – pelagic (P), demersal (D), structural (S), benthic/suprabenthic (B); Behavior – schooling (Sc), shoaling (Sh), solitary (So).

| Type | Family / Species | Common name | 10-m trawl | | | 30-m trawl | | | Ecomorphological traits |
			N	Length	%FO	N	Length	%FO	
Finfish	Achiridae	*Trinectes maculatus*				3	115-155 (141)	13	
	Carangidae	*Caranx crysos*	1	140 (140)	13	27	83-164 (139)	25	
		Selar crumenophthalmus				74	70-138 (109)	75	
		Selene setapinnis	27	52-77 (61)	38	2,775	45-76 (58)	63	
		Trachurus lathami	1	98 (98)	13	17	78-132 (104)	13	
	Clupeidae	*Opisthonema oglinum*	1	80 (80)	13	1	82 (82)	13	
		Etrumeus teres				546	70-136 (121)	38	
	Congridae	*Conger oceanicus*	1	269 (269)	13				
	Cynoglossidae	*Symphurus plagiusa*	2	167-174 (171)	13	1	169 (169)	13	
	Engraulidae	*Anchoa hepsetus*	338	57-133 (99)	63	12,846	70-193 (109)	100	Fu, Ca, P/D, Sc, 90
		Anchoa mitchilli	1,354	38-98 (68)	63	4,405	41-109 (69)	50	Fu, Ca, P/D, Sc, 70
	Merlucciidae	*Merluccius bilinearis*				13	11-152 (119)	38	

Myliobatidae	*Myliobatis freminvillei*	2	320-349 (335)		107	250-1082 (412)	100	
Ophidiidae	*Ophidion marginatum*	11	143-229 (181)	13	53	124-432 (191)	38	
Paralichthyidae	*Etropus microstomus*	81	62-129 (94)	63	12	103-148 (114)	50	Fl, An, B, So, 100
	Paralichthys dentatus	33	133-474 (228)	63	143	137-580 (333)	88	Fl, An, B, So, 270
	Paralichthys oblongus	4	50-55 (53)	25				
Phycidae	*Urophycis regia*	202	128-245 (177)	88	3,205	118-255 (172)	88	
Pomatomidae	*Pomatomus saltatrix*	13	90-151 (135)	38	4,012	101-212 (147)	88	Fu, Ca, P, Sc, 290
Rajidae	*Raja eglanteria*	64	273-461 (374)	88	640	208-488 (366)	100	Fl, Ra, B, So, 230
Sciaenidae	*Bairdiella chrysoura*	7	141-183 (159)	13	55	132-187 (157)	38	Hc, Su, D, Sh, 150
	Cynoscion regalis	3	166-221 (191)	25	2,299	103-282 (201)	100	Fu, Su, D, Sh, 185
	Larimus fasciatus				2	110-190 (150)	25	
	Leiostomus xanthurus	572	95-193 (129)	75	22,276	100-203 (150)	88	Hc, Su, D, Sh, 120
	Menticirrhus spp.	31	166-310 (223)	88	923	162-345 (250)	100	Fu, Su, D, Sh, 220
	Micropogonias undulatus	4	234-296 (269)	38	236	171-322 (233)	88	
Scophthalmidae	*Scophthalmus aquosus*	6	84-242 (188)	25	32	99-275 (222)	100	Fl, An, B, So, 205
Serranidae	*Centropristis striata*				4	122-128 (125)	13	
Sparidae	*Stenotomus chrysops*	1	100 (100)	13	12	102-171 (123)	25	Hc, Su, D/S, Sh, 100
Squalidae	*Squalus acanthias*				5	271-338 (300)	13	
Stromateidae	*Peprilus triacanthus*	970	28-132 (84)	88	41,760	31-221 (113)	100	Hc, Ca, P, Sc, 90
Syngnathidae	*Syngnathus fuscus*	3	197-210 (202)	13				
Tetraodontidae	*Sphoeroides maculatus*	4	74-86 (78)	38				
Triakidae	*Mustelus canis*	4	374-412 (392)	25	9	400-980 (547)	50	
Trichiuridae	*Trichiurus lepturus*	1	125 (125)	13	39	131-206 (164)	25	
Triglidae	*Prionotus carolinus*	22	78-154 (114)	38	3	119-177 (149)	13	
Invertebrate. Loliginidae	*Loligo pealei*	1,082	13-153 (57)	88	6,077	15-236 (72)	100	Fu, Je, D, Sc, 100

[a] Swimming type designations based on characteristics outlined in Helfman et al. 1997

[b] 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)

Chapter 3: Comparing the Nursery Role of Inner Continental Shelf and Estuarine Habitats for Temperate Marine Fishes

Abstract

The marine-estuarine transition represents an important biogeographic boundary. However, 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 composition, biodiversity, size structure, and relative abundance of age-0 fishes were tested using contemporaneous catch data from multiyear trawl surveys of the Middle Atlantic Bight ICS near Assateague Island, MD, and in lower Chesapeake Bay, VA (estuary). Survey data from both habitats showed similar seasonal progression of assemblage structure, biodiversity phenologies, and dominant species. Late summer age-0 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 density of summer flounder *Paralichthys dentatus* was higher in the estuary and density of spot *Leiostomus xanthurus* did not differ between habitats. Apparent daily growth rates of these five species, as estimated by modal length progression, did not differ between the two habitats. Results have provided strong evidence that the ICS of the Middle Atlantic Bight can function 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 due to underlying heterogeneity in biotic and abiotic properties across space and time. Within the mosaic of coastal habitats, the roles of estuaries and inner continental shelf (hereafter "ICS") habitats in particular have received recent attention (see Able 2005 for a review) despite a longstanding recognition that faunal similarities can arise between these habitats (e.g., McHugh's 'offshore estuary', 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 to the boundary paradigm, 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). These physicochemical similarities occur despite evident (e.g., bathymetry, wave action, circulation dynamics) and hypothesized (e.g., predator

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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).

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 1,000 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 use of ICS habitats substantially increases 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 (Houde 2009; Sogard 1997). 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 variation 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, I 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. I used contemporaneous catch data from two multiyear 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, I compared size-structure, growth, and relative abundance of five dominant species.

2. Methods

2.1 Field methods: 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). The 20 m depth contour roughly parallels the coastline at an offshore distance of 7 km, yielding a potential sampling area of approximately 150 km^2. Sampling was conducted approximately bimonthly from June-November of 2004-2006 (Table 1).

The selection of sampling sites was random within shoal (5–10 m) and deep (10–20 m) strata (Fig 1) from a grid of potential sites. Each potential site was separated from adjacent sites by 1.9 km North-to-South and by 0.5 km East-to-West. 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 between northern and southern portions of the sampling region (2-way analysis of similarity [ANOSIM, Clarke 1993] blocked by latitudinal and depth strata, R-statistic = 0.017, p = 0.23).

A Yankee demersal otter trawl with 30-m footrope and 6.4-mm cod-end 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 a transect that generally followed depth contours. All individual fish captured were identified to the species level, sorted, and total weight for each species collected to the nearest practical weight increment (i.e., 10 g for large and 1 g for small species). I used length-based thresholds to separate age-0 from age-1+ individuals; a sub-sample of 30 individuals per age class was measured for total length (TL) and weighed. Depth (m) and water column profiles of temperature (°C), salinity and percent dissolved oxygen saturation (DO) were collected with a Seabird CTD at each site prior to trawl deployment.

2.2 Field methods: Estuary

Survey data were collected by the Virginia Institute of Marine Science Juvenile Fish Trawl Survey (hereafter estuary survey). Monthly sampling within the estuary was

based on a stratified random design based on depth and latitudinal zone (Tuckey and

Fabrizio 2009). With the exception of a few large catches, which were subsampled,

the entire catch was counted (by species) and a subsample (n = 30) of each species or

size class was measured for length (total length or fork length, depending on the

species). Surface and bottom temperature, salinity and DO data were obtained with a

handheld YSI sonde at each site prior to trawl deployment. The estuary survey

utilized a similar trawl design as the ocean survey (demersal semi-balloon otter trawl;

6.4 mm cod-end mesh); but there were large differences in deployment time (estuary

survey: 5 min; marine survey: 20 min) and trawl dimensions (estuary survey: 9.14 m

footrope, 1.3 m vertical gape; Fabrizio unpublished). A gear calibration experiment

was conducted in August 2008 with the *R/V Fish Hawk* (estuary survey vessel) and

the *R/V Seawolf* in which 8 sites were sampled by both vessels in the ICS sampling

area near Assateague Island, MD (Chapter 2, also see Chapter 3 Appendix A). The

estuary survey data included in this study were constrained to sites located in the

lower main stem of the estuary (37° 53′ 10″ N to 36° 56′ 20″ N; depth: 1.5–29.9 m;

salinity range: 11.5–29.2).

2.3 Data analysis: Environmental data

To investigate the relationship between age-0 fish assemblage structure and the

ambient physical environment, I calculated monthly mean and standard deviation

(SD) of depth, temperature, salinity and DO at or near the bottom of each sampled

site. I also calculated the coefficient of variation (CV) for each variable, weighted c.

equivalently on a daily basis (daily n_{ocean} = 3–12 sites, $n_{estuary}$ = 1–17 sites) then

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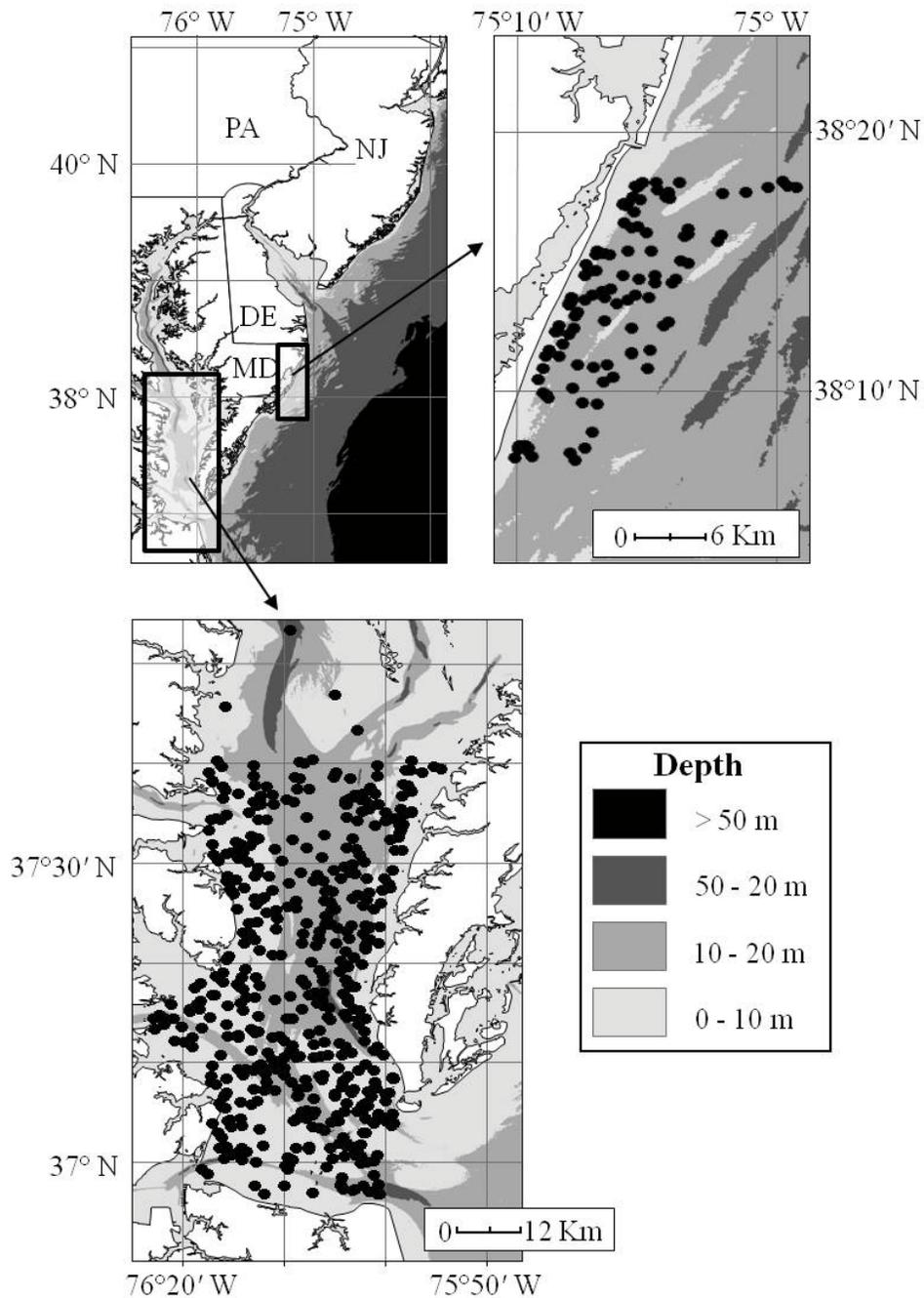
Table 1 Monthly sampling effort of Maryland's inner continental shelf (ICS) and lower Chesapeake Bay (estuary) per year (hauls [total distance trawled, km]) and ambient bottom conditions (mean [SD]): temperature (T, °C), salinity (Sal), percent dissolved oxygen saturation (DO) and depth (z, m).

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)

averaged daily CVs within seasons to estimate relative variability for each habitat.

2.4 Data analysis: 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). In several instances, my length distributions indicated that the age-0 length threshold differed from the published value. In these instances, a normal distribution was fitted to the putative age-0 and adjacent age-1+ cohorts via maximum likelihood procedures (FiSAT II v1.2.2 © FAO 2006). 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 measured tow distance and 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 and Warwick 2001). 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, I

examined paired catch data from the gear calibration experiment (Chapter 2) and found that the two trawls had similar relative efficiencies in sampling dominant species and groups of species with similar ecomorphological attributes (Fig 2). This result suggests that a rank-based approach to direct comparisons of CPUE between surveys is 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.

I applied one and two-way analysis of similarity (ANOSIM, Clarke 1993) to test assemblage structure differences within and between the two habitat types. Comparisons included habitat (ICS, estuary), depth (shallow: < 10 m, deep: ≥ 10 m); season (early summer: June, July; late summer: August, September; fall: October, November) and year (2004-2006). The *R*-statistic from ANOSIM reflects the difference between the average similarity of sites within a group of interest and the average similarity of all site pairs. To enhance interpretability, the *R*-statistic is scaled by sample size to fall between 0-1 (values from -1 to 0 are possible and indicate a greater similarity between sites across groups than within groups, see Clarke 1993 for details). To account for potentially confounding factors in the inter-habitat comparison, I conducted two-way ANOSIMs with season (comparisons: habitat, year, depth) or year (comparison: season) included as block effects. The percent contribution of individual species to seasonal differences in average Bray-Curtis site similarities was assessed using SIMPER analysis (Clarke 1993). Assemblage structure was also visually examined using non-metric multi-dimensional

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 Chapter 1 for model details) of the paired catches. Inset plot shows the same relationship for aggregate catches of ecomorphological species groups before (empty circles) and after (solid circles) gear inter-calibration (B).
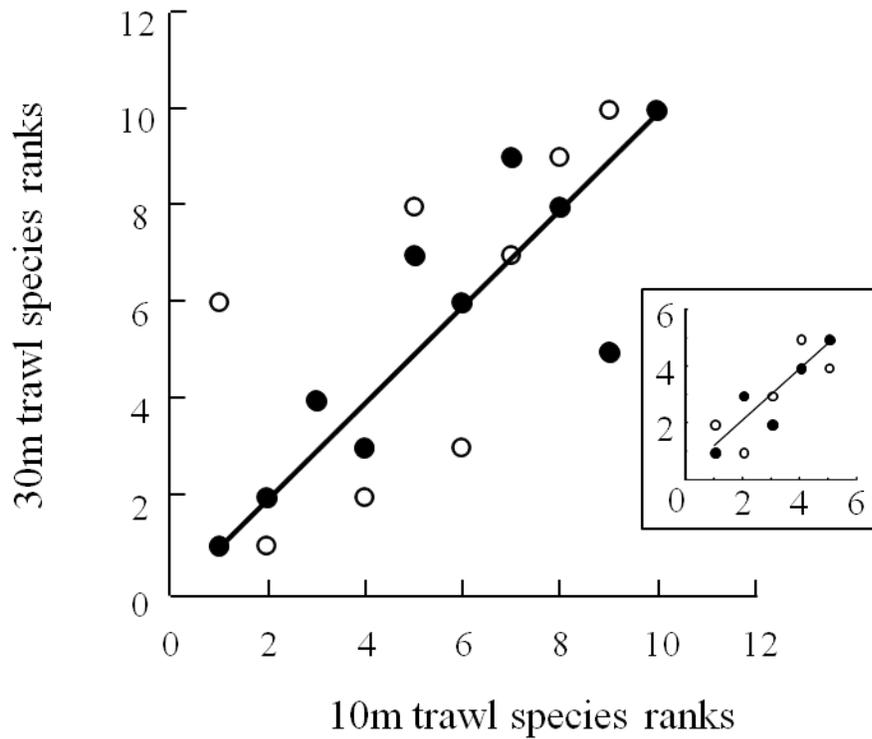
scaling (nMDS). This ordination technique is often applied to multivariate

ecological data (e.g., Kenkel and Orloci 1986; Westera et al. 2003; Murphy and Secor

2006) and, in this case, provides a visual representation of average monthly

assemblage similarity from each year and habitat 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, 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.

2.5 Data analysis: Species CPUE comparisons

Bay anchovy *Anchoa mitchilli*, weakfish *Cynoscion regalis*, spot *Leiostomus*

xanthurus, summer flounder *Paralichthys dentatus*, and Atlantic butterfish *Peprilus*

triacanthus were identified in the multivariate SIMPER analysis as diagnostic of

seasonal trends with habitats and spatial differences between habitats (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, logistic and linear gear

calibration models were alternatively fitted to paired-haul data from the gear

calibration experiment for five species groups (including the five species identified

above) based on 5 mm length-classes using the SELECT method (model development

and additional details regarding the SELECT methodology described in Chapter 1;

also see Millar 1992). An information theoretic model selection criterion ($QAIC_C$,

Burnham and Anderson 2002) was used to identify the best model for each species

group. Observed 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

satisfactorily correct for symptomatic right-skewness in the estuarine $CPUE_{Gear}$ data

(e.g., $log_e(x+1)$ transformation: Kolmogorov-Smirnov $D = 0.05$, $p < 0.01$); therefore

seasonal differences in age-0 $CPUE_{Gear}$ within each habitat were examined using

Kruskal-Wallis non-parametric ANOVA (Quinn and Keough 2003). Comparisons of

catch rates between habitats were also tested with the Wilcoxon rank-sum test and

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) and was used to characterize trends in

species densities.

It is important to note that two types of CPUE calculations were used in the analyses described above – an area-swept standardization (multi-species assemblage analysis), and an inter-gear calibration approach (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. Therefore, I used an area-swept standardization approach to maximize catch similarities between species; this approach is supported by the similarities in rank-abundance of dominant species in both trawls 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-size data were gear-calibrated to maximize the comparability between ICS and estuary samples.

3.0 Results

3.1 Environmental conditions

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 21–23 (salinity), 20–26 °C, 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). Peak temperatures and lowest DO saturation occurred during August in both habitats. Seasonal temperature and DO

saturation was consistently more variable on the ICS (temperature: CV_{ICS} = 9–17%, $CV_{estuary}$ = 1–4%; dissolved oxygen: CV_{ICS} = 20–25%, $CV_{estuary}$ = 8–9%) while salinity was consistently 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 nursery type (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 group that included southern and northern kingfish *Menticirrhus* spp., were numerically dominant in both habitat types (individual species incidence ≥ 38%). These species alone contributed 56% and 25% of the total catch in numbers from the ocean and estuary survey, respectively. Although > 50% (n = 29) of species were present in both habitat types, the majority showed spatial differences in their frequency of occurrence. For example, Atl. butterfish, windowpane flounder *Scophthalmus aquosus*, bluefish *Pomatomus saltatrix* and smooth dogfish *Mustelus canis* were captured more frequently in the ICS (≥ 69% incidence) than in the estuary (≤ 29% incidence). Conversely, smallmouth flounder *Etropus microstomus*, Atlantic croaker *Micropogonias undulatus*, and inshore lizard fish *Synodus foetens* each occurred in ≥ 14% of the estuary samples but < 6% of the ICS samples. Thirteen species, (e.g., northern sennet *Sphyraena borealis*, black drum *Pogonias cromis*, clearnose skate *Raja eglanteria*, round scad *Decapterus punctatus*, rough scad

Trachurus lathami) occurred only in the ocean, whereas twelve species (e.g., North Atlantic harvestfish *Peprilus alepidotus*, Atlantic spadefish *Chaetodipterus faber*, lined seahorse *Hippocampus erectus*, northern searobin *Prionotus carolinus*) were observed only in the estuary (Appendix A).

3.3 Assemblage structure

In both the ICS and estuary samples, assemblages differed between the early summer season and the late summer and fall seasons. Pair-wise comparisons of seasonal assemblage structure within and across both habitat types (Table 2) indicated early summer and late summer ($p = 0.003$), and early summer and fall assemblages ($p = 0.003$) were significantly different although there was not a significant difference between late summer and fall ($p \geq 0.30$) in either habitat. Interannual variability was more pronounced in the estuarine assemblage (Table 2); there were significant interannual differences between 2004 and 2005 ($p = 0.003$) and 2005 and 2006 ($p = 0.003$) but not between 2004 and 2006 ($p = 0.18$). For the ICS assemblage, 2004 was significantly different from 2005 ($p = 0.003$). The effect of depth was not significant for the ICS ($p = 0.68$), but was significant for estuary samples ($p = 0.001$).

Among site similarity, a measure of assemblage homogeneity within each habitat type, was analyzed to represent the influence of season and species on assemblage structure. Site similarities (based on species composition and abundance patterns) for a given habitat were lowest during the early summer ($ICS_{Similarity} = 24.7$ %, estuary$_{Similarity} = 12.0$ %), intermediate in the late summer ($ICS_{Similarity} = 44.4$ %,

estuary$_{Similarity}$ = 33.2 %) and peaked in the fall (ICS$_{Similarity}$ = 55.0 %, estuary$_{Similarity}$ =

43.0 %). A subset of 17 species accounted for > 95 % of the similarity in assemblage

structure (Fig 3). Bay anchovy, weakfish, and Atl. butterfish were seasonally

diagnostic species within both habitats, responsible for 62% and 50% of the average

site similarity across seasons for the ICS and the estuary assemblages, respectively.

Still, the influence of these species was seasonally variable and included declining

(Atl. butterfish – both habitats), modal (bay anchovy – both habitats, weakfish –

estuary), and increasing (weakfish – ICS) trends from early summer to fall.

Contributions of other species (e.g., spot, kingfish, smooth dogfish, windowpane

flounder, spotted hake *Urophycis regia*) to assemblage structure were also seasonally

and spatially dependent (Fig 3). For example, smooth dogfish, windowpane flounder

and spotted hake explained 56% of the early summer ICS$_{Similarity}$ yet only 13% of the

estuary$_{Similarity}$. Conversely in early summer, kingfish, Atl. croaker, and summer

flounder contributed approximately 40% site similarity in the estuary versus only 4%

in the ICS. Spot was one of several species that contributed substantially to

assemblage structure in only one habitat regardless of season: average ICS$_{Similarity}$ < 1

%, average estuary$_{Similarity}$ = 14%.

Differences between the ICS and estuarine assemblages were found in all

direct comparisons except for the 2005 annual contrast (p = 0.12; Table 2). There

was a general divergence in ICS and estuarine assemblages from the early summer to

the fall as evidenced by the increase in seasonal ANOSIM *R*-statistic value from *R* =

Table 2 Results from 1-way ANOSIM of intrahabitat and 2-way ANOSIM (with blocking factor) of interhabitat assemblage structure for juvenile finfish assemblages from Maryland's inner continental shelf (ICS) and the lower main stem of Chesapeake Bay (estuary). Depth strata were defined as shallow (A ≤ 10 m) or deep (B > 10 m), and seasons as early summer (ES: June, July), late summer (LS: August, September), or fall (October, November).

Habitat/effect [a]	Comparison		Block	R	p
Intrahabitat	**ICS**				
Season	ES	LS	-	0.51	0.003
	ES	Fall	-	0.37	0.003
	LS	Fall	-	0.10	0.30
Year	2004	2005	-	0.14	0.003
	2004	2006	-	0.04	0.78
	2005	2006	-	0.08	0.21
Depth	A	B	-	-0.01	0.68
	estuary				
Season	ES	LS	-	0.31	0.003
	ES	Fall	-	0.09	0.003
	LS	Fall	-	-0.01	1.0
Year	2004	2005	-	0.22	0.003
	2004	2006	-	0.03	0.18
	2005	2006	-	0.16	0.003
Depth	A	B	-	0.07	0.001
Interhabitat	**ICS vs. estuary**				
	Global difference		Season	0.14	0.001
	Season	ES	Year	0.08	0.04
		LS	"	0.25	0.008
		Fall	"	0.60	0.008
	Year	2004	Season	0.28	0.008
		2005	"	0.08	0.12
		2006	"	0.31	0.008
	Depth	A	Season	0.28	0.008
		B	"	0.19	0.008

[a] All intrahabitat main effects were significant at $R \geq 0.11$, $p < 0.001$

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, filled bars) and lower Chesapeake Bay (Estuary, open bars). Seasons are defined as: early summer (June, July), late summer (August, September) and fall (October, November).
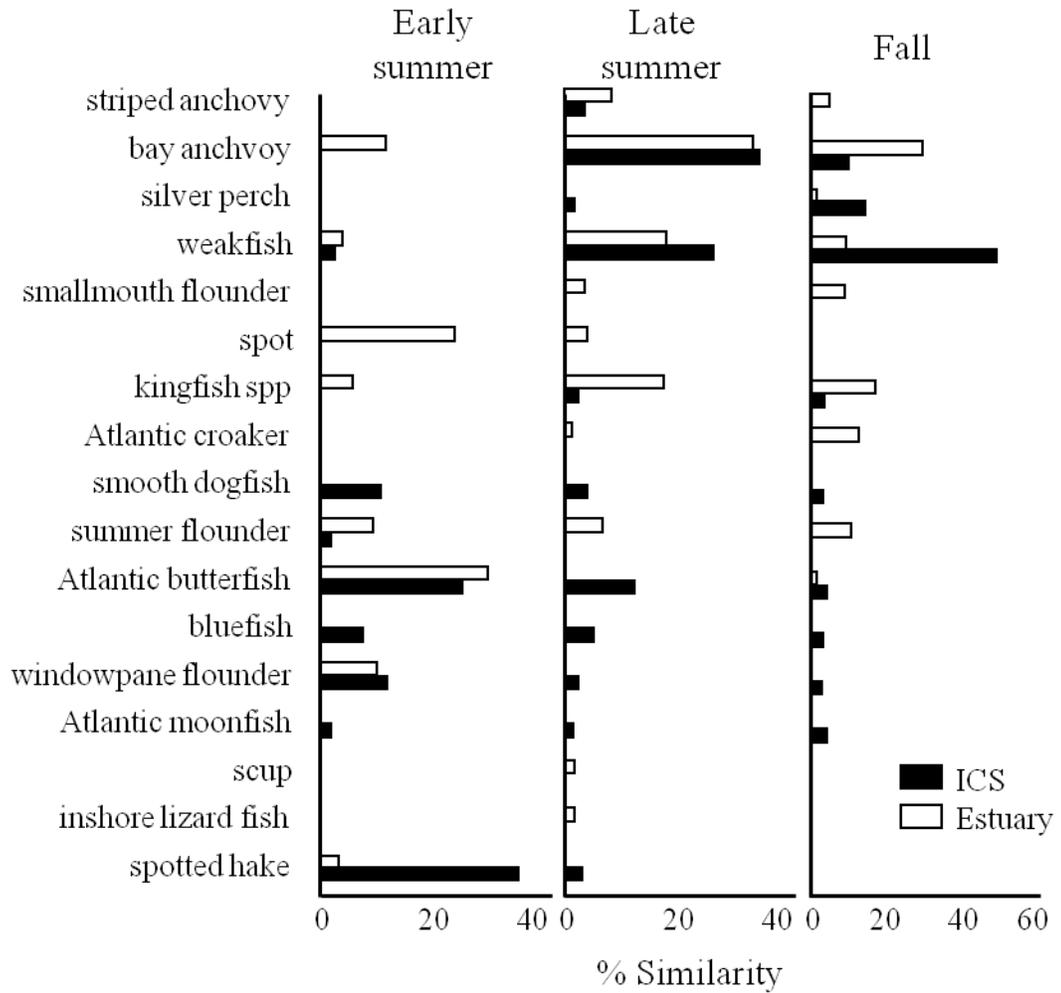
0.08 in the early summer to $R = 0.60$ by the fall. This divergence was due in a large part to the increasing relative dominance of bay anchovy and weakfish over time in each habitat; by the fall, weakfish were numerically dominant in the ICS while bay anchovy dominated in the estuary (Fig 3). Between habitat types, deep areas exhibited greater overlap in assemblage composition than shallow areas ($R_{Deep} = 0.19$ vs. $R_{Shallow} = 0.28$) although the differences in R were modest. In deep areas, bay anchovy, weakfish, and Atl. butterfish explained 61% and 58% of the cumulative site similarity in the ICS and estuary, respectively. The same three species contributed 59% to the shallow $ICS_{Similarity}$. But, a different suite of three species, bay anchovy, kingfish spp., and summer flounder contributed 54% to the shallow estuary$_{Similarity}$.

In nMDS plots of depth-specific monthly averages from each year (Fig 4, upper and middle panels), seasonal patterns dominated ordinations: assemblages associated with summer sampling from both habitats occurred along a continuum between early summer and fall endpoints. The dissimilarity (separation in space) of 2005 from the other years was also apparent, particularly in the estuary. The consistent, seasonal progressions in each habitat were conserved in the combined dataset (Fig 4 lower panel) with a separation between ICS and estuarine assemblages despite parallel temporal patterns.

Seasonal changes in biodiversity corresponded with compositional turnover and shifts in numerical abundance among species (Table 3). Biodiversity indices

Fig 4 Non-metric multidimensional 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.
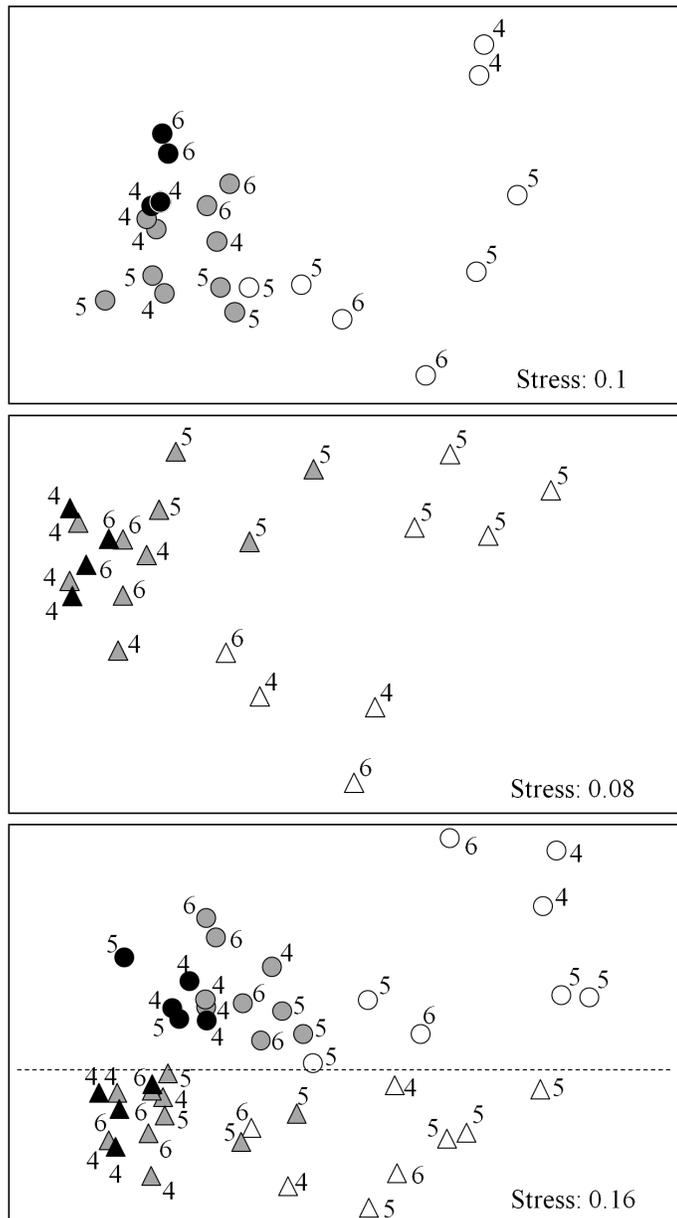
differed significantly among seasonas in species richness S (*ICS*: $F_{2,115} = 68.8$, $p <$ 0.0001; *estuary*: $F_{2,462} = 143.8$, $p < 0.0001$), and evenness J (*ICS*: $F_{2,115} = 7.51$, $p =$ 0.0009; *estuary*: $F_{2,462} = 68.9$, $p < 0.0001$). The year effect was significant for S in both habitats ($p < 0.0001$), but only for J in the ICS ($p = 0.03$). Seasonally, S increased 2–fold in the ICS from early to late summer (Fig 5), corresponding with the appearance of juvenile species such as Atl. menhaden *Brevortia tyrannus*, smallmouth flounder, scup, black drum, striped searobin *Prionotus evolans*, bigeye scad *Selar crumenophthalmus*, lookdown *Selene vomer* and inshore lizard fish. In the estuary, S showed a similar early to late summer increase following the appearance of species such as black sea bass *Centropristis striata*, Atl. spadefish, banded drum *Larimus fasciatus*, Atl. croaker, threadfin shad *Opisthonema oglinum*, northern searobin, and Atl. moonfish. Mean species richness continued to increase from late summer to fall in the estuary despite the disappearance of 7 species and appearance of hogchoker *Trinectes maculatus* and lookdown (Table 3). 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 (Table 3, Fig 5). In both habitats, J declined from early to late summer because of increased abundance of numerically dominant species in both habitats (e.g., bay anchovy, striped anchovy, silver perch, weakfish, spot, weakfish, Atl. croaker, Atl. butterfish, Atl. moonfish, spotted hake), before stabilizing and remaining relatively unchanged from late summer to fall.

Fig 5 Average seasonal patterns in A) average number of species per haul (species richness: Sobs ± SE), and B) species evenness (J ± SE) for age-0 finfish assemblages from Maryland's inner continental shelf (circles) and lower Chesapeake Bay (triangles) from 2004-2006. Seasons are coded as: ES (early summer – June, July), LS (late summer – August, September), and Fall (October, November).
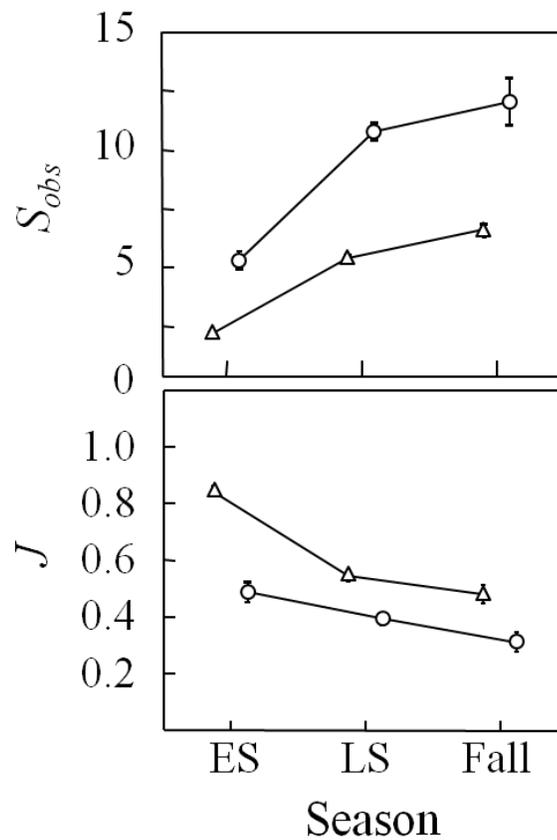
Table 3 Species richness (LSM ± SE), evenness (LSM ± SE) and total age-0 catch (uncorrected) per season for each species from Maryland's inner continental shelf (ICS) and lower mainstem Chesapeake Bay (estuary). Seasons are coded as: ES (early summer – June, July), LS (late summer – August, September), 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 (0.4)[A]	10.9 (0.4)[B]	12.1 (1.0)[B]	2.2 (0.1)[A]	5.5 (0.2)[B]	6.7 (0.2)[C]
species evenness (J)		0.49 (0.04)[A]	0.39 (0.02)[B]	0.31 (0.03)[B]	0.84 (0.02)[A]	0.55 (0.02)[B]	0.48 (0.03)[B]
Alosa aestivalis	blueback herring		9				
Alosa mediocris	hickory shad				2		
Alosa pseudoharengus	alewife				2		
Anchoa hepsetus	striped anchovy	4	5,536		75	1,725	380
Anchoa mitchilli	bay anchovy	1,200	125,482	7,751	665	61,888	49,702
Archosargus probatocephalus	sheepshead			2			
Astroscopus guttatus	northern star gazer				1	3	
Bairdiella chrysoura	silver perch	5	1,791	4,411	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	1,720	86,779	35,229	248	4,917	2,103
Decapterus punctatus	round scad	432	157				
Etropus microstomus	smallmouth flounder		9	20	1	397	199
Etrumeus teres	round herring	2,004	1,439		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	1,228	30	429	1,687	2
Menidia menidia	Atlantic silverside			14			
Menticirrhus spp.	kingfish	80	3,191	838	101	2,374	661
Merluccius bilinearis	silver hake			15			
Micropogonias undulatus	Atlantic croaker			80		547	1,874
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	8,056	16,452	274	189	126	82
Pogonias cromis	black drum		130	7			
Pomatomus saltatrix	bluefish	1,191	5,852	200	7	3	28
Prionotus carolinus	northern searobin					6	10

Species	Common name						
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	1,500	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	4,046	1,969	6	63	11	

3.4 Species growth and CPUE comparisons

Size-structure of bay anchovy, weakfish, spot, summer flounder, and Atl. butterfish over time indicated temporal progression of length modes in each habitat (Fig 6). 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 Atl. butterfish in the estuary.   There was evidence of halted modal progression of bay anchovy from September to the later fall months within the estuary (but not the ICS) as well as increased contribution of smaller summer flounder to 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 6). Estimates of in situ growth rate (based on the monthly progression of length modes) ranged from 0.21–0.59 mm day^{-1} for bay anchovy to 1.00–2.05 mm day^{-1} for summer flounder (Table 4). The rank order of growth rates between habitats varied by species – average growth of spot, summer flounder, and Atl. 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, $p \geq 0.22$).

Increasing seasonal trends in abundance were significant for CPUE$_{Gear}$ of bay anchovy, weakfish, and summer flounder within both habitats ($p < 0.0001$) (Fig 7). Seasonal effects also occurred for spot and Atl. butterfish in the estuary ($p \leq 0.02$).

Fig 6 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, filled bars) and lower Chesapeake Bay (Estuary, open bars). Catches are plotted as percent total catch per length class from each habitat (% Total catch).
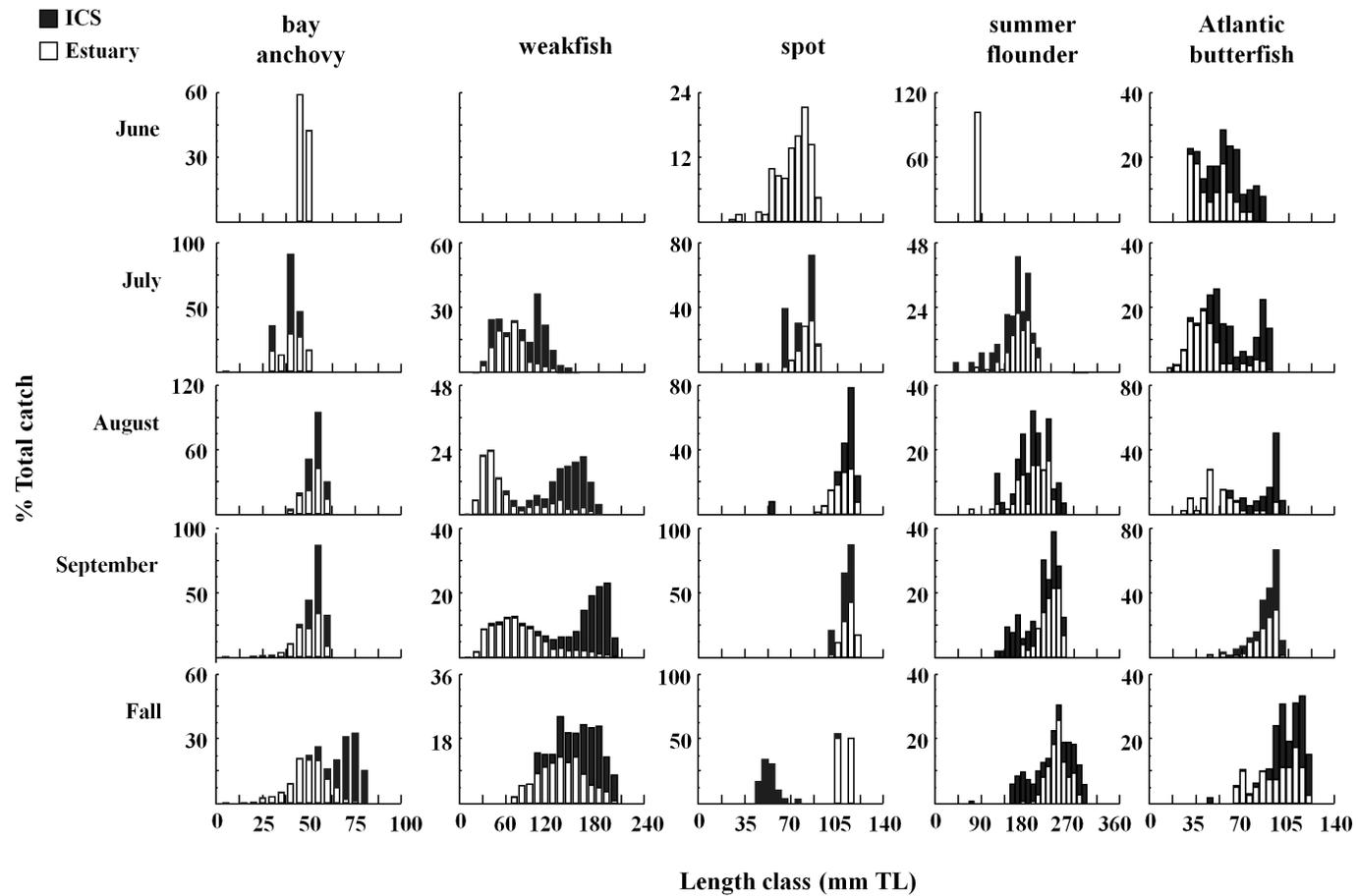
Table 4 Habitat-specific mean growth rates in mm day^{-1} (G [± SD]) and coefficient of variation (%) of five juvenile-stage species from this study and previous studies of regional estuarine environments.

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
	0.53-0.55		estuary	Great South Bay (NJ)	Castro and Cowen 1991
	0.48-0.55		estuary	Hudson River (NY)	Jordan et al. 2000[a]
	0.15		estuary	Narragansett Bay (RI)	Lapolla 2001
	0.32-0.47		estuary	Chesapeake Bay	Zastrow et al. 1991
	0.47		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[b]
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 [c]

	1.3-1.4		estuary	Duplin River (GA)	Reichert and van der Veer 1991[d]
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

[a] Median summer growth rates of larval stage bay anchovy

[b] Late summer growth rates from Table 1, p. 483 of McCambridge and Alden 1984

[c] Field enclosure experiment using juveniles transplanted from NH culture facility

[d] Laboratory study using juveniles (28-46 mm) collected from Duplin River (held at 23.7-24.8 °C)

Peak abundances of spot were observed in late summer in the estuary and although Atl. butterfish densities showed a late summer minimum, seasonal pair-wise comparisons of Atl. butterfish were not significant. Year was a significant factor for three species (spot, summer flounder and Atl. butterfish) in the ICS ($p \leq 0.007$) and all five species in the estuary. Specifically, 2005 was associated with an abundance minimum for bay anchovy and weakfish in the estuary and summer flounder in both habitats. Atlantic butterfish (ICS) and spot (both habitats) abundances were highest in 2005. Only the estuary had significant depth-related differences (Fig 7), where higher abundance of both weakfish and Atl. butterfish occurred in deep (> 10m) areas.

In direct comparisons of $CPUE_{Gear}$ 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 Atl. butterfish ($\chi^2 = 84.2$, $p < 0.0001$) abundances in late summer differed significantly between habitats. Gear-calibrated abundances of bay anchovy, weakfish and Atl. butterfish were 8.1, 4.2 and 12.8-fold higher in the ICS (Table 5). Conversely, spot and summer flounder were 2.4 and 5.8-fold more abundant in the estuary during the late summer.

4. Discussion

The goal of this research was to compare the seasonal assemblages of juvenile fishes that utilize temperate estuaries and the coastal ocean as nursery habitats. I observed similar schedules of species incidence, similar growth rates, and

Fig 7 Log$_e$-transformed age-0 catch-per-unit-effort (CPUE = catch ha^{-1}) ± 1 SE for five species from Maryland's inner continental shelf (ICS, filled bars) and lower Chesapeake Bay (Estuary, open bars). Factor levels within main effects (Year, Season, Depth) with different letters are significantly different (Krusal-Wallis rank-sum test, α = 0.05); an asterisk indicates a significant main effect without significant pairwise comparisons. Seasons: early summer (June, July – ES), late summer (August, September– LS) and fall (October, November); depth strata: shallow (< 10 m), deep (> 10 m).
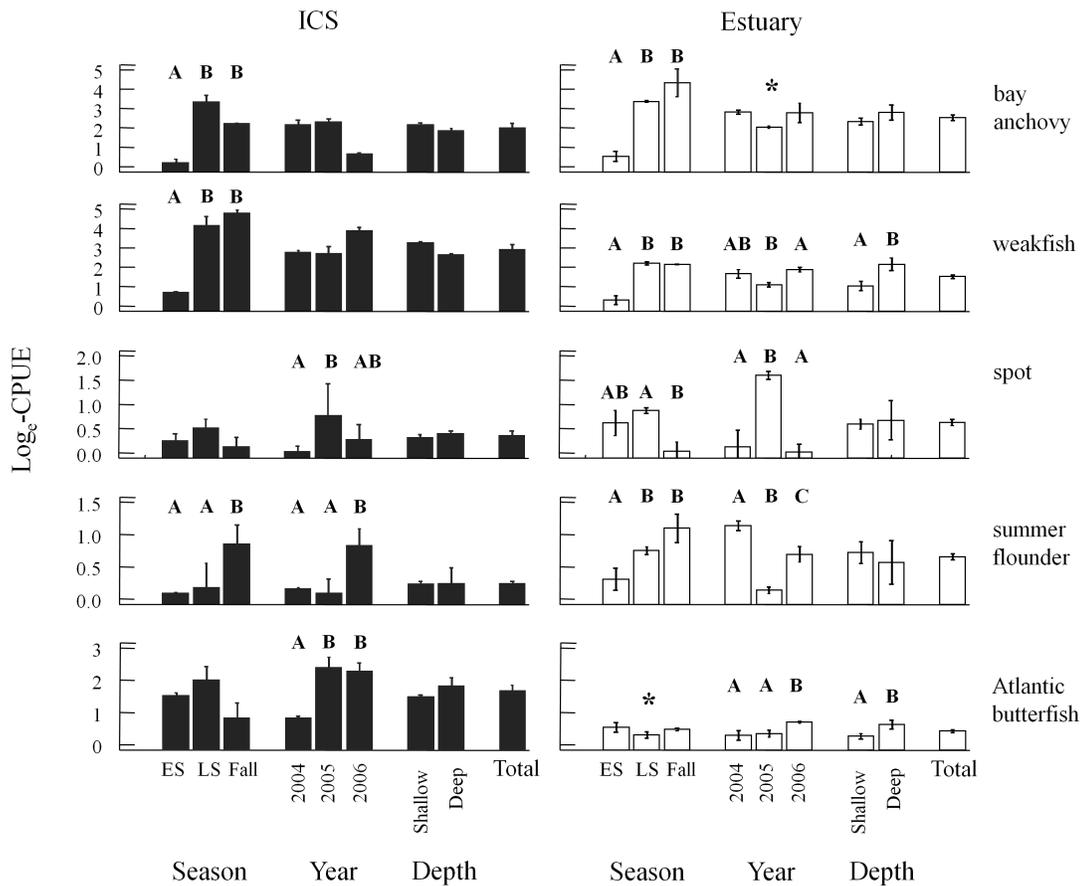
Table 5 Sample size (n – sites with positive catch, [Total late summer sample size –
N_{ICS} = 58, $N_{estuary}$ = 228]) and geometric mean late summer catch ha^{-1} ± 1SE
($CPUE_{Gear}$) for five abundant juvenile-stage species in Maryland's inner continental
shelf (ICS) and lower mainstem Chesapeake Bay (estuary). Includes August and
September sampling.

Species	ICS		estuary	
	n	$CPUE_{Gear}$	n	$CPUE_{Gear}$
bay anchovy [a]	48	27.3 (19.4, 38.2)	162	3.4 (2.9, 3.9)
weakfish [a]	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 [a]	21	0.2 (0.1, 0.2)	96	1.1 (1.0, 1.3)
Atlantic butterfish [a]	47	6.5 (4.9, 8.4)	41	0.5 (0.4, 0.6)

[a] All species CPUE distributions were significantly different between habitats

(Kruskal-Wallis test, α = 0.05)

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: Assemblage phenology

The generalized spring-summer spawning, estuarine 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 that I have demonstrated strong seasonal correspondence between an ICS and estuarine habitat in the progression of age-0 assemblage structure, temporal patterns of biodiversity, species phenologies, and growth rates despite differences in survey design and gear dimensions. 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). In addition to temporal structuring, there was evidence that the estuarine assemblage was responding more coherently to depth than the ICS assemblage. This might reflect differences in the hypsography between the two habitats. The relatively flat expanse of lower Chesapeake Bay is punctuated by deep channel habitats; whereas, the gentle inshore-offshore declivity of the ICS has few well-defined depth breaks (Fig 1). Many demersal fish respond to the availability and complexity of vertical relief in bottom habitats (McCormick 1994) – concentrations of certain species within or along channels (e.g., during up- or

down-estuary movements) might explain the habitat-specific influence of depth in this study.

Juveniles of most temperate transient species (i.e., those that engage seasonal migrations) migrate to southern or offshore shelf (or both) overwintering habitats although some species such as Atl. croaker (Miller et al. 2003), hogchoker *Trinectes maculatus* (Szedlmayer and Able 1996) and summer flounder (Packer et al. 1999) will overwinter within the estuary. For this reason, the high similarity I 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). Still, I did observe a substantial faunal turnover 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, five species were only observed in the ICS during fall sampling (sheepshead *Archosargus probatocephalus*, American conger *Conger oceanicus*, Atlantic silverside *Menidia menidia*, sliver hake *Merluccius bilinearis*, red hake *Urophycis chuss*). Hogchoker appeared in the lower estuary during the fall. The timing of these occurrences is

consistent with the described life-history of these species (i.e., shelf overwintering of Atl. silverside, Am. conger, red hake: Conover and Murawski 1982; Able and Fahay 1998; Steimle et al. 1999; fall settlement of silver hake: Steves and Cowen 2000), suggesting a seasonal turnover in assemblage structure within the study area. However, 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 accurate. The available evidence suggests that such biases are not likely at the species-level (e.g., Fig 2); yet, the better fit of length-variable vs. length-invariant gear-calibration models indicates that relative vulnerability to the gears varies among certain length-classes for most species. The dynamic relative vulnerability of these species to the two trawls indicates a cautionary approach should be taken when interpreting the multispecies results (assemblage analysis) at the species-level.

4.2 The inner continental shelf – evidence for a nursery role: 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

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(i.e., contribution to adult stock). Here, my 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. This suggests that these species are experiencing similar growth trajectories despite observed differences in ambient physicochemical conditions. For example, 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, the effect of temperature on growth was masked by one or more environmental variables, or that growth efficiency and energy allocation strategies varied between the two habitats. 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 settlement. 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 been displayed by bay anchovy in the estuary from late summer to fall (Fig 6), associated with larger juveniles migrating into ICS waters ahead of smaller conspecifics (Vouglitois et al. 1987; Able and Fahay 1998). Weakfish may have shown a similar phenomenon with larger juveniles continuously leaving the estuary for the ICS throughout the summer growth period.

There was evidence of decreased variability in age-0 growth conditions within the ICS relative to the estuary (Table 4; exception is summer flounder). This suggests that growth conditions may be more stable year-to-year in the ICS than in lower Chesapeake Bay. It is not clear why growth rates were less variable on the ICS given the comparable environmental variability I measured between these habitats. Two potentially contributing factors were: 1) analytical – modal estimates of growth could be biased in ways that decrease variance in the ICS relative to the estuary, and 2) environmental – increased environmental variability experienced by estuarine fish at the microhabitat scale could yield a wider spectrum of growth trajectories (e.g., trophic, Sogard 1992; bioenergetic, Claireaux and Lefrancois 2007). A third possibility is that differences in the size-selectivity of the two trawls resulted in higher variability into the estuarine survey. If the smaller area-swept and lower sampling efficiency for large fish increased the patchiness of catch-at-size in the estuary gear, it could inflate variance in growth estimates despite gear calibration.

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 Atl. 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 hrs, weakfish ~ 50 hrs; 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 Atl. butterfish to be three of the most abundant species co-occurring in polyhaline and euhaline habitats.

Although I 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 Atl. butterfish during August and September. In lower Chesapeake Bay (c. 1,000,526 ha within the potential sampling polygon), estimated estuarine relative densities ($CPUE_{Gear}$) 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 Atl. 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% (Atl. 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 ICS (e.g., NEMAP program, Bonzek et al. 2007) 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 bay anchovy were substantially lower than those presented in an earlier study. In the earlier study, baywide abundance of bay anchovy, weakfish, spot, and Atl. butterfish (Jung and Houde 2003) were all higher than those estimated here. This is particularly true for bay anchovy. From 1995-2000, estimated abundance of bay anchovy (age-0 and adult) from April-October in Chesapeake bay was approximately 11.2×10^9 (Jung and Houde 2003), or 5.7×10^9 if adjusted to the volume of lower Chesapeake Bay alone (Cronin 1971) versus the 3.37×10^6 estimated for trawlable abundance in this study. The discrepancy is most likely due to three interacting factors: 1) gear differences; 2) habitat sampled; and 3) estimation method. The earlier study was based on data from a mid-water trawl survey (3-mm codend liner) that obliquely sampled the entire water column; a sampling design that almost certainly sampled juveniles of pelagic species such as bay anchovy and Atl. butterfish more effectively than the bottom trawls (6.4-mm codend liner) used in this study. Despite the larger mesh codend liner, a comparison of mean individual weight per species suggests that

the bottom trawl captured smaller individuals on average, an unexpected result (Table 6). Scaling by volume (Jung and Houde 2003) vs. area would have a substantial effect on final abundance estimates (e.g., volumetric abundances would include a depth multiplier of ~ 10). Finally, abundance in the Jung and Houde (2003) study was derived from arithmetic mean CPUE on a volumetric basis; whereas geometric mean CPUE estimates were used in the current study due to high skew in the data.

A recalculation of ICS and estuary species densities (from this study) based on arithmetic means was compared to values reported in Jung and Houde (2003) to investigate the effect of this particular difference in estimation method (Table 6). The results suggest that when treated similarly, estimates from both studies yield similar abundances (within 2 orders of magnitude) if scaled to a common area. Still, bay anchovy estimates were nearly 100-fold higher in the Jung and Houde study, indicating that the bottom trawl used in my study was substantially less efficient gear than the mid-water trawl in sampling this species. Ultimately, the goal of this analysis was a robust comparison of relative abundance between ICS and estuary habitats. Therefore, while the relative abundances reported in Table 5 may not be accurate estimates of true abundance of these species (especially pelagic spp.), they do provide calibrated estimates of abundance suitable for direct comparisons between habitats.

4.3 Summary

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. My 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 their recognized role as latitudinal and longitudinal movement corridors.

Table 6. Comparative metrics from the current study (ICS, estuary [here given as L. Ches.]) and a previous study of Chesapeake Bay finfish assemblage structure (Jung and Houde 2003 [J-H 2003], L. Ches.). Shown are weight-per-individual (directly measured for ICS and estuary, calculated from total abundance and biomass reported in J-H 2003), arithmetic mean catch-per-unit-effort based on areal (ICS, estuary) or volumetric (J-H 2003) estimators, and projected total relative abundance for lower Chesapeake Bay based on CPUE from each habitat/study.

| Species | Wt ind^{-1} (g) | | | CPUE ($m^2 \times 10^3$) [a] | | CPUE ($m^3 \times 10^3$) | Expanded Abundances [b] | | |
	ICS this study	L. Ches. this study	L. Ches. J-H 2003	ICS this study	L. Ches. this study	L. Ches. J-H 2003	ICS this study	L. Ches. this study	L. Ches. J-H 2003 [c]
bay anchovy	0.97	0.83	0.82	39.52	3.09	214.23	3.95E+08	3.09E+07	2.14E+09
weakfish	25.11	5.88	41.4	17.93	9	0.68	1.79E+08	9.00E+07	6.82E+06
spot	12.29	14.19	74.43	0.47	2.22	0.41	4.70E+06	2.22E+07	4.15E+06
summer flounder	77.53	93.6	-	0.03	0.35	-	3.00E+05	3.50E+06	-
Atlantic butterfish	8.45	4.77	35.96	5.99	0.32	0.2	5.99E+07	3.20E+06	2.04E+06

[a] Arthimetic means (instead of geometric means) have been provided for ICS and estuary habitats from this study to increase comparability with Jung and Houde 2003

[b] A lower Chesapeake Bay area of 1,000,526 ha (1 x 10^{10} m^2) was used

[c] Volumetric CPUE (m^3) from Jung and Houde 2003 was substituted for areal calculations (i.e., CPUE m^3 = CPUE m^2)

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Chapter 3 Appendix

Appendix A Total catch (N), geometric mean density (CPUE = C 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[a],

habitat, behavior and maximum length[b] (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	ICS			Estuary			Ecomophological traits
		N	CPUE	% FO	N	CPUE	% FO	
Achiridae	*Trinectes maculatus*	-	-	-	1	1.89	<1%	
Atherinopsidae	*Menidia menidia*	14	0.25	1%	-	-	-	
Batrachoididae	*Opsanus tau*	-	-	-	9	2.19	1%	
Blenniidae	*Hypsoblennius hentzi*	-	-	-	4	2.03	1%	
Carangidae	*Decapterus punctatus*	589	0.99	9%	-	-	-	
	Selar crumenophthalmus	9	0.20	2%	-	-	-	
	Selene setapinnis	1,781	0.46	49%	19	2.67	1%	
	Selene vomer	21	0.25	2%	4	2.25	<1%	
	Trachurus lathami	796	0.82	10%	-	-	-	
Clupeidae	*Alosa aestivalis*	9	0.17	3%	-	-	-	

	Alosa mediocris	-	-	-	2	2.46	<1%	
	Alosa pseudoharengus	-	-	-	2	2.49	<1%	
	Brevoortia tyrannus	95	0.22	18%	4	2.46	1%	
	Clupea harengus	5	0.17	2%	-	-	-	
	Etrumeus teres	3,443	2.90	11%	7	2.67	1%	
	Opisthonema oglinum	14	0.22	4%	180	3.71	6%	
Congridae	*Conger oceanicus*	1	0.17	1%	-	-	-	
Engraulidae	*Anchoa hepsetus*	5,540	4.31	21%	2,179	3.85	31%	Fu, Ca, P/D, Sc, 90
	Anchoa mitchilli	134,434	14.64	54%	112,255	23.78	55%	Fu, Ca, P/D, Sc, 80
Ephippidae	*Chaetodipterus faber*	-	-	-	45	2.19	6%	
Gobiidae	*Gobiosoma bosci*	3	0.17	2%	2	2.06	<1%	
	Gobiosoma ginsburgi	-	-	-	7	2.78	1%	
Haemulidae	*Orthopristis chrysoptera*	46	0.31	4%	3	2.46	1%	
Merlucciidae	*Merluccius bilinearis*	15	0.19	3%	-	-	-	
Ophidiidae	*Ophidion marginatum*	2	0.16	2%	-	-	-	
Paralichthyidae	*Etropus microstomus*	30	0.25	5%	597	2.46	24%	Fl, An, B, So, 100
	Paralichthys dentatus	290	0.20	40%	553	2.35	38%	Fl, An, B, So, 300
Phycidae	*Urophycis chuss*	2	0.19	1%	-	-	-	
	Urophycis regia	6,022	0.68	70%	74	2.16	4%	
Pomatomidae	*Pomatomus saltatrix*	7,244	0.38	76%	38	2.46	4%	Fu, Ca, P, Sc, 270
Rajidae	*Raja eglanteria*	42	0.40	13%	2	2.10	<1%	
Sciaenidae	*Bairdiella chrysoura*	6,207	1.16	37%	419	2.63	13%	Hc, Su, D, Sh, 150
	Cynoscion regalis	123,728	4.93	66%	7,268	3.26	45%	Fu, Su, D, Sh, 185
	Larimus fasciatus	20	0.20	8%	134	2.42	8%	
	Leiostomus xanthurus	1,548	2.63	20%	2,118	4.42	23%	Hc, Su, D, Sh, 120
	Menticirrhus spp.	4,109	0.70	49%	3,136	3.22	50%	Fu, Su, D, Sh, 220
	Micropogonias undulatus	80	0.46	3%	2,421	4.26	21%	
	Pogonias cromis	137	0.27	11%	-	-	-	

Scombridae	*Scomberomorus maculatus*	-	-	-	4	2.60	<1%	
Scophthalmidae	*Scophthalmus aquosus*	846	0.23	69%	91	2.10	11%	Fl, An, B, So, 205
Serranidae	*Centropristis striata*	1	0.17	1%	6	1.89	1%	
Sparidae	*Archosargus probatocephalus*	2	0.17	1%	-	-	-	
	Stenotomus chrysops	415	0.77	15%	245	2.56	14%	Hc, Su, D/S, Sh, 100
Sphyraenidae	*Sphyraena borealis*	31	0.20	14%	-	-	-	
Stromateidae	*Peprilus alepidotus*	-	-	-	223	2.49	11%	
	Peprilus triacanthus	24,782	3.06	73%	397	2.39	23%	Hc, Ca, P, Sc, 90
Syngnathidae	*Hippocampus erectus*	-	-	-	32	2.16	4%	
	Syngnathus fuscus	4	0.15	3%	67	2.19	7%	
Synodontidae	*Synodus foetens*	16	0.16	6%	157	2.22	14%	
Tetraodontidae	*Sphoeroides maculatus*	266	0.26	36%	63	2.19	7%	
Triakidae	*Mustelus canis*	986	0.23	78%	5	1.86	1%	
Triglidae	*Prionotus carolinus*	-	-	-	16	2.16	3%	
	Prionotus evolans	9	0.20	3%	16	2.16	3%	
Uranoscopidae	*Astroscopus guttatus*	-	-	-	4	2.25	1%	

[a] Swimming type designations based on characteristics outlined in Helfman et al. 1997

[b] 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)

Chapter 4: Differences in Juvenile Trophic Niche for Two Coastal Fish Species that use Marine and Estuarine Nursery Habitats

Abstract

In coastal regions, age-0 juveniles of many fish species occur in both marine and estuarine nursery habitats, yet the ecological consequences of specific nursery habitat use is poorly understood. Here, I analyzed muscle $\delta^{13}C$ and $\delta^{15}N$ and gut contents to compare trophic ecology associated with differential age-0 habitat use for bay anchovy *Anchoa mitchilli* and bluefish *Pomatomus saltatrix* from two habitats: Maryland's inner continental shelf (ICS) and lower Chesapeake Bay (estuary). Bluefish occupied equivalent trophic positions (TP) in the ICS and estuary (3.9-4.2 ~ tertiary consumers). In contrast, bay anchovy TP was higher in the ICS (3.6-3.8 ~ secondary-tertiary consumers) than the estuarine habitat (3.4-3.5). Percent lipid in muscle tissue and condition (weight-at-length) was higher in the ICS than estuary for both species. Isotopic diversity metrics (average nearest neighbor distance and standard deviation, convex hull area) suggested that trophic niche width was 57 and 35% narrower in ICS habitats for bluefish and bay anchovy, respectively. This study provides evidence that juvenile marine fish species recruiting to coastal ocean habitats may realize superior foraging conditions (i.e., equal/increased TP, increased lipid storage and condition) despite narrower total niche width relative to those recruiting to proximal estuaries.

1. Introduction

The survival, growth and eventual recruitment of juvenile marine fish to adult populations depend on a suite of interacting biotic and abiotic environmental factors (Cushing 1975; Beck et al. 2001). Exposure to unique combinations of these factors in different natal habitats, often mediated through parental reproductive strategies (e.g., cohort structure; Secor 2007), is considered an important determinant of spatially-explicit patterns in juvenile production (Beck et al. 2001). Isolating and quantifying juvenile production from individual habitats is an important endpoint from the population perspective as well as potentially useful for management (e.g., prioritization of conservation effort; Beck et al. 2001; Kraus and Secor 2005; Dahlgren et al. 2006). Still, without an understanding of the ecological mechanisms that support differential juvenile production between habitats and the realized condition of recruits, knowledge of spatial production patterns alone are insufficient for holistic spatially-explicit decision making (Sheaves et al. 2006). For example, if a particular reef supports a high density of juveniles due to the consistent arrival of a dominant prey type from an adjacent seagrass bed, protection of the reef alone would not be sufficient to maintain juvenile production – the prey source (i.e., seagrass bed) would also need to be protected.

One critical component of juvenile habitat quality is the availability of an accessible forage base that supports basal metabolic processes while allowing positive somatic growth and energy storage (e.g., Gibson 1994; Nislow et al. 2000; Rosenfeld et al. 2005). Among conspecifics, an individual's realized trophic niche (sensu

Hutchinson 1957) can vary between habitats depending on the composition of local prey fields, presence of physical habitat (e.g., sea grasses, oyster reefs), physicochemical conditions, anthropogenic effects, and density-dependent effects (Gerking 1994) . By influencing growth rate and the duration of size-dependent predation vulnerabilities, spatial variability in realized trophic niche can influence early survivorship patterns (Werner and Gilliam 1984); thereby linking intra-cohort foraging dynamics to recruitment success and population persistence at ecologically relevant time scales. Energy storage dynamics during the juvenile-phase may be particularly important for species inhabiting temperate coastal ecosystems that require sufficient energy reserves to sustain recruits during seasonal migrations and(or) overwintering periods (Schultz and Conover 1997).

Metrics that assess realized trophic niche are either based on direct observations of food habits such as quantification of stomach contents (e.g., Scharf et al. 2000) or indicators of time-integrated foraging history such as stable isotope ratios or fatty acid composition (Graeve et al. 1997; Bearhop et al. 2004). For the latter group of niche metrics, the advancement of ecological applications using stable isotopes in trophic studies are providing new representations of trophic niche width and variability ranging from the individual to the community level (Bearhop et al. 2004; Layman et al. 2007). By integrating assimilated nutrient characteristics over a period of weeks to months, stable isotope-based approaches can provide a holistic representation of trophic ecology throughout the nursery residence period (Herzka 2005).

In this study, I conducted a comparative analysis of ecological and physiological consequences arising from the use of different juvenile habitats by age-0 bluefish *Pomatomus saltatrix* and bay anchovy *Anchoa mitchilli*. Substantial ecological research exists for bluefish and bay anchovy in estuarine habitats of the Middle Atlantic Bight (MAB) (e.g., Hartman and Brandt 1995; Wang and Houde 1995; Harding and Mann 2001; Jung and Houde 2003; Scharf et al. 2006), yet both species are known to utilize inner continental shelf (ICS) nursery habitats in addition to estuaries (Able and Fahay 1998). Mature bluefish spawn in offshore continental shelf habitats as the population migrates northward along the US Atlantic coast in the spring and the summer; a process that typically results in two temporally segregated juvenile cohorts that preferentially recruit to estuary and ICS habitats of the MAB during the spring and summer, respectively (Kendall and Walford 1979; Hare and Cowen 1996; Able and Fahay 1998; Callihan et al. 2008). Bay anchovy spawn within estuaries and ICS waters (Able and Fahay 1998) with juveniles apparently recruiting to proximal suitable nursery areas although the natal source of juveniles captured in either region has not been fully verified. Juvenile cohorts of both species recruiting to estuarine and marine habitats are likely to experience dissimilar nursery conditions.

Here, I use morphometric, isotopic and dietary data to test three hypotheses relating nursery habitat suitability at the seascape scale (i.e., 1-100 km) to trophic ecology for two species, representing contrasting trophic positions. Specifically, I hypothesized that 1) vertical trophic position does not differ significantly between

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ICS and estuarine cohorts despite the likelihood of spatial differences in specific diet composition; 2) trophic niche width is wider for estuarine cohorts due to the increased heterogeneity of physical and geochemical attributes of estuarine habitats; and 3) cohorts from each habitat will exhibit similar physiological condition.

2. Materials and Methods

2.1 Fish collections

Specimens of both species were collected by trawl or seine during August 2008 (Table 1). Ocean samples were collected from Maryland's inner continental shelf (ICS, 5–20 m depth; Fig 1) as part of a larger, multi-year fisheries independent trawl survey (see Woodland et al. *in press*). The majority of ocean specimens (bluefish = 100%, bay anchovy = 50%) were collected with a demersal Yankee otter trawl (n = 8, 20-min tow duration) with 30-m foot-rope and 6.4-mm cod-end mesh. The remaining bay anchovy specimens were taken in a fixed frame 1-m^2 Tucker trawl (280-μm cod-end mesh) that was towed in a stepped, oblique pattern from the bottom to the surface at 45 sec intervals (n = 4, 6-min tow duration). Both trawls were towed along North-South transects that generally followed depth contours. Contemporaneous estuarine specimens were collected from the polyhaline lower mainstem Chesapeake Bay, VA (hereafter "estuary", salinity: 14.5–30.5) during the Virginia Institute of Marine Science Juvenile Fish and Blue Crab Trawl Survey's August sampling period (Fig 1). The estuary survey utilizes a similar trawl design (demersal semi-balloon otter trawl; 6.4-mm codend mesh); yet deployment time (5 min) and gape dimensions (e.g., 9-m footrope, Hata 1997) differ from the ICS survey methodology

Table 1 Sampling effort (N) by gear (OT = demersal otter trawl; TT = Tucker trawl) in Maryland's inner continental shelf (ICS) and lower mainstem Chesapeake Bay (estuary) from August 2008. Average environmental conditions (Depth m, Temp = temperature °C, Sal = salinity, DO = dissolved oxygen mg L^{-1}) and number/type of samples collected (diet, stable istope) for juvenile bluefish and bay anchovy shown per habitat-gear combination.

							Samples		
Habitat	Gear	N	Depth	Temp	Sal	DO	Bluefish	bay anchovy	eastern oyster
ICS	30-m OT	8	12.0	23.3	31.8	3.6	36, 14	10, 9	-
	1-m^2 TT	4	13.6	17.6	31.6	4.8	-	21, 6	-
Estuary	10-m OT	4	9.1	24.8	23.7	6.0	30,15	45, 16	-
	Oyster cages [a]								
	location 1	3	~1.5	27.2	18.9	6.5	-	-	5
	location 2	3	~1.5	27.9	19.9	6.7	-	-	5

[a] see Fig 1 for geographic placement of oyster cages at estuary locations 1 & 2 in Chesapeake Bay

Fig 1 Locations of fish (empty symbols) and bivalve (solid symbols) collection/cage sites in Maryland's inner continental shelf (circles), lower mainstem Chesapeake Bay (triangles) and Chesapeake Biological Laboratory (square).
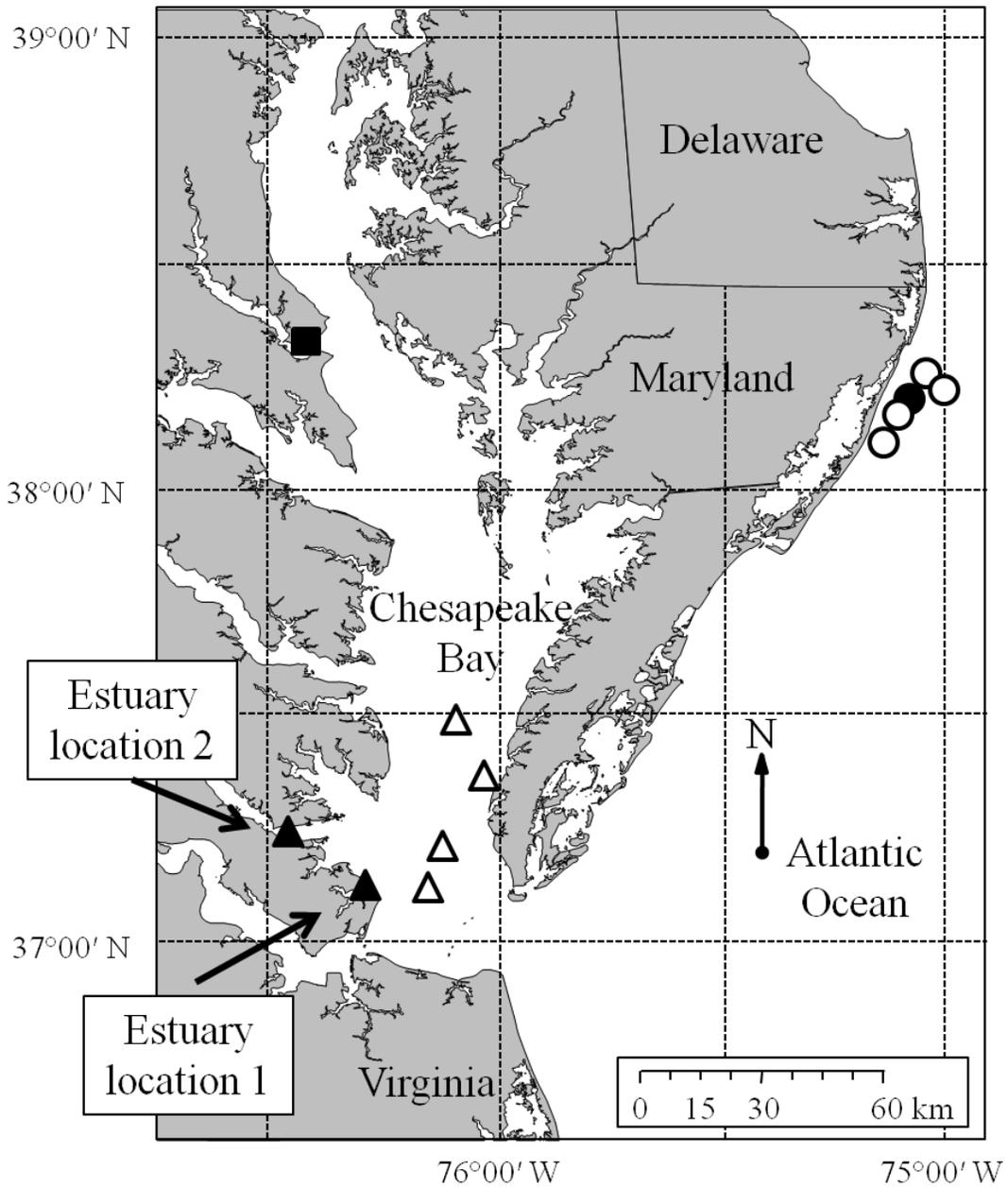
(see Tuckey and Fabrizio 2009 for additional survey details). Specimens were collected from depths of approximately 11.1 m ± 3.2 m (SD) in the ICS and 9.1 m ± 3.8 m in the estuary. Specimens retained for stable isotope (SI) and stomach contents (SC) analysis were either flash-frozen on dry ice immediately following capture (ICS) or immersed in an ice bath and transferred to a -20°C freezer prior to the end of the date of capture (estuary). All specimens were stored at -20°C until analyzed.

Bluefish collected in the ICS (TL = 154 ± 19 mm SD) were significantly smaller (2-sample t-test, $t = -5.26$, $df = 42$, $p < 0.0001$) than those collected in the estuary (211 ± 36 mm). There was no difference ($t = -2.86$, $df = 34$, $p = 0.10$) in size distribution of bay anchovy specimens between habitats (ICS = 46 ± 5 mm, estuary = 49 ± 5 mm). Due to the size difference of ICS and estuary bluefish, I used an ancillary multi-year dataset of bluefish stomach contents (SC) to test the hypothesis that diet varies significantly between length-classes of age-0 bluefish pertinent to this study. These SC data were collected from 570 age-0 bluefish from Maryland's coastal habitats (coastal lagoons, surf zone [0–2 m], ICS [5–20 m) and mainstem Chesapeake Bay (upper [mesohaline], lower [polyhaline]) from June-July (early summer) and August-September (late summer) of 1999-2001. Only bluefish 75–274 mm TL were included in the analysis (n = 430 with prey present); these were separated into 50-mm length-classes and biomass of SC aggregated into dominant prey categories. Biomass SC data (g) were log(x+1) transformed, Bray-Curtis similarities calculated among individuals and analysis of similarity (ANOSIM, Clarke 1993) used to compare diet across length-classes. Season, year, habitat and length-

class were all identified as significant main effects (1-way ANOSIM, Table 2); therefore, a single dummy variable was created from every combination of season, year and habitat (e.g., early summer 1999 ICS). This dummy variable was used as a block effect to account for external variation in pair-wise contrasts of diet between length-classes (2-way ANOSIM).

2.2 Oyster deployments

I selected eastern oyster *Crassostrea virginica* as a reference species to provide a standardized isotopic baseline, an approach that has been applied successfully using aquatic bivalve and gastropod species (Post 2002). Eastern oysters (hereafter "oyster") are euryhaline (naturally occur in salinities 2-40, Shumway 1996) primary consumers (i.e., trophic level [TL] = 2) in many estuarine and coastal ecosystems of the eastern United States (MacKenzie Jr. 1996). Age-1 cultured oysters were held in an unfiltered ambient flow-through raceway at Chesapeake Biological Laboratory (CBL, 38° 19.1′ N, 76° 27.1′ W, salinity = 9.3–16.1) from May-September 2008. In July, a subsample of these oysters were transferred to two locations proximal to fish collection sites in the estuary – location 1: 37° 05.6′ N, 76° 20.7′ W, and location 2: 37° 14.9′ N, 76° 30.4′ W. At each location, oysters were held in polyethylene 2.54-cm^2 bar mesh cages (n = 4 oysters cage^{-1}), suspended 0.5 m above the bottom on a vertical tether stretched between a cement anchor and surface float at depths of approximately 1.5–2 m. Oysters were allowed to equilibrate in situ at estuarine locations for 70 d, at which time all surviving specimens from the cages were retrieved, frozen and stored at -20°C. To verify equilibration of the planted oysters to

local biogeochemical conditions, I collected wild oysters at estuary location 1 for SI analysis (Fig 2; see Data analysis: *Trophic niche characteristics* below).

2.3 Stable isotope analysis

Teleost specimens were partially thawed and a sample of dorsal epaxial muscle tissue removed and cleaned of residual intermuscular bones. Samples were rinsed in de-ionized water, held at 60°C for $\geq$ 48 hours until completely dried, then pulverized to a fine homogenous powder using a mortar and pestle. The adductor muscle from individual bivalves was removed and handled identically to teleost tissue. Powdered samples were stored in a desiccator until sent for carbon and nitrogen SI analysis on a continuous-flow isotope ratio mass spectrometer coupled with an elemental analyzer (EA-CFIRMS; Colorado Plateau Stable Isotope Laboratory, Northern Arizona University). Stable isotope values are reported as a ratio in the "δ" notation (Peterson and Fry 1987) relative to international standards - Pee Dee Belemnite (C) and ambient air (N). All $\delta^{13}C$ values were mathematically normalized using the C:N ratio of the sample in conjunction with published correction models (Kiljunen et al. 2006; Post et al. 2007).

2.4 Condition factors

Species condition was compared between habitats using two independent methods. First, I derived the residual index of individual condition (CI; Gould 1975; as cited by Jakob et al. 1996) by regressing $\log_e$(body mass) against $\log_e$ (total length) for each

Table 2 Analysis of similarity (*R*-statistic [*R*]) of age-0 bluefish diet dataset from mainstem Chesapeake Bay [a] (Estuary), Maryland coastal bays and inner continental shelf [b] (Coast) and all habitats combined. Main effects: Season (June, July – early summer; August, September – late summer), Year (1999-2001), Habitat [a, b], Length-class (Lclass – 50 mm intervals, 75 to 274 mm total length). Results from 1-way ANOSIM (Main effects), 2-way ANOSIM (Lclass blocked by dummy variable – Season, Year, Habitat; e.g., early summer 1999 ICS) and pair-wise Lclass contrasts from 2-way ANOSIM. Significant effects are embolded ($\alpha \le 0.05$).

Factors/Groups	Estuary (n = 191)		Coast (n = 239)		All (N = 430)	
	R	*p*	*R*	*p*	*R*	*p*
Main effects (1-way ANOSIM)						
Season	**0.10**	**0.006**	**0.25**	**0.001**	**0.21**	**0.001**
Year	**0.10**	**0.001**	**0.13**	**0.002**	**0.08**	**0.001**
Habitat	**0.09**	**0.004**	**0.26**	**0.001**	**0.22**	**0.001**
Lclass	**0.08**	**0.001**	0.02	0.13	**0.03**	**0.005**
Main effects (2-way ANOSIM)						
Lclass	0.07	0.07	0.02	0.25	0.04	0.09
Block effect	**0.08**	**0.0001**	**0.19**	**0.002**	**0.21**	**0.001**
Lclass contrasts (from 2-way ANOSIM)						
75-124 vs 125-174	0.07	0.07	-0.01	0.55	0.03	0.23
75-124 vs 175-224	0.06	0.35	0.001	0.39	0.01	0.32
75-124 vs 225-274	-	-	0.20	0.12	0.20	0.12
125-174 vs 175-224	0.001	0.43	0.03	0.23	0.03	0.23

125-174 vs 225-274	0.20	0.18	0.13	0.22	0.13	0.21
175-224 vs 225-274	-	-	0.03	0.44	0.03	0.43

[a] lower (polyhaline) and upper (oligo–mesohaline) mainstem Chesapeake Bay

[b] Chincoteague Bay, Assateague Bay, Assateague Island surf zone, Maryland inner continental shelf (5–20 m)

Fig 2 δ^{15}N mixing models (solid lines) for age-1 oysters from two locations in lower

Chesapeake Bay (Location 1 – upper panel, Location 2 – lower panel; see Fig 1 for

geographic reference) for a 1-yr equilibration period. Empirical δ^{15}N ($\pm$ SD) values

at time = 0 d (R_i, caged oysters) and 70 d (R_t, caged and wild oysters) given as open

circles. Local δ^{15}N equilibria (R_f) = dashed lines and represent observed (Location 1)

and modeled (Location 2) estimates; grey dotted lines (upper panel only) = $R_f \pm 1$ SD.
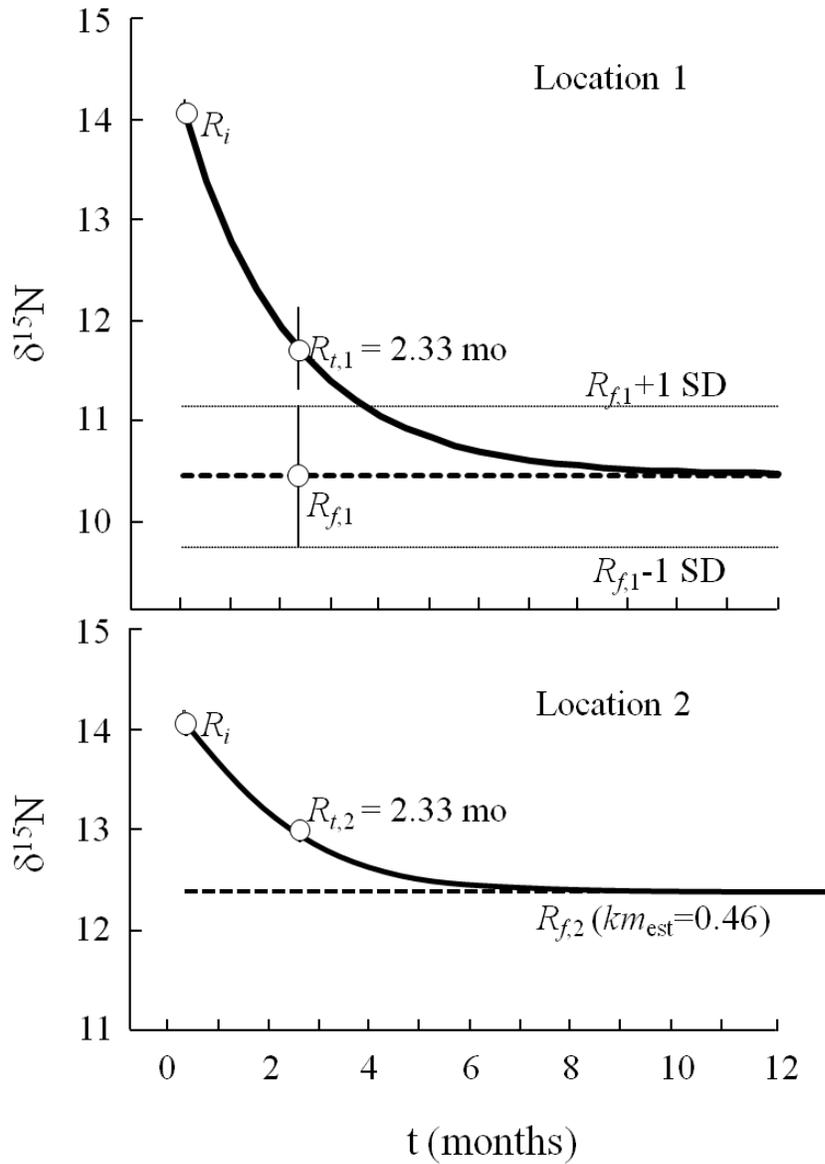
species and calculating the residual for each observation (i.e., individual). The

regression of $\log_e$ (body mass) against $\log_e$ (total length) was significant for both

species (bluefish slope $= 3.36 \pm 0.05$ SE, $F_{1, 58} = 3,936$, $p < 0.001$; bay anchovy slope

$= 3.44 \pm 0.16$ SE; $F_{1, 59} = 488$, $p < 0.001$). Species residuals were compared between

habitats with t-tests. I used the C:N ratio of epaxial muscle tissue, calculated during

mass spectroscopy, as a physiochemical index of individual condition representing

energy storage (i.e., proxy for sample % lipid content, Mcconnaughey and Mcroy

1979; Post et al. 2007; Buchheister and Latour 2010).

2.5 Trophic niche characteristics

A comparison of planted to wild oysters indicated planted oysters had not yet

equilibrated to local isotopic conditions after the 70-d period (2-sample t-test, $t =$

3.51, $df = 8$, $p = 0.008$; Fig 2); therefore, I used a 2 end-member mixing model to

estimate the equilibration rate of oysters planted at estuary location 1:

$$R_t = R_f + (R_i - R_f) * e^{-(k+m)*t}$$

where R_t is the sample δ^{15}N value measured at time t, R_f is the local equilibrium δ^{15}N

value, R_i is the initial δ^{15}N value, $k + m$ represents the isotopic equilibration rate

based on somatic growth (k) and metabolic turnover (m) and t is the length of time the

oysters were allowed to equilibrate. All parameters were known except for k and m

($R_f =$ wild caught oyster δ^{15}N value). For simplicity, $k + m$ were modeled as a single

term km_{est} representing the integrated isotopic equilibration rate. A maximum-

likelihood estimate of km_{est} at estuary location 1 was solved numerically based on my

empirical R_i, R_t and R_f measurements (Fig 2). This km_{est} was then used at estuary

location 2 in conjunction with empirical R_i and R_t values from this location to estimate R_f. The empirical R_f from estuary location 1 and modeled R_f from estuary location 2 were averaged and the mean used as the $\delta^{15}N$ isotopic baseline for the estuary.

One of the assumptions of using stable isotopes to compare trophic niche differences between habitats is that the sampled tissue of the consumer(s) of interest has equilibrated to the geochemistry of the local food web (Post 2002; Herzka 2005). I modeled isotopic equilibration time using biomass specific growth rates and simple exponential growth models (Herzka 2005), making the implicit assumption that dilution was principally responsible for equilibration dynamics (Fry and Arnold 1982). Absolute average daily growth rates $\bar{g}$ of 2.01 mm d^{-1} (bluefish, Callihan 2005) and 0.40 mm d^{-1} (bay anchovy, Able and Fahay 1998) were used to calculate biomass specific growth rates G (d^{-1}) for bluefish feeding on a novel forage base at 30, 50, 70 and 80 mm (endpoint = 150 mm) and bay anchovy at 15, 20, 25, 30 mm (endpoint = 50 mm) using the length-to-weight conversions:

$$Wt_{\text{bluefish}} = 3 \times 10^{-6} * TL^{3.2062}$$

$$Wt_{\text{bay anchovy}} = 2 \times 10^{-6} * TL^{3.2647}.$$

I assumed that juveniles equilibrated to the isotopic characteristics of a novel forage base after a 4–6-fold increase in initial biomass (Herzka 2005). The residency period required to achieve isotopic equilibrium t_{equil} in days was estimated for each species and initial size combination as

$$t_{equil} = \frac{Wt_{initial}/Wt_t}{G}$$

where $Wt_{initial}$ is the biomass at $t = 0$ (i.e., first day of foraging within novel food web)
and Wt_t is the biomass at day t.

I used species distributions in bivariate SI space to analyze spatial differences
in trophic ecology, including indicators of trophic variability, dispersion and total
niche area. Species-specific $\delta^{15}N$ and $\delta^{13}C$ variance patterns were compared
(Levene's test) to determine if niche width differed between habitats (Bearhop et al.
2004). Packing of individuals within species niche space (i.e., dispersion metrics,
Layman et al. 2007) was compared by mean Euclidean nearest neighbor distance
(NND) and the standard deviation of mean NND (NNDSD). Total niche area (TA)
was calculated as the minimum convex hull area in $\delta^{15}N$ and $\delta^{13}C$ space (Cornwell et
al. 2006, Layman et al. 2007). Convex hull area provides an index of realized niche
space while minimizing the unnecessary empty space inherent in areal bivariate
minima associated with rectangular or circular bounding containers (Cornwell et al.
2006). Bootstrapping (unrestricted random sampling with replacement, n = 1000)
was used to generate replicate distributions of NND, NNDSD and TA metrics to
allow statistical comparisons between habitats for each species. For each metric, the
between-habitat difference was calculated for each bootstrap replicate. The number
of replicates resulting in a higher metric value than the observed value was used to
calculate a p-value for the bootstrapped difference of means.

Trophic position of bluefish and bay anchovy from each habitat was estimated directly from diet (SC) and δ^{15}N signatures (SI analysis). Stomachs were excised from thawed specimens and fixed in 10% buffered formalin solution prior to SC analysis. Prey items were identified to the lowest possible taxon, enumerated, blotted dry and weighed (mg). Percent diet composition by weight (Hyslop 1980) was aggregated into 17 (bluefish) or 8 (bay anchovy) unique prey categories (Table 2). Trophic position of species i in habitat j was then calculated from SC data as:

$$TP_{SC,ij} = 1.0 + \sum_{k=1}^{n} TP_k(p_{ijk})$$

where TP_k is the trophic position of forage species k and p_{ijk} is the proportion of the total stomach contents biomass contributed by prey species k to the diet of species i in habitat j (Winemiller et al. 2007). Stable isotope estimation of trophic position was calculated as:

$$TP_{SI,ij} = \frac{\left[\left(\delta^{15}N_{ij} - \delta^{15}N_{base,j}\right)\right]}{\Delta_N} + \lambda$$

where $\delta^{15}N_{ij}$ is the isotopic signature of species i in habitat j, $\delta^{15}N_{base,j}$ is the mean δ^{15}N value of the baseline bivalve sampled in habitat j, Δ_N is the mean trophic fractionation of N between trophic levels (assumed = 3.4‰), and λ is the trophic level of the organism used to estimate $\delta^{15}N_{base}$ ($\lambda_{bivales}$ = 2; Post 2002). Spatial differences in species $TP_{SI\ was}$ tested with ANOVA and one-sample t-tests were used to test for agreement between TP_{SI} distributions and TP_{SC} point estimates.

3. Results

3.1 Bluefish diet analysis

Small-bodied forage fish (e.g., *Anchoa* spp., *Menidia* spp.) contributed 57–92% of the identifiable prey biomass across bluefish length-classes (Fig 3). The contribution of juvenile moronid species to SC biomass declined from 2% in fish 125–174 mm to 0% in fish 225–274 mm; whereas clupeids (e.g., Atlantic menhaden *Brevoortia tyrannus*) increased from 4% SC biomass in fish 125–174 mm to 27% in fish 225–274 mm. The three dominant invertebrate categories contributed relatively little (<1–6%) to SC across length-classes.

Due to unbalanced sample size among habitats, years and seasons, 1-way tests of length-class as a main effect yielded biased tests of length effects (Table 2). For example, bluefish 75–124mm were captured during early and late summer in the ICS yet bluefish 125–174 mm were only captured during late summer. A 1-way test of length-class as a main effect was therefore confounded with temporal changes in diet between early and late summer. Spatiotemporal changes in diet explained much of the variation present in the 1-way tests of main effects; but importantly, bluefish 75–274 mm in length did not exhibit significant differences among length-classes in diet composition after accounting for geographic, seasonal and annual variability (2-way ANOSIM, Table 2). Specific to the isotopic analysis that follows, there was no difference (2-way ANOSIM, R-stat $= 0.20$, $p = 0.18$) between length-classes of bluefish 125–174 mm and 225–274 mm in the 1998-2001 dataset from mainstem Chesapeake Bay habitats.

Fig 3 Percent diet composition by weight for 4 length-classes (Lclass: 50-mm intervals) of age-0 bluefish (N = 430, n per Lclass given above bars) from mainstem Chesapeake Bay, Maryland's coastal bays and inner continental shelf (see Table 2 for habitat details) collected from June-September 1999-2001. *Miscellaneous prey category includes rare vertebrate and invertebrate prey types.
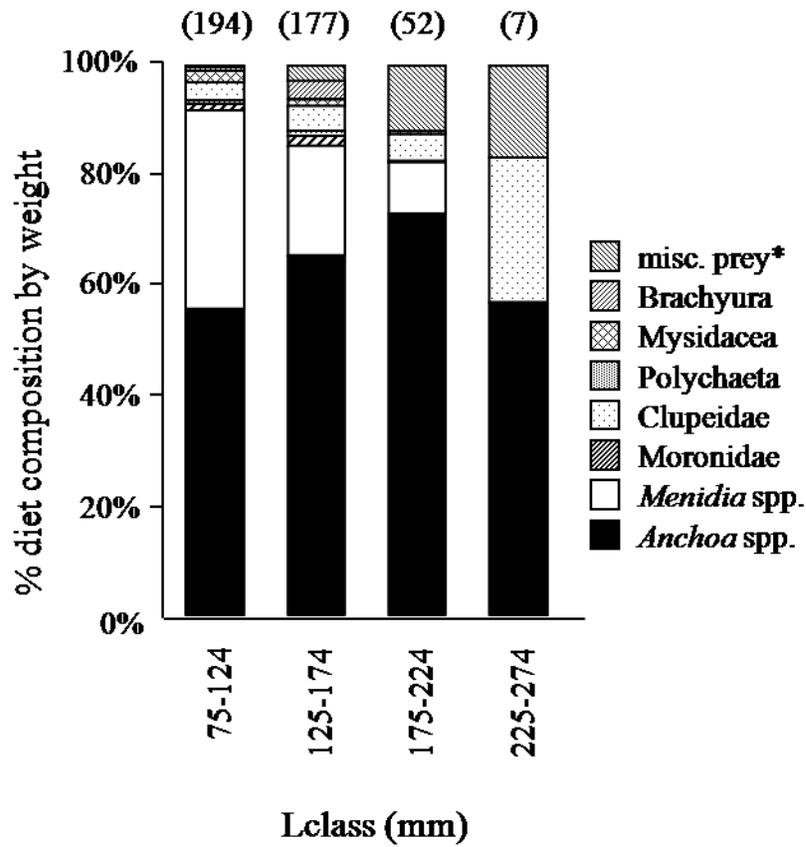
3.2 Isotopic baseline and equilibration estimates

Baseline isotopic measurements indicated C became more enriched (e.g., salinity =

12.6, 30.1; $\delta^{13}C$ at TL_2 = -21.04, -17.53) and N became more depleted (e.g., salinity =

12.6, 30.1; $\delta^{15}N$ at TL_2 = 14.12, 8.71) with increasing salinity conditions. These

patterns follow expected enrichment patterns (Fry 2002) and were consistent from

mesohaline to polyhaline to euhaline salinity regimes. The empirically measured R_f

from estuary location 2 was 10.37 ± 0.71 ‰ (SD) and the ML estimate of km_{est} was

0.46 ± 0.04 (ASD) (Fig 2). Based on km_{est} from location 1, the modeled R_f value for

location 2 was 12.42 ± 0.07 ‰ (ASD). The final average of the estuary $\delta^{15}N_{base}$ was

11.40 ‰. This was 2.69 ‰ higher than the ICS $\delta^{15}N_{base}$ of 8.71± 0.74 ‰ (SD) and

2.72 ‰ less than the CBL $\delta^{15}N_{base}$ of 14.12 ± 0.40 ‰.

Biomass specific growth rates for bluefish ranged 0.058–0.087 d^{-1}; whereas G

ranged 0.044–0.033 d^{-1} for bay anchovy. Equilibration models for bluefish and bay

anchovy indicate that a 4–6-fold increase in biomass requires t_{equil} = 16–31 d for

bluefish after switching to a novel forage base at 30–80 mm; whereas t_{equil} = 31–54 d

for 15–30 mm bay anchovy (Fig 4). The models were relatively insensitive to

changes in absolute growth rate ($\Delta\bar{g}$). This was examined by recalculating t_{equil} for $\bar{g}$

= 1.71 and 2.31 mm d^{-1} for bluefish (i.e., $\Delta\bar{g}$ = ± 0.30 mm d^{-1}) and for $\bar{g}$ = 0.35 and

0.45 mm d^{-1} for bay anchovy (i.e., $\Delta\bar{g}$ = ± 0.05 mm d^{-1}). Bluefish t_{equil} increased by

2.9–5.7 d (-$\Delta\bar{g}$) and decreased by 2.0–3.9 d (+$\Delta\bar{g}$). Bay anchovy showed changes of

similar magnitude: t_{equil} increased by 4.0–7.0 d (-$\Delta\bar{g}$) and decreased by 3.8–6.6 d

(+$\Delta\bar{g}$).

3.3 Condition factors

There was no difference in CI of bluefish between habitats ($t = 1.65$, $df = 58$, $p = 0.11$) although the mean residual value of ICS bluefish (0.01 ± 0.09 SD) was higher than that of estuary bluefish (-0.03 ± 0.09, Fig 5). Two observations, one from each habitat, were statistical outliers (studentized residuals = -4.21, 4.37). The ICS outlier was the shortest specimen analyzed from either habitat (TL = 112 mm) whereas the estuarine outlier was the longest (TL = 249 mm). After removing the statistical outliers (studentized residuals = -4.21, 4.37), the difference between ICS (mean residual = 0.02 ± 0.07) and estuary (-0.04 ± 0.06) bluefish CI was significant ($t = 3.61$, $df = 56$, $p = 0.001$).

Lipid content was also significantly higher ($t = 5.37$, $df = 27$, $p < 0.001$) in ICS ($2.53\% \pm 0.20$ SD) versus estuary bluefish ($2.18\% \pm 0.16$; Fig 5). For bay anchovy, CI was significantly higher ($t = 2.84$, $df = 53.01$, $p = 0.006$) in fish from the ICS (mean residual = 0.05 ± 0.09) than the estuary (-0.05 ± 0.17). Similarly, percent lipid was significantly higher ($t = 6.52$, $df = 29$, $p < 0.001$) among bay anchovy from the ICS ($3.57\% \pm 0.23$) versus those from the estuary ($2.90\% \pm 0.33$).

As a supporting analysis, ANCOVA (Factor: habitat, dependent variable: $\log_e$[body mass], covariate: $\log_e$[total length]) was used to test for differences in slope of the body mass-to-total length relationship between habitats as well as differences in average $\log_e$(body mass) by habitat following adjustment for the covariate. Results

Fig 4 Isotopic equilibration schedule models for juvenile bluefish (left panel) and bay anchovy (right panel) based on average individual growth rates in coastal Mid-Atlantic Bight habitats. Time interval (days) corresponding to a 4–6-fold increase in $Wt_t/Wt_{initial}$ (ratio of body weight at time t to initial body weight) for four hypothetical sizes at the switch to a novel forage base (TL_{switch}) is shown by surface trajectories (solid lines) and ancillary axis intercepts (dashed lines).
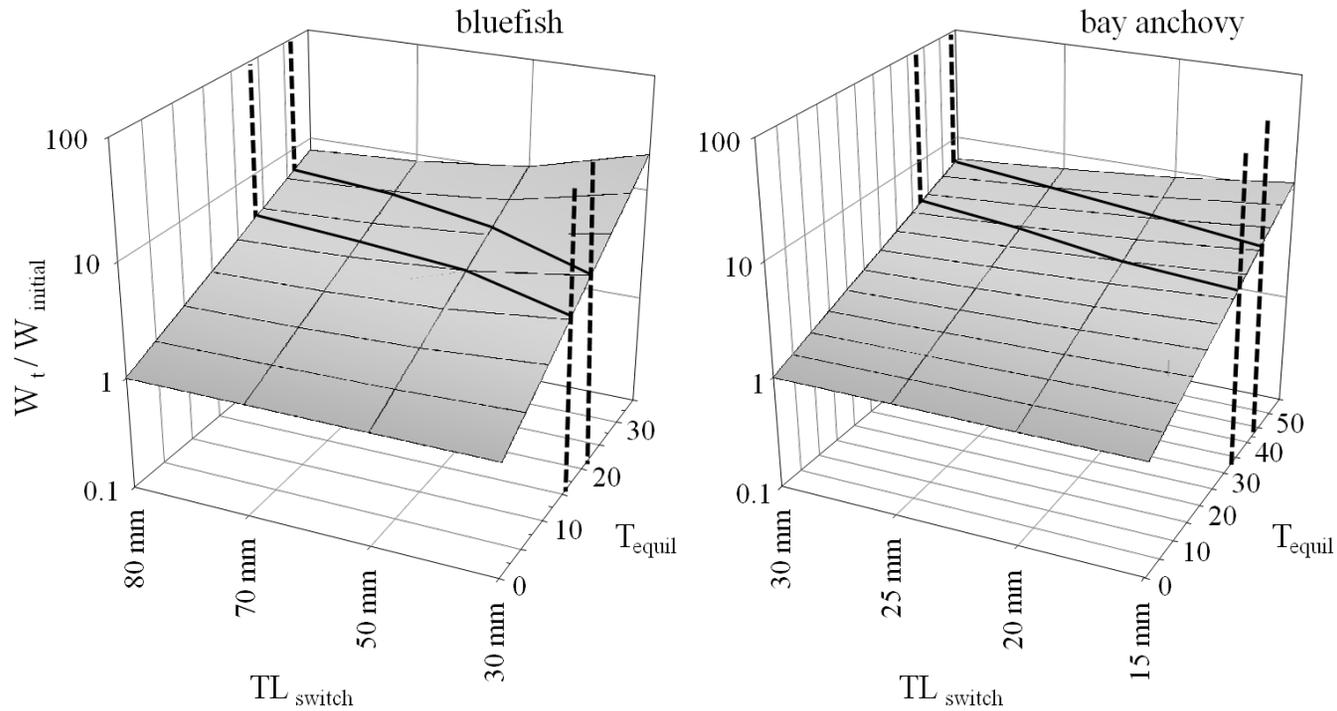
Fig 5 Residuals from linear regression of $\log_e$(body mass) on $\log_e$(length) for bluefish (upper left panel) and bay anchovy (lower left panel) plotted against body length (TL) from Maryland's inner continental shelf (ICS – open circles) and lower mainstem Chesapeake Bay (estuary – filled squares). Normal distributions fitted to ICS (solid lines) and estuary (dashed lines) data are given along the secondary axes and 2 statistical outliers in the upper panel are indicated by arrows. Box plots show distributions of percent lipid content of white muscle tissue from each habitat (ICS – open box, estuary – filled box) for bluefish (upper right panel) and bay anchovy (lower right panel). Box plots show median (line), 50% range of values (box), and 1.5*the interquartile range (whiskers).
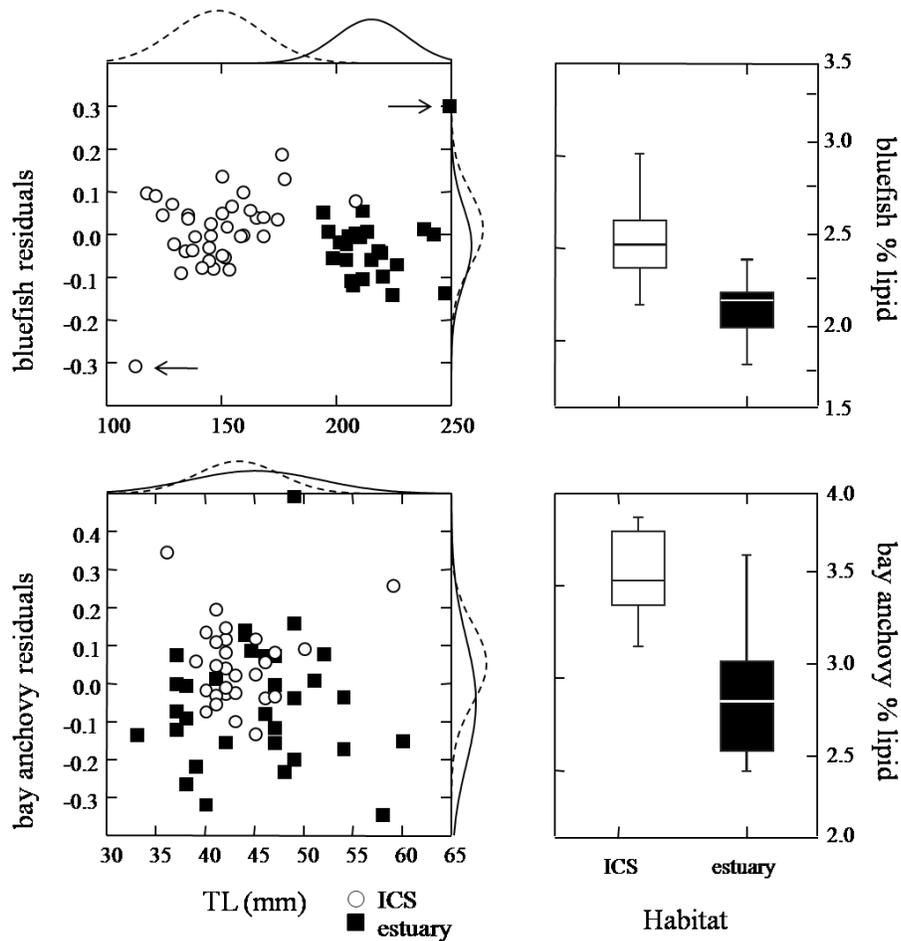
from the ANCOVA indicated that the slopes relating $\log_e$(body mass) to $\log_e$(total length) were parallel for bluefish ($F = 0.55$, $df = 1$, $p = 0.46$) and nearly parallel for bay anchovy ($F = 0.05$, $df = 1$, $p = 0.05$). After adjusting for body length, $\log_e$(body mass) was higher in ICS bluefish ($F = 5.15$, $df = 1$, $p = 0.027$) but not bay anchovy ($F = 1.16$, $df = 1$, $p = 0.29$). The ANCOVA results recapitulate the residual analysis for bluefish (ICS condition > estuary condition) but conflict for bay anchovy (ICS condition = estuary condition). Given the statistical significance of the homogeneity of slopes test for bay anchovy ($p = 0.05$, see above), I selected the residual analysis as the most appropriate analysis of morphometric condition and provided interpretation of that analysis alone in the Discussion.

3.4 Trophic niche characteristics

Observed (i.e., not standardized to reference bivalves) $\delta^{13}C$ and $\delta^{15}N$ values of each fish species varied by habitat but generally showed similar levels of variance. Carbon isotopic signatures for bluefish ranged from -19.18 to -17.72‰ in the ICS and -20.61 to -18.01‰ in the estuary (Table 3; Fig 6). Bluefish nitrogen signatures ranged from 13.88 – 16.21‰ (ICS) and 16.21 – 18.73‰ (estuary). Bay anchovy isotopic signatures ranged from -20.43 to -17.23‰ (ICS) and -24.43 to -18.66‰ (estuary) for carbon, and 14.13 to 15.14‰ (ICS) and 15.51 to 17.11‰ (estuary) for nitrogen. Delta-^{13}C variance was similar ($F_{13, 14} = 0.42$, $p = 0.13$) between habitats for bluefish ($s_{ICS}^2 = 0.25$, $s_{estuary}^2 = 0.59$) but it was less variable ($F_{14, 15} = 2.33$, $p = 0.009$) for ICS bay anchovy ($s_{ICS}^{22} = 0.62$) than estuary bay anchovy ($s_{estuary}^2 = 2.67$). Isotopic

variance was similar for $\delta^{15}N$ ($F \geq 0.54$, $p \geq 0.26$) between habitats for bluefish (s_{ICS}^2 = 0.59, $s_{estuary}^2$ = 0.54) and bay anchovy (s_{ICS}^2 = 0.12, $s_{estuary}^2$ = 0.23).

Prior to dispersion (i.e., NND, NNDSD) and total niche area (TA) calculations, one outlier from the estuary bay anchovy dataset ($\delta^{13}C$ = -24.43‰, $\delta^{15}N$ = 17.11‰, studentized residual = -4.2) was removed. This individual (TL = 45 mm) was significantly shorter than the specimen mean of 49 mm for estuary bay anchovy (1-sample t = 3.57, df = 15, p = 0.003), but showed no other anomalous characteristics. Bluefish NNDSD was significantly lower in the ICS than the estuary (bootstrap estimate of difference of means, p = 0.011; Table 3). Although not statistically significant ($p \geq 0.35$), all other dispersion metrics for bluefish and bay anchovy (Table 3) were lower in ICS niche space than the estuary. Dispersion was ~ 40 and 22% (NND), or 55 and 14% (NNDSD) lower for bluefish and bay anchovy respectively in the ICS than the estuary (Fig 7), consistent with greater individual packing (i.e., reduced individual variability) in ICS niche space. Bootstrapped differences in mean TA between habitats were not significant for either species ($p \geq$ 0.19); yet the observed ICS TA was 43% lower than estuary TA for bluefish and 65% lower for bay anchovy. Lower TA in the ICS habitat suggests a narrower, less isotopically diverse forage base among individuals.

Stomach contents of bluefish in the ICS (n = 27; TP_{SC} = 4.20 ± 0.09 SD) were primarily composed of fish and cephalopod remains that included anchovy (*Anchoa* spp. = 59% of total stomach contents biomass), squid (*Loligo* spp. = 13%), and

Atlantic butterfish (*Peprilus triacanthus* = 13%) (Fig 8). Conversely, the diet of estuarine bluefish (n = 26; TP_{SC} = 4.15 ± 0.06) was dominated by anchovy (88%) and clupeids (unidentified Clupeidae = 9%), with mantis shrimp (*Squilla empusa* = 2%) representing the only invertebrate consumed. Despite a statistical difference in TP_{SC} of bluefish between habitats (t = 2.26, df = 44.98, p = 0.03), the magnitude of the difference (ΔTP_{SC} = 0.05) suggests it is unlikely to be ecologically significant. Stable isotope-based estimates of bluefish TP_{SI} (ICS = 3.86 ± 0.23 SD, estuary = 3.84 ± 0.22) did not differ between habitats (t = 0.30, df = 27, p = 0.77) and were less than TP_{SC} in both habitats ($t \geq 5.34$, $df \sim 15.3$, $p < 0.001$).

Bay anchovy diets were more evenly distributed than bluefish diets with 4 prey categories – Copepoda, mixed zooplankton (e.g., fish eggs, bivalve larvae, ostracods), Mysidacea, and larval (i.e., zoea/mysis stage) crustaceans contributing 86% of total stomach contents biomass of the ICS sample (n = 31; prey categories = 31%, 29%, 13% and 13% respectively) and 94% of the estuary sample (n = 45; prey categories = 17%, 11%, 9% and 57%) specimens (Fig 8). Bay anchovy TP_{SC} was 3.51 ± 0.17 in the ICS and 3.44 ± 0.40 in the estuary although this difference was not significant (t = 0.20, df = 66, p = 0.83). Bay anchovy TP_{SI} showed the same pattern but was significantly higher (t = 8.70, df = 29, $p < 0.001$) in the ICS (3.75 ± 0.10) than the estuary (3.37 ± 0.14). A comparison of estimation methods showed that TP_{SI} was higher than TP_{SC} in the ICS (t = -5.99, df = 41.3, $p < 0.001$) and lower than TP_{SC} in the estuary (t = 3.71, df = 17.2, p = 0.002).

Table 3 Stable isotope (δ^{13}C, δ^{15}N) and diet-based trophic niche metric values ($\pm$SD) for age-0 bluefish and bay anchovy from Maryland's inner continental shelf (ICS) and lower mainstem Chesapeake Bay (estuary) from August 2008. Metric abbreviations: TP = trophic position (SI – stable isotope, SC – stomach contents), NND = nearest neighbor distance, NNDSD = stnd. dev. of NND, TA = convex hull area.

Species	Niche metric	Habitat	
		ICS	estuary
bluefish	δ^{13}C	-18.57 ± 0.50	-19.21 ± 0.77
	δ^{15}N	15.03 ± 0.77	17.76 ± 0.73
	TP_{SI} / TP_{SC}	3.86 / 4.20	3.84 / 4.15
	NND	0.39	0.65
	NNDSD	0.28	0.63
	TA	1.51	4.35
bay anchovy	δ^{13}C	-18.49 ± 0.79	-20.22 ± 1.63
	δ^{15}N	14.66 ± 0.35	16.17 ± 0.48
	TP_{SI} / TP_{SC}	3.75 / 3.51	3.37 / 3.44
	NND	0.37	0.47
	NNDSD	0.40	0.47
	TA	1.52	2.68

Fig 6 Age-0 bluefish (upper panel) and bay anchovy (lower panel) from Maryland's inner continental shelf (ICS – open circles) and lower mainstem Chesapeake Bay (estuary – filled squares) in $\delta^{13}C$ and $\delta^{15}N$ niche space. Minimum convex hull in isotopic niche space (ICS: dashed line, estuary: solid line) shown for each species-habitat combination.
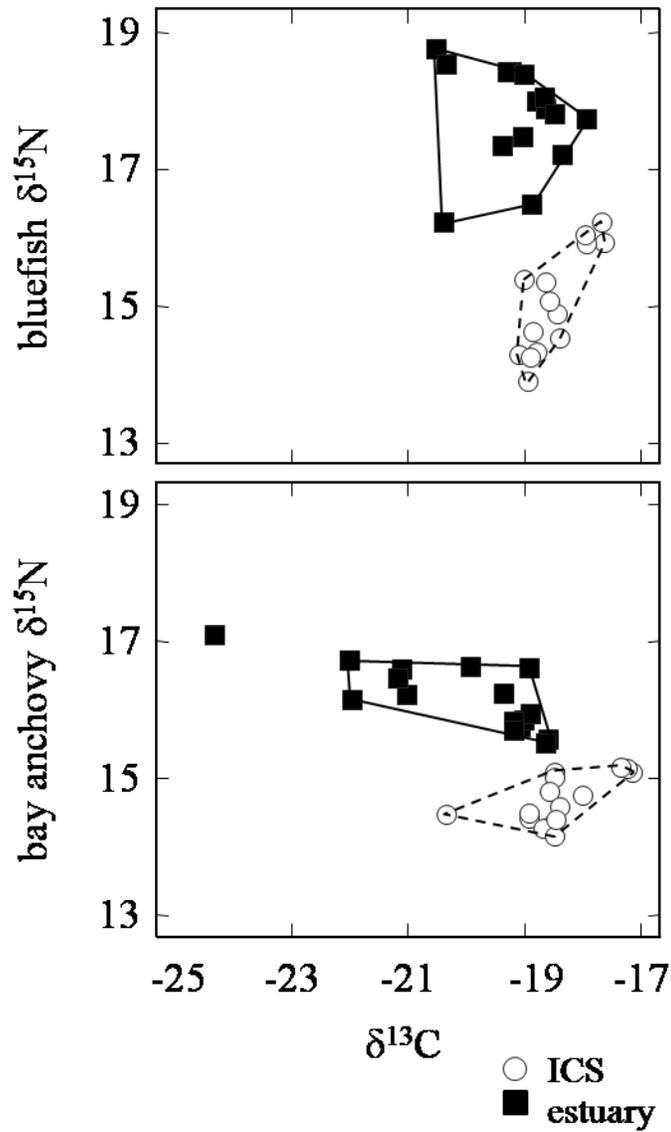
Fig 7 Bootstrap histogram (n = 1000) of nearest neighbor distance (NND), standard deviation of nearest neighbor distance (NNDSD) (primary y-axis) and total area (TA) (secondary y-axis) of age-0 bluefish (upper panel) and bay anchovy (lower panel) from Maryland's inner continental shelf (ICS – open bars) and lower mainstem Chesapeake Bay (estuary – filled bars) in δ^{13}C and δ^{15}N niche space.

Fig 8 Stomach contents data (n per habitat given above bars) for age-0 bluefish (upper panel) and bay anchovy (lower panel) from Maryland's inner continental shelf (ICS) and lower mainstem Chesapeake Bay (estuary).
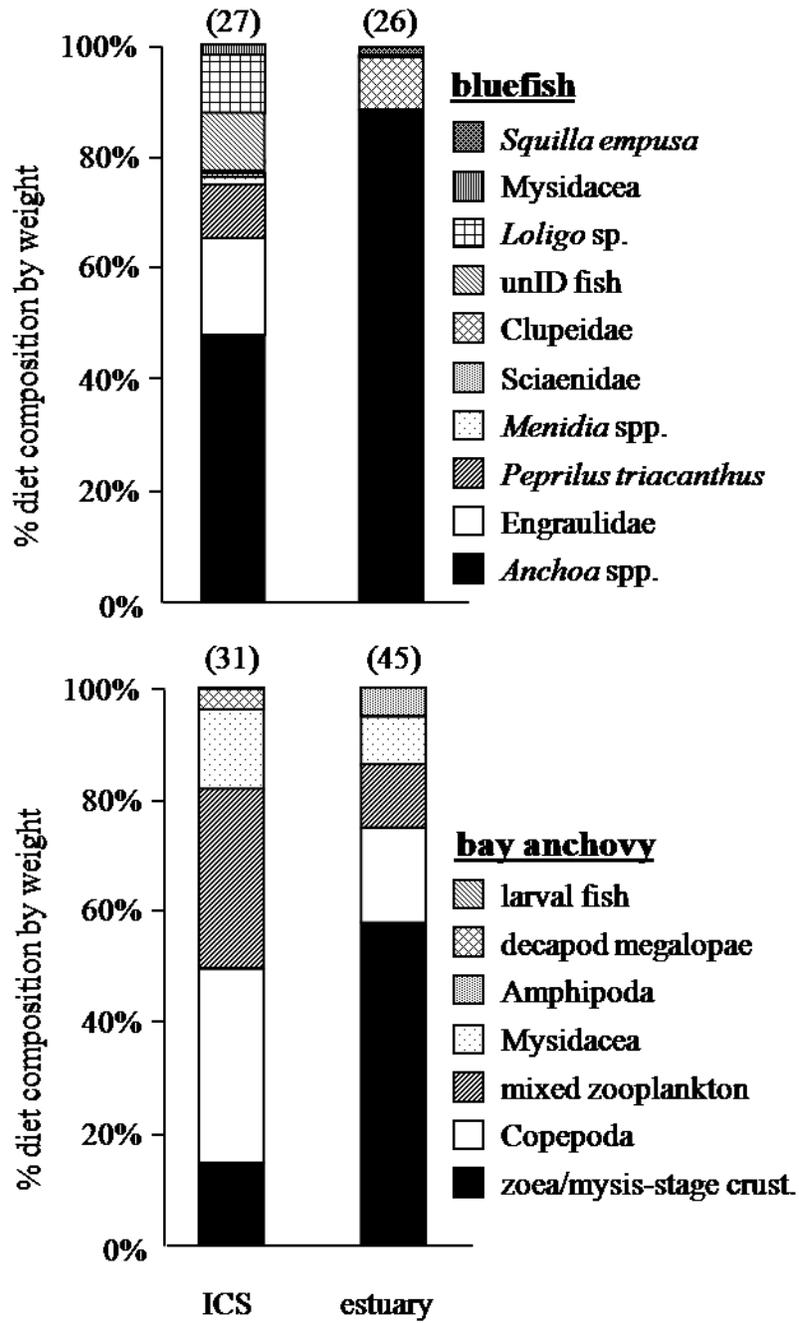
4. Discussion

Despite underlying environmental similarities that allow many marine finfish species to facultatively recruit (sensu Able 2005) to either inner continental shelf or estuarine nurseries, significant differences in trophic ecology can arise between cohorts depending on the recruitment habitat. The simultaneous use of stable isotope, stomach contents, and allometric L-W data supported spatial differences in foraging ecology between two principal nursery habitat types over temporal scales relevant to juvenile residency periods and related physiological consequences of local foraging conditions.

4.1 Inner continental shelf vs. estuarine foraging conditions

Lower species packing and higher total area in estuarine isotopic niche space supports the hypothesis that individuals in estuaries encounter more variable foraging conditions and realize higher overall niche breadth (Layman et al. 2007) than those recruiting to ICS habitats. Consumers recapitulate food web geochemistry at multiple spatial scales (Hobson 1999), a process influenced by the dispersiveness of basal nutrient source(s) (e.g., rooted seagrass vs. pelagic phytoplankton), reticulation of trophic channels (i.e., integration of prey foraging habits) and mobility of the consumer. Individual modalities in spatial foraging behavior in an isotopically heterogeneous environment would therefore be expected to correlate with a larger population-level isotopic niche. There is some evidence that age-0 bluefish display resident spatial foraging behavior in estuaries. For example, although juvenile bluefish < 270 mm FL are capable of movements ≥ 10 km d^{-1} (Morton et al. 1993;

Young et al. 1999), evidence from tagging studies in US and Australian estuaries suggests individuals may remain resident in localized habitats for periods of weeks to months (Morton et al. 1993; Able et al. 2003). In contrast, juvenile bluefish tagged in exposed coastal ocean habitats displayed higher mobility and reduced site fidelity (Morton et al. 1993; Able et al. 2003). Individual movement data for bay anchovy are limited, but environmental reconstructions inferred from otolith microchemistry (Kimura et al. 2000) indicate age-0 bay anchovy 35–45 mm (SL) captured in polyhaline Chesapeake Bay habitats were spawned in that same salinity regime. Converesely, dispersive juveniles originating in poly-, meso-, or oligohaline salinities showed up-estuary movements only. Habitat-specific differences in habitat use (e.g., local residence behavior) by both species, coupled with the greater underlying biogeochemical heterogeneity of estuaries (e.g., $\delta^{13}C$ – see Table 1 vs. Table 2 in Raymond and Bauer 2001), could explain the larger isotopic niche occupied by estuarine cohorts.

As a corollary, spatial structuring of prey assemblages in response to biotic or abiotic factors will determine the composition and isotopic characteristics of the local forage base. Bluefish and bay anchovy are opportunistic predators capable of diet switching among or between prey types (e.g., teleost versus crustacean prey) and stomach contents of both species generally reflect local prey availability (Din and Gunter 1986; Buckel and Conover 1997; Harding and Mann 2001). Spatial heterogeneity in prey availability is therefore another mechanism by which the estuarine habitat mosaic could support wider niche widths for consumers than the

more homogeneous ICS habitats. Still, it should be noted that bluefish and bay anchovy do not forage indiscriminately – juvenile bluefish are predominantly piscivorous and size-selective (Juanes and Conover 1995; Buckel et al. 1999a; Buckel et al. 1999b) and bay anchovy are selective particle feeders (Din and Gunter 1986; Morton 1989). In contrast to purely opportunistic feeding behaviors, prey-selective foraging strategies could reduce the isotopic variability of assimilated nutrients if similarly sized yet spatially segregated and taxonomically distinct prey species are functioning as ecological equivalents (e.g., same basal carbon sources, similar TP). Finally, it is possible that bluefish and bay anchovy in the ICS experience different isotopic assimilation and equilibration dynamics than estuarine fish due to endogenous feedbacks between environmental conditions, prey type, metabolism, growth and physiological condition (e.g., McCutchan et al. 2003).

4.2 Trophic position

Juvenile bay anchovy occupied a slightly higher vertical trophic niche in ICS habitats relative to estuarine conspecifics, whereas there was no evidence of spatial differences in TP of juvenile bluefish. Due to inefficiencies in trophic transfers, even small differences in TP can have a substantial effect on the amount of primary production needed to support fish production on an annual basis. For example, Jung and Houde (2004) estimated standing biomass of bay anchovy > 30 mm TL (age-0 and age-1+) was ~ 23.5 x 10^3 MT in Chesapeake Bay from June-August of 1995-2000. Assuming a trophic transfer efficiency of 10% per trophic level (Pauly and Christensen 1995) and applying my estimates of TP_{SI} for bay anchovy (Table 3), the

photosynthetic biomass pool required to produce the mid-summer population of bay anchovy > 30 mm TL in Chesapeake Bay would equate to either 88.1×10^4 MT (ICS TP_{SI} estimate) or 79.2×10^4 MT (estuary TP_{SI} estimate). Under this scenario, a positive $\Delta TP_{SI} = 0.38$ translates to an 8.93×10^4 MT increase in primary production demand or conversely, the loss of 2.65×10^3 MT of potential bay anchovy production. Repeating these calculations using TP_{SC} values for bay anchovy ($\Delta TP_{SC} = 0.07$) yield similar results (basal primary production demand increase = 1.65×10^4 MT, bay anchovy production lost = 4.78×10^2 MT). Assuming a conservative primary production rate of 1.0 g C m^{-2} d^{-1} (Flemer 1970) and an area of approximately 1.0×10^{10} m^2 in lower mainstem Chesapeake Bay (Woodland unpublished), local primary production approaches 1×10^4 MT C d^{-1} and an annual total of 3.7×10^6 MT C (or ~4.2×10^6 MT total photosynthetic biomass based on the Redfield ratio of C:N:P = 106:16:1). Using these numbers, a positive $\Delta TP_{SI} = 0.38$ for bay anchovy increases trophic demand by 2.1% of total annual production of pelagic photosynthetic biomass for lower Chesapeake Bay. While admittedly coarse, these simple calculations underscore the importance of relatively small changes in realized TP in constraining potential nursery production.

Unlike juvenile bay anchovy, which occupied different vertical trophic niches in ICS and estuarine nurseries, bluefish TP was functionally equivalent despite taxonomic differences in prey composition. Piscivorous species are typically associated with a higher vertical trophic niche than invertivores yet bluefish TP did not vary between ICS and estuarine habitats despite the increased importance of

invertebrates in the diet of ICS fish. This is likely due to the high TP of the specific

invertebrates consumed by juvenile ICS bluefish, particularly *Loligo* spp. – juvenile

coastal squid species are primarily zooplanktivores (Hendrickson and Holmes 2004;

Jacobson 2005) and occupy a similar TP as juvenile bay anchovy. This is supported

by ancillary stable isotope data collected during the ICS trawl survey in which the

$\delta^{15}N$ of juvenile squid (14.80 ± 0.38‰, 53–87 mm ML, n = 2; see Chapter 6 for full

dataset) is very similar to that of juvenile bay anchovy (Table 3). It is interesting to

note that despite juvenile bluefish consuming juvenile bay anchovy similar in size to

those analyzed for this study (bay anchovy in SC of bluefish from ICS = 35–76 mm

TL; estuary = 28–69 mm), TP_{SI} estimates of bluefish and bay anchovy were separated

by less than one full trophic "level" (i.e., $\delta^{15}N_{predator}$ - $\delta^{15}N_{prey}$ < 3.4 ‰) regardless of

habitat. This blurring of trophic separation between consumer and a primary prey

species underscores the failure of discrete trophic levels to accurately represent the

adaptive foraging behaviors exhibited by most fish (Wootton 1990; Gerking 2004).

Mechanistically, isotopic deviations from expected isotopic predator-prey trophic

separation could arise from a temporal lag in isotopic equilibrium arising from prey

switching by the consumer or prey, species-specific variability in trophic

fractionation of $\delta^{15}N$ (McCutchan et al. 2003), or the influence of unobserved or rare

prey on integrated isotopic signatures.

4.3 Condition

Increased lipid content and morphological condition of juvenile bluefish and bay

anchovy from the ICS suggests these fish may be better conditioned for overwinter

survival relative to those recruiting from the estuary. My use of the C:N ratio as a proxy for lipid content is predicated on the carbon-rich elemental composition of lipid relative to the nitrogenous protein structure of lean muscle mass (e.g., Kiljunen et al. 2006, Post et al. 2007) and this relationship is the basis for mathematical C:N normalization of lipid content prior to interpretation of $\delta^{13}C$ data. One potential drawback to using the C:N ratio obtained during SI analysis as an indicator of juvenile condition is that it reflects a bulk lipid estimate inclusive of all lipid classes present in the epaxial musculature (e.g., triacylglycerols, sterols). It also does not distinguish between C incorporated in lipids versus carbohydrates, although the latter are generally negligible in fish muscle tissues (Gnaiger and Bitterlich 1984).

The scope for inference is somewhat constrained for bluefish because I was unable to directly compare physiological condition of the same cohort between habitats. Recent work by Slater et al. (2007) and Morley et al. (2007) found spring and summer cohorts of bluefish displayed different energy allocation strategies; members of the spring-spawned cohort entered the overwintering period with higher lipid reserves than summer-spawned fish that presumably shunted more energy into somatic growth. I observed the opposite pattern – larger (spring cohort, estuary) fish possessed lower lipid stores per unit muscle mass than the smaller summer-spawned bluefish from the ICS. If bluefish or bay anchovy metabolism is elevated in the estuary due to chronic exposure to bioenergetically suboptimal environmental conditions (e.g., hyperthermia, hypoxia), the fraction of the total energy budget available for somatic growth is reduced. The subsequent reduction in energy

available for storage could be one potential explanation for the difference in percent

lipid between ICS and estuarine bluefish. Another possibility is that the taxon-

specific lipid content of prey varies between habitats, resulting in spatially-explicit

energetic profitability despite similar dietary composition. This is evident from bay

anchovy in this study – as a prey item, juvenile bay anchovy in the ICS would

provide increased lipid per unit biomass to juvenile bluefish than juvenile bay

anchovy in the estuary.

The use of stable isotopes as spatially-explicit indicators of consumer trophic

ecology is contingent on several assumptions. One of the most important

assumptions is that the appropriate isotopic baseline has been accurately measured for

a given habitat and consumer. Our ability to model equilibration rates with wild

oysters collected in situ at estuary location 1 provided a mechanism for avoiding bias

in the estimation of $\delta^{15}N_{base}$ due to the premature collection of planted oysters from

the cage-experiment. This approach relies on the assumption that the average growth

rate of oysters at estuary location 1 was equivalent to that of oysters at estuary

location 2. I do not believe this is an unreasonable assumption; oysters at both

locations were of similar size and exposed to comparable environmental regimes

during the summer equilibration period (Table 1). A corollary assumption is that the

baseline reference species is assimilating carbon from the same primary trophic

pathway (e.g., pelagic, benthic, autochthonous, allochthonous) as the consumer of

interest. In this case, diet analysis showed juvenile bluefish and bay anchovy relied

heavily upon the same pelagic food web that would have served as a primary carbon

source for the filter feeding bivalves. Finally, consumer equilibration models for bay anchovy and bluefish showed that a residency period of c. 15-50 d was sufficient for isotopic equilibration to local food webs. At the body size analyzed in this study, growth rates from the literature indicate individuals of both species were substantially older than the required equilibration schedules (Able and Fahay 1998) and were most likely resident in each habitat as either larvae (bay anchovy, Kimura et al. 2000) or early juveniles (bluefish, Callihan et al. 2008).

Overall, I found substantial evidence that juvenile marine finfish can realize significant differences in trophic niche when recruiting to coastal ocean versus estuarine nursery habitats. Spatial patterns in realized trophic niche at the seascape scale indicate these cohorts are either exposed to forage bases that differ significantly in composition, availability, and potentially quality; or the cohorts are experiencing environmental conditions (biotic or abiotic) that are sufficiently different so as to manifest alterations in foraging behavior or metabolism. By integrating information on consumed and(or) assimilated prey into a single index, trophic niche indices provide a potentially valuable class of explanatory variables for examining spatially explicit juvenile production patterns.

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Chapter 5: Trophic Resource Overlap between Small Elasmobranchs and Sympatric Teleosts in Mid-Atlantic Bight Nearshore Habitats

Abstract

Small, abundant elasmobranchs use shallow marine areas (< 20 m depth) of the U.S. Middle Atlantic coast as nurseries and adult foraging habitat, an area also used by a diverse assemblage of economically important juvenile and adult teleost species. Specimens of three small elasmobranch species (smooth dogfish *Mustelus canis*, clearnose skate *Raja eglanteria*, and bullnose ray *Myliobatis freminvillii*) were collected in August 2007 and 2008 from a study area of ~ 150 km^2, extending 22 km south from Ocean City, Maryland, USA (38° 19' N) and offshore from 5 to 20-m depth. Stomach contents indicated that fish were part of the diets of smooth dogfish and clearnose skate at a level comparable to sympatric piscivorous teleosts. However, stable isotope data suggest that piscivory is likely an opportunistic foraging behavior in this habitat. Studied elasmobranchs were secondary-tertiary consumers with diets composed primarily of decapod crustaceans, fish, and mollusks. There was significant overlap in diet composition, spatial distribution, and diel stomach fullness patterns between clearnose skate, southern kingfish *Menticirrhus americanus* (teleost) and, to a lesser extent, smooth dogfish. Despite this evidence for piscivory, their relatively low densities suggest that predation by these elasmobranchs is unlikely to

affect teleost populations in shallow coastal ocean habitats. If shared prey were to become scarce, then competitive interactions are possible.

1. Introduction

Several recent studies (Fogarty and Murawski 1998; Shepherd and Myers 2005; Myers et al. 2007) that suggest increasing abundance and biomass of small, mid-trophic level elasmobranchs (i.e., mesopredators, Soule et al. 1988; Myers et al. 2007) have precipitated interest in potential trophic interactions with sympatric fisheries species (Link et al. 2002b; Myers et al. 2007). Several explanations have been advanced to account for increased abundances of small elasmobranchs: (1) reduced predation pressure from large sharks (Shepherd and Myers 2005; Myers et al. 2007); (2) competitive release due to large-scale fishery removals of sympatric groundfish species (Fogarty and Murawski 1998); (3) metapopulation dynamics associated with oceanic regime shifts (Frisk et al. 2008); (4) bycatch reduction in coastal trawl fisheries (Brewer et al. 1998); and (5) density-dependent habitat selection (Swain and Benoit 2006). Regardless of the cause(s), this potential shift in community structure has raised concerns about the effects on local food web dynamics and the recovery and productivity of economically valuable species (Fogarty and Murawski 1998; Myers et al. 2007).

A diverse group of small elasmobranchs use inner continental shelf (ICS) waters of the U.S. Middle Atlantic coast as nurseries and adult foraging habitats (Castro 1993; Musick et al. 1993; Murdy et al. 1997; Packer et al. 2003). These

coastal areas also serve as transitional migration corridors and summer habitats for juvenile and adult stages of many commercially and ecologically important teleosts (Able and Fahay 1998). Many small elasmobranchs occupy an intermediate position in coastal food webs (Polis and Strong 1996; Shurin et al. 2006; Prugh et al. 2009), mediating flows of energy and biomass by foraging at multiple trophic levels (top-down), and serving as prey for larger shark species (bottom-up). These elasmobranchs thus occupy a potentially influential trophic niche within ICS communities; yet quantitative diet information is incomplete for this ecological group, particularly for non-shark species and subadult life-stages.

Two ways in which small elasmobranchs might negatively affect sympatric teleosts within a food web are: 1) piscivorous foraging behavior (i.e., direct predation – especially upon smaller juvenile stages) and 2) exploitative competition for the same prey (Link et al. 2002b). In contrast to knowledge gaps in the trophic ecology of small elasmobranchs, foraging habits of many teleosts are well documented and provide a framework for examining piscivory in the elasmobranchs. Exploitative competition between species is difficult to detect from field studies (Link et al. 2002b). Niche overlap or partitioning of food resources is more readily observed and information on the extent of niche overlap is relevant to future studies on competition.

The present study provides an evaluation of diet and spatial overlap between three small elasmobranchs and a group of co-occurring teleosts in a shallow (< 20 m) ICS habitat of the U.S. Middle Atlantic coast. We focus on the trophic status of three

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representative elasmobranchs common to the study area: smooth dogfish *Mustelus canis*, clearnose skate *Raja eglanteria*, and bullnose ray *Myliobatis freminvillii* (Fig. 1). Studies from proximal coastal (Rountree and Able 1996; Gelsleichter et al. 1999) and deeper continental shelf (> 20 m) areas (Bowman et al. 2000; Link et al. 2002b) indicate that smooth dogfish, clearnose skate, and bullnose ray are primarily invertivores although fish have been identified as possible prey for smooth dogfish and clearnose skate. Trophic data from these elasmobranchs were compared with seven sympatric teleost species with varying affinities for demersal habitat and foraging behaviors that are either typically piscivorous (weakfish *Cynoscion regalis*, bluefish *Pomatomus saltatrix*, Hartman and Brandt 1995; summer flounder *Paralichthys dentatus*, Packer et al. 1999) or invertebrate-based (southern kingfish *Menticirrhus americanus*, northern kingfish *Menticirrhus saxatilis*, Bowman et al. 2000; spotted hake *Urophycis regia*, Garrison and Link 2000; windowpane flounder *Scophthalmus aquosus*, Link et al. 2002a). Stomach contents, stable isotope, and catch data were used to pose two hypotheses about negative food web interactions among elasmobranchs and teleosts: 1) piscivory is less important in the diet of smooth dogfish and clearnose skate relative to that of known piscivorous teleosts (direct predation hypothesis), and 2) there is significant overlap in the diet and spatiotemporal catch patterns between elasmobranchs and sympatric demersal teleost invertivores (niche overlap hypothesis).

Fig 1 Monthly catch-per-unit-effort (CPUE = catch haul^{-1} ± SE) of small elasmobranchs (upper panel) from a 30-m footrope demersal trawl survey of Maryland's inner continental shelf from 2004-2008 and percent contribution to the catch (% catch, lower panel) by smooth dogfish (filled bars), clearnose skate (empty bars), and bullnose ray (shaded bars). Additional small elasmobranchs from trawl survey *Carcharhinus isodon*, *Squatina dumeril*, *Squalus acanthias*, *Rhizoprionodon terraenovae*, *Rhinoptera bonasus*, *Raja erinacea*, *Raja ocellata*, *Gymnura micrura*, *Gymnura altavela*, *Dasyatis americana*, *Dasyatis centroura*, *Dasyatis sabina*, and *Dasyatis say*.
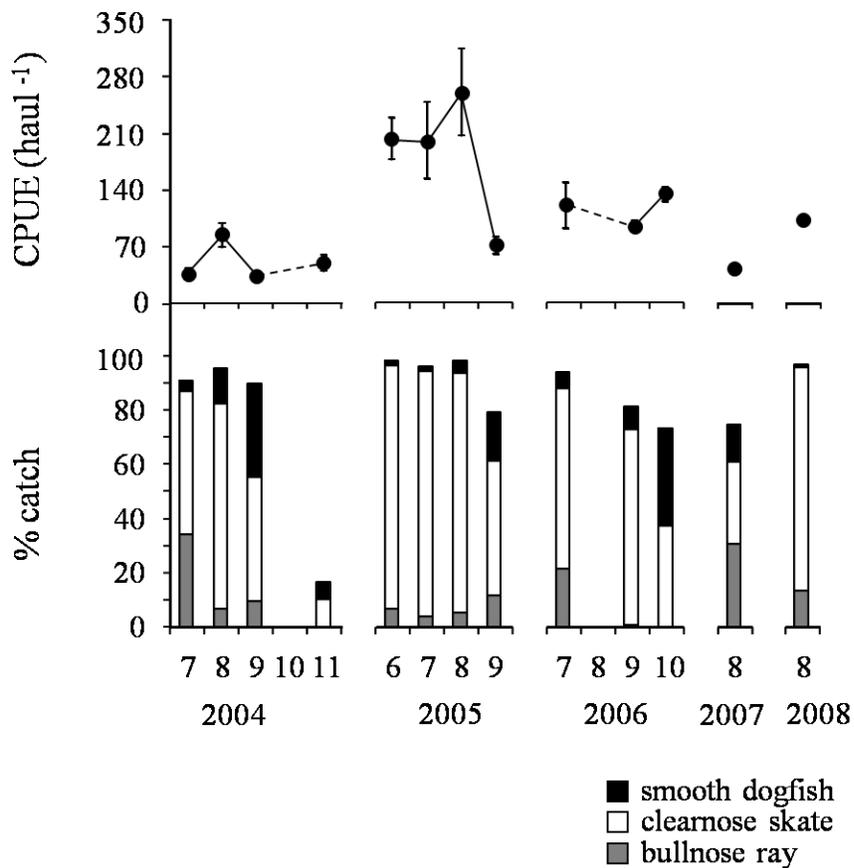
2. Methods

2.1 Field and laboratory methods

Trawling was conducted roughly bimonthly from June-November 2004-2006, and in August of 2007 and 2008 on the inner continental shelf (ICS, 5-20 m) along the southern edge of the northeastern U.S. continental shelf, extending southward from the Ocean City inlet, MD (38° 19′ N) approximately 22 km along the Assateague Island National Seashore (Fig. 2). The study area was divided into a grid of 52 potential sites and site selection was randomly stratified between shoal (5-10 m) and deep (10-20 m) strata to ensure equal sampling effort across the available depth gradient. In the study area, the 20-m isobath roughly parallels the coastline at an offshore distance of 7 km, yielding a potential sampling area of 150 km^2.

Specimen samples for trophic analysis were collected during August 2007 and 2008. The primary collecting gear was a demersal Yankee otter trawl with 30-m foot-rope and 6.4-mm cod-end mesh. Samples collected with this gear were also supplemented with a few specimens (bullnose ray [n = 1], bluefish [n = 2] , weakfish [n = 9]) taken in a smaller semi-balloon mid-water trawl (5.7-m foot-rope, 6.4-mm cod-end mesh) that was initially deployed to the bottom and raised every 4 min thereafter, resulting in oblique sampling of the water column. Both trawls were towed at 3 knots for 20 min along North-South transects that generally followed depth contours. Prior to deploying trawls, depth (m) and water column profiles of temperature (°C), salinity, and dissolved oxygen (DO = mg L^{-1}) were collected with a

Seabird CTD at each site. In addition to elasmobranch and teleost species, Atlantic moon snails *Neverita duplicata*, a predatory gastropod, and a mysid shrimp *Neomysis americana* were collected to provide in situ isotopic reference values for estimating finfish trophic positions (Post 2002). Moon snails were incidentally captured by the bottom trawl and mysids were collected with a Tucker trawl (1-m^2 opening, 280-μm cod-end mesh) that sampled the lower and upper water column in stepped 45-sec intervals (6-min total tow duration). During each cruise, gear deployments were temporally staggered over 2 to 3-d to sample the full diel period.

All fish and invertebrates were identified to the species level, sorted, and weighed to the nearest practical weight increment (i.e., 10 g for large and 1 g for small species). A sub-sample of 30 individuals per species was measured for total length (TL mm) or disc width (DW mm [linear distance between wingtips – skate and ray species only]) and weighed to allow gravimetric conversion of total weight to an estimate of total number caught per site. Specimens destined for stable isotope (SI) and stomach contents (SC) analysis were flash frozen on dry ice immediately following capture. The stomach and a fillet of dorsal white muscle tissue (Pinnegar and Polunin 1999) were removed from larger individuals in the field and flash frozen. All fish and invertebrates not retained for analysis were immediately released.

Samples frozen in the field were stored at -20°C until analyzed; at which point samples were partially thawed, stomachs excised from whole specimens, and a fillet of white muscle tissue removed. After thawing, stomachs and contents were fixed in

a 10% buffered formalin solution then preserved in ethanol. Prey items were identified to the lowest possible taxon, enumerated, blotted dry, and weighed to the nearest milligram. Very fresh fish prey (i.e., showing no apparent digestion) was discounted to avoid the possibility of net feeding introducing bias into our piscivory estimates.

A random sub-sample of 3-13 individuals per species and age-class was selected for SI analysis. These samples were rinsed in de-ionized water, held at 60°C for ≥ 48 hours until completely dried, then pulverized to a fine homogeneous powder using a mortar and pestle. Invertebrates were treated similarly. Tissue samples were removed from the muscular foot of individual moon snails for SI analysis. Conversely, five to ten whole mysids were aggregated, dried and pulverized, then split into two separate samples. One sample was acid-fumigated with 1N HCL for 24 h within a sealed desiccator, then redried and sent out for carbon isotope analysis (Bunn et al. 1995). The second sample, analyzed for nitrogen, was not acidified. Powdered samples were stored in a desiccator until sent for carbon and nitrogen analysis using continuous-flow isotope ratio mass spectrometry coupled with an elemental analyzer (EA-CFIRMS; Colorado Plateau Stable Isotope Laboratory, Northern Arizona University).

Stable isotope values are reported as a ratio in the "δ" notation following established convention in the ecological literature (Peterson and Fry 1987). All $\delta^{13}C$ values were normalized using the C/N ratio of the sample in conjunction with

Fig 2 Map of study area in Maryland's inner continental shelf showing August
bottom trawl sampling locations from 2004-2005 (n = 24), 2007 (n = 8) and 2008 (n =
8).
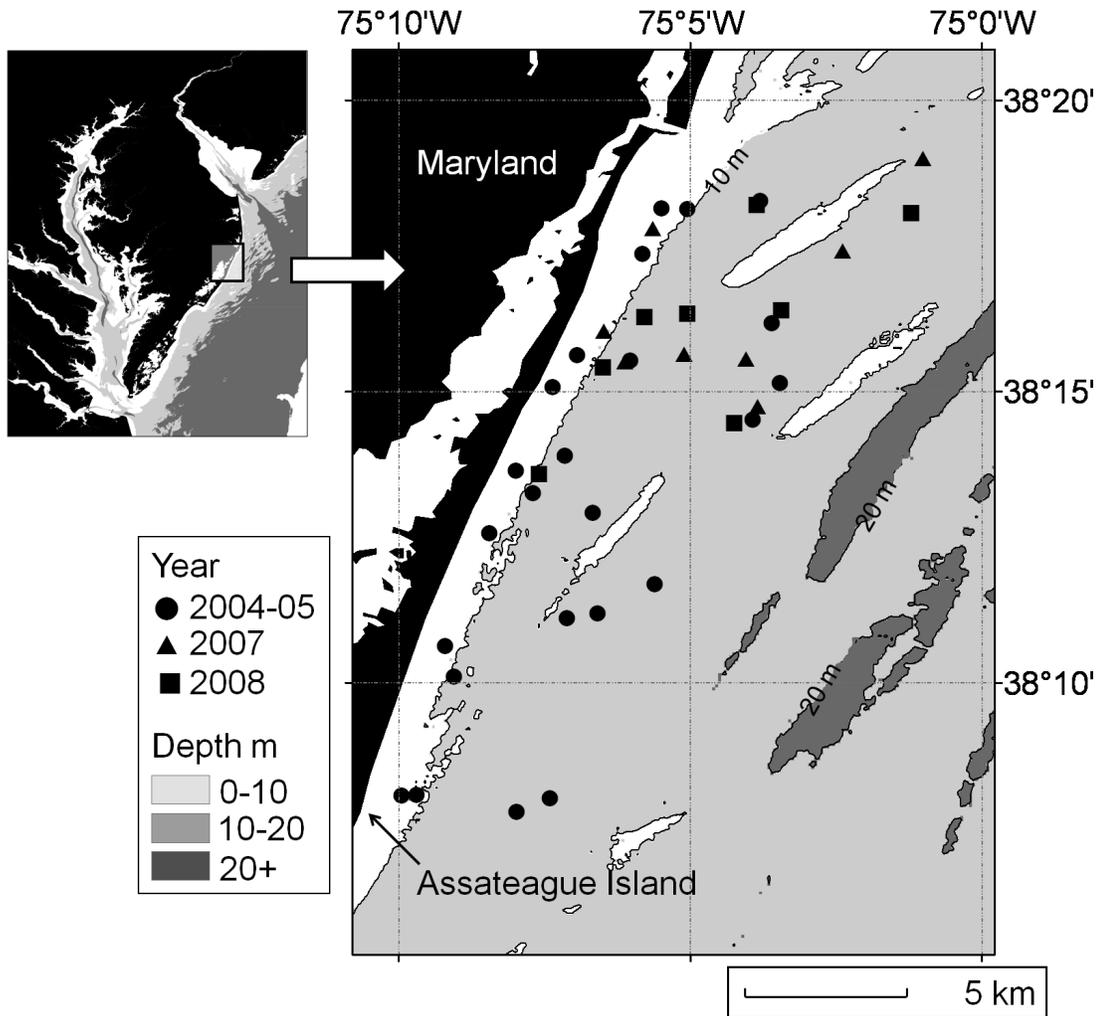
published correction curves (Post et al. 2007). Mathematical lipid normalization (as compared to chemical lipid extraction) was chosen to reduce sample preparation time and ensure sample integrity for both $\delta^{13}C$ and $\delta^{15}N$ analysis (Post et al. 2007).

   2.2 Data analysis

Age-0 smooth dogfish and two age-classes of clearnose skate (subadult – adult) and bullnose ray (age-0 – age-1+) were available from 2007 (SI and SC data) and 2008 (SI data) for analysis. Tests for annual differences in intraspecific mean and variance of $\delta^{13}C$ and $\delta^{15}N$ were not significant (t-tests, $p \geq 0.16$; F-tests: $p \geq 0.30$) for smooth dogfish, adult clearnose skate, and bullnose ray; therefore SI results from 2007 and 2008 were pooled for all subsequent analyses. Stable isotope data from 2007 and 2008 were not pooled for subadult clearnose skate due to significant interannual differences in mean $\delta^{15}N$ ($t = 4.36$, $df = 12$, $p < 0.001$) and $\delta^{13}C$ variance ($F_{6, 6} = 11.49$, $p = 0.009$). Preliminary rarefaction of prey categories by age-class (not shown) indicated sample sizes were not sufficient to describe the age-specific diets of clearnose skate and bullnose ray; therefore elasmobranch SC data were analyzed at the species level.

   Teleost trophic data for selected age-classes were available from 2007 (SI and SC) and 2008 (SC). Stable isotope and SC data were analyzed for age-1+ (all species) and select age-0 (summer flounder and bluefish) teleosts. Age-0 summer flounder and bluefish attain total lengths ≥ 250 mm by late summer (Able and Fahay 1998) and were considered big enough to eat the same prey as the elasmobranchs.

Rarefaction of spotted hake diet data suggested sample size was not sufficient to adequately describe the complete diet for this species; however, to provide a preliminary perspective, we decided to retain the species in the analysis.

Percent diet composition by weight (Hyslop 1980) was summarized into 17 unique prey categories per species or age-class using a 2-stage weighting approach to account for autocorrelation in diet among individuals captured from the same site (Buckel et al. 1999a, 1999b). Elasmobranch diet composition was visually inspected using a graphical method that simultaneously presents species-level and among-individual diet variability (Amundsen et al. 1996), allowing for interpretation of trophic niche within and between species. For each prey category, the % frequency of occurrence was plotted against prey-specific biomass. Prey-specific biomass of prey category i for consumer j (P_{ij}) was calculated as:

$$P_{ij} = 100 * \frac{\sum_{j=1}^{n} B_i}{\sum_{j=1}^{n} B_{ti}}$$

where B_i is the biomass of prey category i in the stomach of an individual of consumer j, and B_{ti} is the total biomass of all prey categories combined in the stomachs of consumer j that also contained prey category i (Chipps and Garvey 2007).

2.3 Direct predation hypothesis

To examine the importance of fish prey in the diets of smooth dogfish and clearnose skate, the incidence of piscivory was compared between these elasmobranch species and the teleosts: weakfish, summer flounder (age-0, age-1+), and bluefish (age-0, age-1+). Contingency table analysis was used to test for group-level differences in the incidence of piscivory between elasmobranchs versus teleosts (all stomachs – empty or prey present). Pair-wise contrasts with 1-sided Fisher's exact test (H_a: teleost incidence > elasmobranch incidence) were used to test for significance of inter-species differences. Odds ratios (Quinn and Keough 2003) were calculated to estimate the differential probability of observing fish prey in the teleosts relative to the elasmobranchs. The proportion by weight of fish prey to elasmobranch and teleost diets (using non-empty stomachs only) was compared with Kruskal-Wallis rank-sum tests and differences quantified with the Hodges-Lehman estimator of location shift (Hodges and Lehmann 1963).

2.4 Niche overlap hypothesis

Potential niche overlap between elasmobranchs and teleosts was evaluated using multivariate and univariate approaches. First, a Bray-Curtis similarity matrix (Clarke 1993) was constructed among species using the square-root transformed percent diet composition data. We used group-average agglomerative cluster analysis to examine similarities among elasmobranchs and teleosts and identify general food web groupings. Significance in the underlying cluster structure was tested by means of a permutation test of the observed similarity profiles (SIMPROF procedure, $\alpha = 0.05$)

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between species pairs (Potter et al. 2001). Species clusters identified as significant by the permutation test were further analyzed to determine the identity and relative contribution of specific prey categories to the within-cluster similarity (SIMPER procedure, Clarke 1993). Prey categories that contributed $\geq 90\%$ of the cumulative within cluster Bray-Curtis similarity were considered sufficiently descriptive of prey types for that species cluster. All multivariate analyses were conducted using the *PRIMER* v.6 software package.

Patterns in spatial overlap were assessed by calculating Spearman rank correlation coefficients (r_S) between elasmobranch and teleost species pairs. All four years of August trawl data (30-m bottom trawl: 2004, 2005, 2007, 2008) were used to analyze site-specific catches by species or age-class as a means of incorporating potentially broader patterns of interannual variability in our spatial overlap estimates. To maintain comparability with the stomach contents analysis, clearnose skate and bullnose ray catch data were not age-delineated. We used principal components analysis (PCA; Kwak and Peterson 2007) to summarize the four normalized environmental variables recorded at each trawl site (temperature, salinity, DO, and depth). Spearman rank correlations were calculated between PC-scores and species catches to compare patterns of environmental associations among species. Spatial and environmental correlations between species were planned tests; therefore, *p*-values were not corrected for multiple comparisons (Moran 2003).

Species pairs that demonstrated trophic and spatial overlap were evaluated for common diel patterns in relative stomach fullness (= [total biomass of stomach contents] / [total body wt − total biomass of stomach contents]) and CPUE. Sampling days were separated into four 6-h periods (e.g., 0000-0559 hrs, 0600-1159 hrs), and then the stomach fullness index and CPUE was calculated for each 6-h period. Temporal patterns were visually and statistically (1-way ANOVA) analyzed for each species.

Trophic position was estimated from stomach contents (TP$_{SC}$) at the species level using percent diet composition by prey weight after correction for subsample autocorrelation. An average TP was assigned to each prey category based on estimates of TP for each prey item (or closely related taxon) from the literature (Akin and Winemiller 2006; Ebert and Bizzarro 2007). The TP of consumer j was then estimated as

$$TP_{SC,j} = 1.0 + \sum_{i=1}^{n} TP_i\left(p_{ij}\right)$$

where p$_{ij}$ is the fraction of prey category i in the diet of consumer j (Winemiller et al. 2007).

Estimates of elasmobranch and teleost TP were derived from SI data (TP$_{SI,j}$) (Winemiller et al. 2007) as

$$TP_{SI,j} = \left[\frac{\left(\delta^{15}N_j - \delta^{15}N_{base}\right)}{\Delta_N}\right] + \lambda$$

where $\delta^{15}N_j$ is the nitrogen isotope signature of consumer j, $\delta^{15}N_{base}$ is the mean $\delta^{15}N$ value of the baseline food web reference(s), Δ_N is the mean trophic fractionation (enrichment) of N between trophic levels, and λ is the trophic position of the organism(s) used to estimate $\delta^{15}N_{base}$ (Post 2002). Delta^{15}N values for moon snails ($\lambda = 3$, Gosner 1999) and mysids ($\lambda = 2.75$, Winkler et al. 2007) were used as $\delta^{15}N_{base}$ values to calculate independent estimates of $TP_{SI,j}$ that were then averaged to provide a final estimate of TP_{SI} for each individual.

Stable isotope-based TP estimates were compared to those derived from stomach contents (one sample t-test) at the species level to test for differences between the two metrics. The significance of group (elasmobranch versus teleost) effects on TP_{SC} and TP_{SI} was tested using two-sample t-tests. One-way ANOVA with Tukey-adjusted least-squares means comparisons was used to test for pair-wise differences in TP_{SI} between species and a second 1-way ANOVA (with Tukey-adjusted means comparisons) was used to test for an age-effect among species with multiple age-classes. Tests of residual non-normality and heteroskedasticity were not significant for all parametric analyses and *a priori* significance for all statistical tests was set at $\alpha = 0.05$.

3. Results

3.1 Elasmobranch diets

Results from the stomach contents analysis are provided in detail for the three elasmobranch species (Table 1) and summarized for all species (Table 2). Overall,

diet composition of smooth dogfish and clearnose skate was consistent with a generalist mid-trophic level foraging strategy, characterized by high between- and within-individual diversity in stomach contents (Fig. 3). Conversely, bullnose ray appeared to specialize on molluscan prey and displayed limited consumption of other prey types.

Stomach contents of smooth dogfish and bullnose ray consisted primarily of invertebrate prey (92-94% of total biomass); whereas fish prey constituted nearly half the identifiable biomass in clearnose skate stomachs (46%; Table 2). Smooth dogfish diet was dominated by epifaunal invertebrates, particularly brachyuran and anomuran crab species. Errant polychaetes and bivalves occurred frequently in the stomachs of smooth dogfish but contributed relatively little to the overall prey biomass. Demersal fish species (e.g., weakfish, striped cusk eel *Ophidion marginatum*, scup *Stenotomus chrysops*) were infrequent in the diet of smooth dogfish (12% frequency of occurrence [FO]), clearnose skate (10% FO), and bullnose ray (3% FO); yet when present, this prey category contributed the bulk of the prey biomass (49%, 91%, and 28% of prey-specific biomass, respectively [Fig. 3]). Similarly, schooling fishes (*Anchoa* sp.) were uncommon in the stomachs of clearnose skate but had a relatively high prey-specific biomass. Several species of brachyuran occurred frequently in the stomachs of clearnose skate (75% FO), had a high prey-specific biomass (42%, Fig. 3), and contributed a substantial proportion to the overall prey biomass for the species (41%; Table 1). Other invertebrates (e.g., bivalves, anomurans) were frequently encountered in the stomachs of clearnose skate but were typified by low prey-specific

biomasses. Stomach contents of bullnose ray were composed almost exclusively of gastropods and bivalves by weight (Fig. 3). Together, these prey categories accounted for 93% of the total identified biomass for bullnose ray.

3.2 Piscivory

We did not observe a group-level difference in incidence of piscivory ($\chi^2 = 1.02$, $df = 1$, $p = 0.31$) between elasmobranchs (smooth dogfish and clearnose skate) and teleosts (weakfish, summer flounder, bluefish); however, fish prey did constitute a lower proportion of total diet biomass ($\chi^2 = 16.05$, $df = 1$, $p < 0.0001$) in the elasmobranch group relative to the teleost group. The odds of observing fish prey among teleosts were 1.4 (0.7-2.7 CI [95%]) times higher than elasmobranchs and fish prey contributed approximately 17% (<1-33% CI) more biomass to teleost diets. Species level differences in incidence were not significant ($\chi^2 < 2.29$, $p > 0.13$); odds ratios indicated the probability of piscivory was 1.6-2.0 times higher in weakfish and bluefish (both age-classes), and 1.0-1.3 times lower in summer flounder than smooth dogfish and clearnose skate. Fish prey represented a higher proportion of total diet in weakfish and age-0 bluefish than either smooth dogfish ($\chi^2 > 14.95$, $p < 0.0001$) or clearnose skate ($\chi^2 > 14.03$, $p \leq 0.0002$). Fish prey constituted 66% (40-90% CI) and 48% (10-90% CI) more biomass in weakfish and 89% (80-100% CI) and 77% (50-100% CI) more biomass in age-0 bluefish diets than smooth dogfish and clearnose skate, respectively.

Table 1 Detailed stomach contents by total weight (g) of three small elasmobranchs collected from Maryland's inner continental shelf

during August 2007-2008. All smooth dogfish = age-0, clearnose skate and bullnose ray = mixed age-classes.

Prey category	Family	Genus and species	smooth dogfish	clearnose skate	bullnose ray
Fish prey					
schooling	Engraulidae	*Anchoa mitchilli*	-	2.6	-
		Anchoa sp.	0.04	0.25	-
demersal	Sciaenidae	*Cynoscion regalis*	7.58	28.52	-
		Unidentified	0.08	-	-
	Ophidiidae	*Ophidion marginatum*	-	30.05	-
	Sparidae	*Stenotomus chrysops*	-	-	12.38
	Paralichthyidae	*Paralichthys* sp.	0.02	1.53	-
Invertebrate prey					
Mysidacea	Mysidae	*Neomysis americana*	<0.01	0.02	-
Amphipoda	Gammaridae	*Gammarus* sp.	0.02	0.08	-
Brachyura	Portunidae	*Ovalipes ocellatus*	-	9.96	-
	Cancridae	*Cancer irroratus*	13.58	13.03	0.52
	Majidae	*Libinia emarginata*	0.07	24.02	-
		Unidentified	46.37	8.82	0.07
Anomura	Paguridae	*Pagurus* sp.	13.09	6.2	0.12
Crangonidae	Crangonidae	*Crangon septemspinosa*	0.04	0.61	<0.01
Gastropoda	Naticidae	*Neverita duplicata*	0.52	-	97.01
		Unidentified	-	-	26.4
bivalves	Solenidae	*Ensis directus*	5.03	6.1	1.09
	Mytilidae	*Mytilus edulis*	0.02	-	-

		Unidentified	3.13	2.36	61.26
Polychaetea	Opheliidae	*Ophelia denticulata*	-	0.29	-
	Glyceridae	*Glycera americana*	0.49	-	0.12
	Nereidae	*Nereis diversicolor*	-	0.23	-
	Unidentified		2.01	0.19	-
Nemertea	Lineidae	*Cerebratulus lacteus*	-	-	0.53
Cephalopoda	Loliginidae	*Loligo pealei*	0.2	-	-
other shrimp	Penaeidae	*Penaeus* sp.	0.8	-	-
	Squillidae	*Squilla empusa*	3.73	2.67	-
	Upogebiidae	*Upogebia affinis*	0.11	-	-
		Upogebia sp.	0.14	-	-
other invertebrates	Isopoda (order)	Unidentified	0.14	<0.01	-
	Sesillia (order)	Unidentified	<0.01	-	-
amphioxus	Branchiostomatidae	*Branchiostoma* sp.	-	0.17	-
plant matter			0.54	-	0.35
unidentified biomass			18.05	6.56	10.79
inorganic material			0.04	-	-

Table 2 Prey categories (with trophic position TP) and percent diet composition by weight for elasmobranch and teleost species collected from Maryland's inner continental shelf during August 2007-2008. Abbreviations (based on Latin names) are as follows, Species: Mc – smooth dogfish, Re – clearnose skate, Mf – bullnose ray, Cr – weakfish, Pd – summer flounder, Ps – bluefish, Ma – southern kingfish, Ms – northern kingfish, Sa – windowpane flounder, Ur – spotted hake. Total sample size is given in parentheses following each species/age-class.

Prey category [a]	TP	Mc (22)	Re (39)	Mf (34)	Cr (35)	Pd age-0 (34)	Pd age-1+ (46)	Ps age-0 (98)	Ps age-1+ (16)	Ma (34)	Ms (25)	Sa (73)	Ur (12)
Fish prey													
schooling	3.2	<0.1	2.1	-	92.0	58.7	11.1	85.4	10.0	1.5	-	-	-
larval fish	3.0	-	-	-	<0.1	0.1	0.1	-	-	<0.1	-	0.3	0.2
demersal	3.6	7.9	43.6	6.2	-	19.5	29.2	2.8	79.9	0.4	-	-	-
Fish prey incidence		31.8	30.8	11.8	46.8	41.2	36.8	69.0	52.0	11.8	-	3.2	8.3
% total diet biomass		8.0	45.7	6.2	92.0	78.3	40.3	87.6	89.9	1.9	-	0.3	0.2
Invertebrate prey													
Mysidacea	2.8	-	<0.1	-	5.9	6.5	5.6	<0.1	-	<0.1	<0.1	96.1	0.2
Amphipoda	2.2	<0.1	0.1	-	0.1	-	<0.1	-	-	0.6	0.5	-	12.2
Brachyura	2.5	61.7	40.5	0.3	1.2	2.8	6.7	-	-	12.7	-	-	-
Anomura	3.0	13.5	4.5	0.1	-	-	-	-	-	12.4	0.3	-	13.1
Crangonidae	2.8	<0.1	0.4	-	-	0.1	<0.1	-	-	6.2	0.5	0.4	72.3
Gastropoda	2.7	0.4	-	61.9	0.1	-	-	-	-	3.2	-	-	-

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bivalves	2.0	8.4	6.1	31.3	<0.1	-	-	-	-	16.9	0.4	-	-
Polychaeta	2.5	2.6	0.5	0.1	-	-	-	-	-	19.8	14.3	-	2.1
Nemertea	3.0	-	-	0.3	0.7	-	-	-	-	-	-	-	-
Cephalopoda	3.2	0.2	-	-	-	8.7	46.4	11.8	10.1	-	-	-	-
other shrimp	2.8	4.9	1.9	-	-	3.6	1.0	-	-	22.3	<0.1	-	-
other invertebrates	2.5	0.1	-	-	-	-	-	-	-	1.9	-	-	-
amphioxus	2.3	-	0.1	-	-	-	-	-	-	2.1	83.9	-	-
zooplankton	2.5	-	-	-	-	-	-	<0.1	-	<0.1	-	3.1	<0.1
Invert. prey incidence		100.0	84.6	97.1	54.1	70.6	17.4	8.2	12.5	84.2	84.0	64.4	41.7
% total diet biomass		72.0	54.3	93.8	8.0	21.7	59.7	12.4	10.1	98.1	100.0	99.7	99.8

Fig 3 Prey-specific biomass plotted against percent frequency of occurrence for 12 primary prey categories identified within stomachs of smooth dogfish, clearnose skate, and bullnose ray from Maryland's inner continental shelf during August 2007-2008. Prey categories are coded as: Am – Amphipoda, An – Anomura, bi – bivalve, Br – Brachyura, Cr – Crangonidae, Ce – Cephalopoda, de – demersal fish, Ga – Gastropoda, Ne – Nermertea, Po – Polychaeta, os – other shrimp, Sc – schooling fish. Only prey categories with values > 2 % on both axes are plotted.
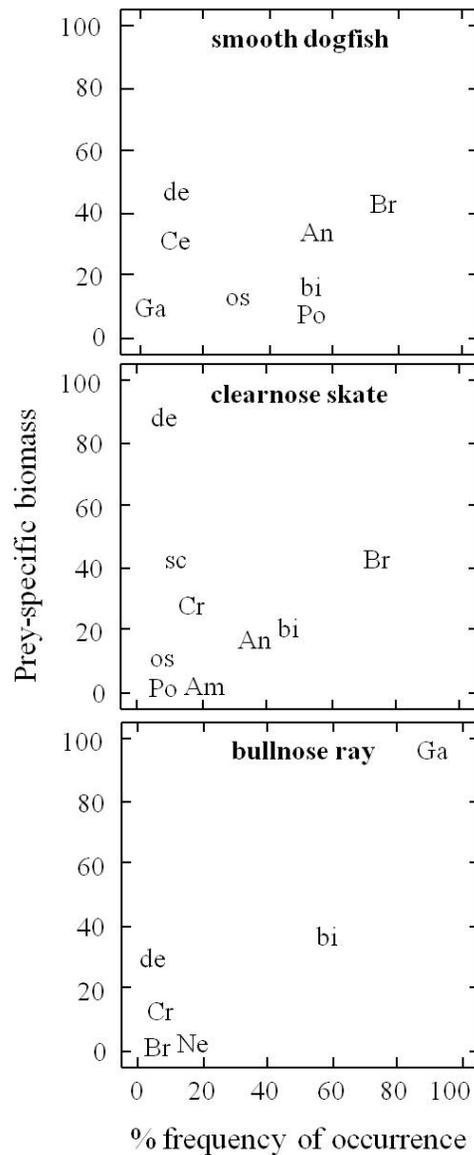
3.3 Diet overlap

Multivariate analysis of SC data (Fig. 4) revealed six significant species clusters, two of which were multispecies clusters. One multispecies cluster was a mixed elasmobranch-teleost cluster (Cluster 5) and the other was composed solely of teleosts (Cluster 6). Decapod crustacean (brachyuran spp. explained 29% of within-cluster similarity, anomuran spp. – 16%, and other shrimp – 11%), bivalve (17% within-cluster similarity), and demersal fish (9% within-cluster similarity) consumption explained 82% of the diet similarities (SIMPER analysis) within the elasmobranch-teleost cluster (smooth dogfish, clearnose skate, and southern kingfish). The teleost cluster included all of the species identified as piscivorous. This cluster was typified by piscivory (schooling spp. – 49% within-cluster similarity and demersal fish prey – 19% within-cluster similarity) and cephalopod predation (19% within-cluster similarity); these three categories explained 87% of the within cluster similarity. Among the remaining single species clusters (Clusters 1-4), bullnose ray, spotted hake and northern kingfish were more similar to the mixed elasmobranch-teleost cluster (32-25% diet similarity) than the teleost cluster (4-13% diet similarity; Fig. 4). This was due to the relatively high biomass of invertebrates in the diets of bullnose ray, spotted hake and northern kingfish (Table 2). Conversely, windowpane flounder was more similar to the teleost cluster (12% diet similarity) than the elasmobranch-teleost cluster (4% diet similarity), primarily based on the importance of mysids and zooplankton to the diet of windowpane flounder (Table 2).

3.4 Spatial overlap

There was evidence of positive and negative spatial associations among species pairs. Smooth dogfish catches showed a weak yet significant positive correlation with weakfish ($r_S = 0.34$, $p = 0.03$). Clearnose skate were positively correlated with southern kingfish ($r_S = 0.39$, $p = 0.01$) and bullnose ray ($r_S = 0.31$, $p = 0.05$), and negatively correlated with age-0 summer flounder ($r_S = -0.55$, $p = 0.0003$), northern kingfish ($r_S = -0.37$, $p = 0.02$), and windowpane flounder ($r_S = -0.32$, $p = 0.04$). Catches of bullnose ray were also significantly correlated with spotted hake ($r_S = 0.34$, $p = 0.03$).

Environmental conditions showed substantial variability during the four-year sampling period (Table 3). Average salinities ranged from 30.4-31.7, water temperatures from 18-24 °C, and DO concentrations from 3.6-7.5 mg L^{-1}. The average site depth increased over the time series although the difference was not significant (ANOVA, $F_{3, 36} = 2.44$, $p = 0.08$). The first two principal components (PC-1, PC-2) from the eigenanalysis explained 71 % of the total variability in the data: 41 % by PC-1 (eigenvalue = 1.62) and 31 % by PC-2 (eigenvalue = 1.22). Factor loadings of depth, salinity, and water temperature were highest on PC-1; whereas DO concentration loaded most heavily on PC-2. The first PC corresponds roughly to the inshore-offshore gradient and the second PC appears to be associated with vertical stratification as indicated by the gradient in DO concentration. Smooth dogfish catches showed significant correlation with PC-2 ($r_S = -0.37$, $p = 0.02$) in positive covariance with DO conditions. Clearnose skate correlated with PC-1 ($r_S = -$

0.41, $p = 0.01$), suggesting a warmer, more inshore distribution. Bullnose ray correlations were not significant with either PC ($p \geq 0.7$). Among the teleosts, weakfish ($r_S = -0.32$, $p = 0.05$), age-0 bluefish ($r_S = -0.52$, $p = 0.0007$), and windowpane flounder ($r_S = 0.38$, $p = 0.02$) were significantly correlated with PC-1, indicative of a more inshore distribution of weakfish and age-0 bluefish than windowpane flounder. Age-1+ summer flounder ($r_S = 0.49$, $p = 0.002$) and northern kingfish ($r_S = 0.40$, $p = 0.01$) were significantly correlated with PC-2, suggesting increased abundance or catchability associated with lower DO concentrations (< 4.5 mg L^{-1}). Southern kingfish was not significantly correlated with either PC although it demonstrated the same negative correlation with PC-1 ($r_S = -0.28$, $p = 0.09$) as clearnose skate.

Due to the similarity in diet and positive correlation in site-specific catches between clearnose skate and southern kingfish, we compared diel trends in relative stomach fullness and CPUE (Fig. 5). Changes in CPUE ($F \leq 1.60$, $p \geq 0.21$) and stomach fullness ($F \leq 1.76$, $p \geq 0.17$) across 6-h period were not statistically significant for either species although visual examination of the data indicated similar temporal trends. Average CPUE peaked between the hours of 1200-1759 for clearnose skate (167 ± 55 SE haul^{-1}) and southern kingfish (113 ± 49 SE) and maximum average stomach fullness occurred in specimens of both species during the following 6 h period (1800-2359 hrs: clearnose skate = 0.005 ± 0.002 SE, southern kingfish = 0.007 ± 0.002 SE).

Fig 4 Dendrogram of diet similarity among elasmobranch (filled circles) and teleost (shaded squares) species from Maryland's inner continental shelf during August 2007-2008. Species clusters (separated by dotted lines) are significantly different at α ≤ 0.05 (permutation test).
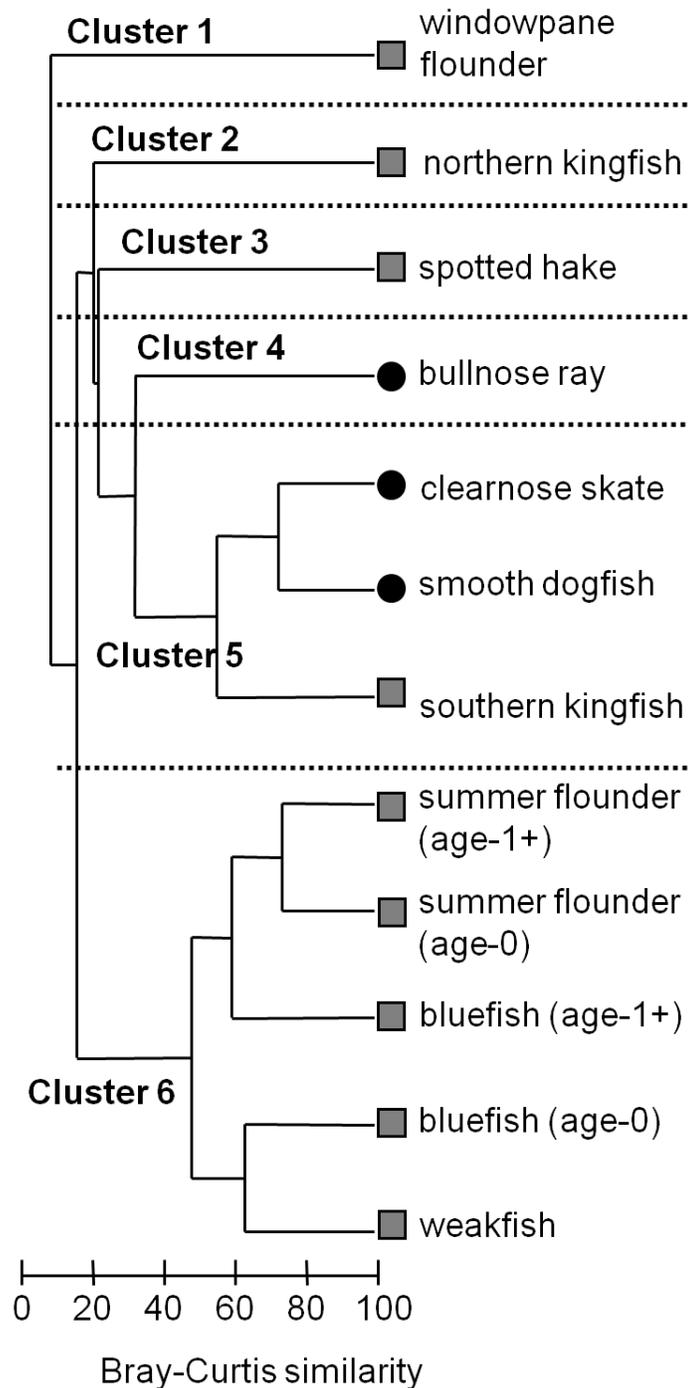
3.5 Trophic position

Stable isotope analysis indicated a pattern of increasing nitrogen enrichment from the
isotopic reference species to the elasmobranchs, and finally, to the teleosts (Fig. 6).
Elasmobranch TP estimates ranged from 3.5-4.1 based on SC data and 3.2-3.7 based
on SI data (Table 4); whereas teleost TP estimates ranged from 3.3-4.5 (SC) and from
3.8-4.2 (SI). Significant differences (*t*-test, $p \leq 0.05$) in TP between estimation
methods occurred for six of the twelve species (Table 4) with no obvious taxonomic
or age-related pattern in bias. The mean discrepancy between TP_{SC} and TP_{SI}
estimates across species was 0.30 and ranged from < 0.05 for smooth dogfish,
weakfish, and spotted hake to ≥ 0.5 for clearnose skate, age-1+ bluefish, southern
kingfish, and northern kingfish.

Group-level differences between elasmobranch and teleost species were not
significant for TP_{SC} (t = -0.77, df = 10, p = 0.46) but were significant for TP_{SI} (t = -
9.21, df = 96, p < 0.0001). Differences in TP_{SI} were present among species ($F_{11, 86}$ =
11.41, p < 0.0001) with significant pair-wise differences occurring between and
among elasmobranchs and teleosts (Table 4). The 2008 subadult clearnose skate and
age-1+ bullnose ray occupied a significantly lower TP_{SI} than all the teleost species
and age-classes (Tukey HSD, p < 0.05). Smooth dogfish, 2007 subadult clearnose
skate, and age-0 bullnose ray showed intermediate levels of overlap in TP_{SI} with the
teleosts. There were no significant differences in TP_{SI} between age-classes within
species; yet TP_{SI} did increase from younger to older age-classes of clearnose skate

Table 3 Trawl deployments (N) with annual means (SD) and loadings on principal components 1 (PC-1) and 2 (PC-2) for depth (m), temperature (°C), salinity, and dissolved oxygen concentrations (mg L^{-1}) from Maryland's inner continental shelf during August.

Year	N	Depth	Temperature	Salinity	DO
2004	12	10.2 (3.7)	19.8 (1.1)	31.2 (0.3)	7.5 (0.6)
2005	12	10.7 (3.3)	19.9 (1.6)	30.4 (0.1)	3.6 (0.2)
2007	8	13.2 (3.0)	23.6 (0.7)	31.7 (0.1)	3.7 (0.4)
2008	8	13.0 (3.5)	17.8 (2.5)	31.6 (0.2)	6.1 (2.7)
Total means	40	11.7 (3.5)	20.3 (2.4)	31.2 (0.6)	5.2 (2.1)
PC-loadings					
PC-1		0.725	-0.443	0.523	-0.069
PC-2		0.269	0.239	-0.287	-0.888

Fig 5 Diel patterns in an index of relative stomach fullness (primary y-axis: clearnose skate – filled circles, southern kingfish – shaded squares) and catch-per-unit-effort (CPUE haul^{-1}, secondary y-axis: clearnose skate – empty circles, southern kingfish – empty squares) for two species. Solid (clearnose skate) and dotted (southern kingfish) lines indicate average stomach fullness and CPUE per 6-h period.
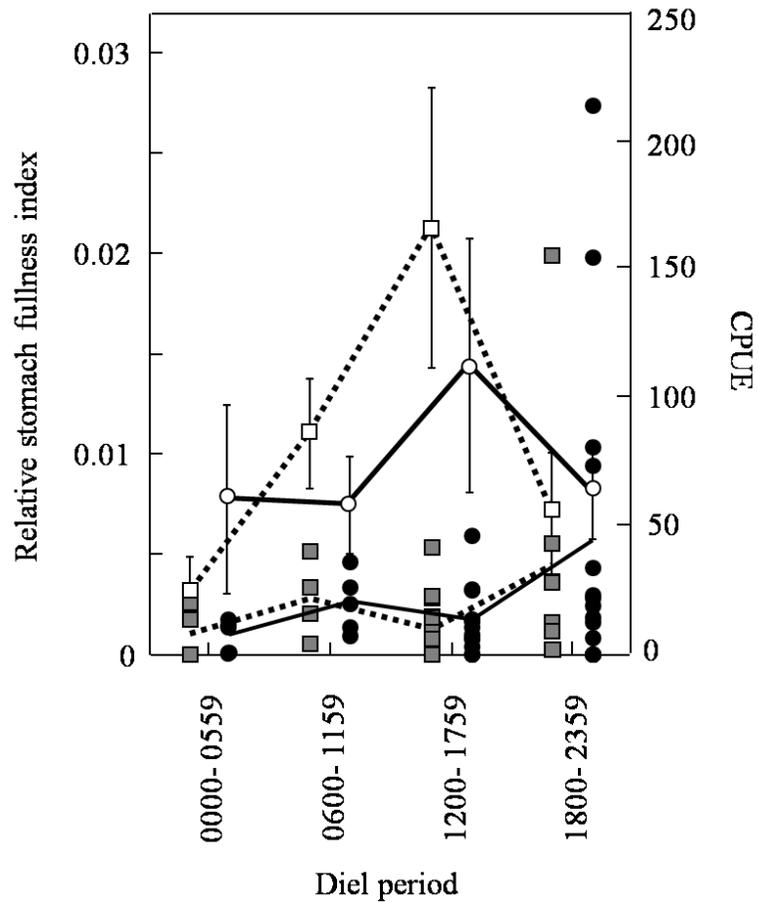
Fig 6 δ13C and δ15N signatures (± 1 SE) from elasmobranch (filled circle), teleost (shaded square), and isotopic baseline (open circle) species from Maryland's inner continental shelf during August 2007-2008. Abbreviations are based on Latin names as follows, Species: Mc – smooth dogfish, Re – clearnose skate, Mf – bullnose ray, Cr – weakfish, Ma – southern kingfish, Ms – northern kingfish, Pd – summer flounder, Ps – bluefish, Sa – windowpane flounder, Ur – spotted hake; Age: "0" = age-0 or subadult (clearnose skate: "07" for 2007 samples, "08" = 2008 samples), "1" = age-1+ or adult (clearnose skate). δ15N signatures corresponding to trophic levels (TL) 3 (secondary consumer) and 4 (tertiary consumer) are plotted for reference (dot-dot-dash lines).
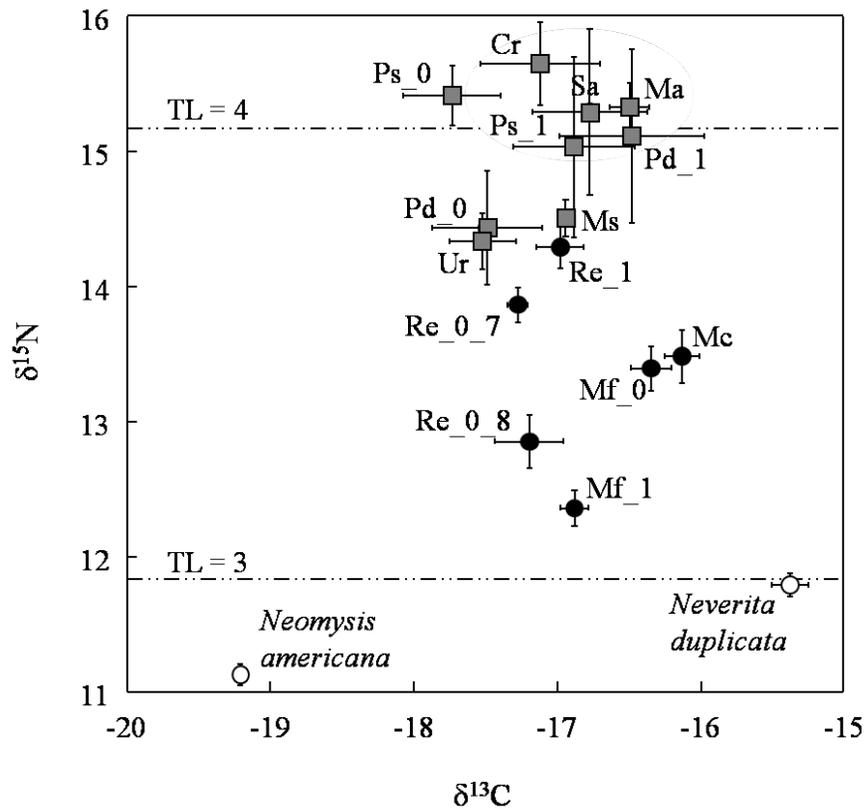
Table 4 Trophic positions based on stomach contents (TP_{SC}) and stable isotope analysis (TP_{SI}) for three elasmobranch and seven teleost species collected from Maryland's inner continental shelf during August 2007-2008. Bold fonts indicate significant differences between TP_{SC} and TP_{SI} estimates. Species or age-classes with different letters (TP_{SI} grouping) have significantly different TP_{SI} estimates at α=0.05 (Tukey HSD).

Species	Age class	TP_{SC}	TP_{SI}	TP_{SI} grouping
smooth dogfish	age-0	3.56	3.51	A,B,C
clearnose skate	Pooled	**4.10**	**3.50**	
	Adult		3.73	B,C,D,E
	subadult (2007)		3.61	B,C,D
	subadult (2008)		3.30	A,B
bullnose ray	Pooled	**3.53**	**3.32**	
	age-0		3.47	A,B,C
	age-1+		3.16	A
spotted hake	age-1+	3.75	3.76	C,D,E
northern kingfish	age-1+	**3.30**	**3.80**	C,D,E
summer flounder	age-0	**4.22**	**3.80**	C,D,E
	age-1+	4.28	3.98	D,E
bluefish	age-0	4.17	4.08	E
	age-1+	**4.52**	**3.96**	D,E
windowpane flounder	age-1+	3.75	4.07	E
southern kingfish	age-1+	**3.60**	**4.07**	E
weakfish	age-1+	4.12	4.16	E

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and summer flounder. Conversely, TP_{SI} of age-0 bullnose ray and bluefish was higher than that of older conspecifics.

4. Discussion

Despite the lack of formal stock assessments, fisheries-independent and commercial harvest data indicate regional abundances of a variety of small elasmobranchs have fluctuated in recent decades (Shepherd and Myers 2005; Sosebee 2006; Myers et al. 2007; Frisk et al. 2008; Vonderweidt et al. 2008). These changes could potentially affect co-occurring teleosts by modulating trophic demand for shared resources, diverting basal production into alternative species biomass, and influencing predation pressure, particularly on small or juvenile teleosts. In this study, the stomach content data for several species (smooth dogfish, clearnose skate, and southern kingfish) indicated that they interact with multiple local prey resources. We found that piscivory represents a relatively common, although likely opportunistic, foraging strategy by smooth dogfish and clearnose skate. We also detected niche overlap between and within elasmobranch and teleost species groups arising from overlap in forage or spatial resources. Thus, changes in local abundance of these three elasmobranchs could influence some species within the sympatric teleost assemblage by altering trophic demand for the shared forage base.

The relatively high rates of piscivory and proportion of the diet contributed by fish to smooth dogfish and clearnose skate diets indicate that teleosts can constitute important prey for these species in ICS habitats. Link et al. (2002b) noted a

significantly lower incidence of groundfish in the diets of smooth dogfish (< 1% FO

in 3,806 stomachs) taken in deeper continental shelf habitats (27-366 m depth).

Conversely, piscivory approached 10% for age-0 (Breder 1921; Rountree and Able

1996) and 28% among larger (460-1260+ mm TL, Gelsleichter et al. 1999) smooth

dogfish collected from coastal lagoon and shelf waters of the Mid-Atlantic region.

Piscivory appears to be more common in clearnose skate; a meta-analysis of three

independent studies (including Bowman et al. 2000) found fish prey represented

approximately 27% of the standardized diet composition (Ebert and Bizzarro 2007).

Among specimens collected from the northeastern U.S. continental shelf, the

incidence of piscivory ranged from 16-29% (Packer et al. 2003) with the percent diet

proportion by weight increasing from 0-79% across seven size-classes of clearnose

skate (Bowman et al. 2000). In the present study we were unable to determine

whether the observed fish prey were actively captured or scavenged, yet direct

observation of stomach contents suggests that piscivory is more common in the ICS

versus estuarine or offshore continental shelf habitats for both smooth dogfish and

clearnose skate.

Our stable isotope analysis suggests that fish are probably not a major source

of assimilated biomass for these elasmobranchs in the ICS. Observed $\delta^{15}N$ values

indicated they were feeding at trophic positions of 3.2 to 3.7; yet analysis of the most

important demersal fish species (by weight) consumed by both smooth dogfish and

clearnose skate in this study (juvenile weakfish) had a mean $\delta^{15}N$ of 13.12 ± 1.05 SE

($n = 5$, Woodland unpublished data), which corresponds to $TL_{SI} = 3.4$. This does not

conform to the pattern of source-to-consumer fractionation of nitrogen expected from a dominant predator-prey relationship (Peterson and Fry 1987; Phillips and Gregg 2001). Rather, the observed elasmobranch $\delta^{15}N$ signatures are indicative of diets primarily composed of prey in lower trophic positions, such as the mollusks and decapod crustaceans that formed the bulk (>50%) of the stomach content biomass of all elasmobranchs. Based on the SC and SI analyses, we infer that piscivory (or scavenging fish remains) represents an opportunistic foraging strategy for juvenile smooth dogfish and clearnose skate in ICS habitats. The importance of teleosts in the diet of these species may be density dependent or rely on other factors that modulate prey availability and/or vulnerability to predation.

Decoupling of an organism's immediate diet and isotopic tissue composition can arise from the movements of organisms (Hobson 1999; Herzka et al. 2001; Post 2002), whether due to biogeochemical differences between habitats or spatially varying forage conditions. This could explain the difference in TP estimates using SC and SI data for species such as southern kingfish. Many of these species undertake seasonal migrations to offshore or southern overwintering habitats (Murdy et al. 1997; Able and Fahay 1998), so the isotopic tissue signature (particularly among age-1+ fish) may reflect spatial changes in the individual's prior feeding history (Hobson 1999; Winemiller et al. 2007). Alternatively, ontogenetic changes in diet may underlie observed differences in TP_{SC} and TP_{SI} between age-classes within species (e.g., increased importance of demersal fish prey for age-1 bluefish) in which

SI tissue signatures have not yet reached equilibrium following age- or size-related trophic shifts (MacNeil et al. 2005).

Although small teleosts constituted a common diet item for three small elasmobranchs in ICS habitats, it is not clear what effects they might exert on prey populations. In this study, the densities of prey species (e.g., bay anchovy CPUE = 1,778 haul^{-1}, age-0 weakfish CPUE = 1,031) were much higher than those of the elasmobranchs (i.e., juvenile smooth dogfish CPUE = 7.4, clearnose skate CPUE = 102, bullnose ray CPUE = 10.3) in the trawl survey. Corresponding area-swept regional abundances were estimated at roughly 2.00×10^4, 2.75×10^5, and 2.77×10^4 individuals for smooth dogfish, clearnose skate, and bullnose ray within the 150-km^2 sampling area during August. While substantial, these abundances are low compared to contemporaneous abundances of weakfish (1.96×10^6 [age-1+]), summer flounder (6.40×10^4), and bluefish (4.24×10^5). Therefore, it seems unlikely that current densities of these elasmobranchs exert significant predation pressure on teleost prey populations relative to the abundance and foraging habits of sympatric piscivorous teleosts.

We found evidence of resource sharing between clearnose skate and southern kingfish in the study area (i.e., trophic and spatial overlap) and weaker evidence of overlap between clearnose skate and smooth dogfish, and smooth dogfish and southern kingfish. The environmental conditions under which these species co-occur suggest that smooth dogfish are less common in areas with low DO concentrations

than either clearnose skate or southern kingfish. The availability of suitable DO conditions might therefore contribute to niche separation between smooth dogfish juveniles and the two other species. At the same time, both clearnose skate and southern kingfish tended to be captured in shallower locations typified by warmer, less saline waters. The open, unstructured nature of Maryland's ICS should reduce the likelihood of observing spatial exclusion of species despite shared environmental niche preferences. Here, we interpret spatial overlap as a prerequisite for ecologically meaningful species interactions and do not necessarily infer that species are 'competing' for space.

Although these patterns suggest similar environmental correlates with catch patterns, diet overlap in particular provides unequivocal evidence of shared prey resources and similar trophic pathways. Diel trends in CPUE and stomach fullness of clearnose skate and southern kingfish suggest higher crepuscular activity and foraging behavior. Temporal shifts in CPUE may indicate these species use the sampling area prior to foraging in either shoal (< 5 m) or deep (> 20 m) waters during the night and early morning. The primary diet overlap between clearnose skate and southern kingfish occurred for invertebrates, so if the observed level of piscivory by clearnose skate was anomalously high (as suggested by TP_{SI}), the overlap in shared prey resources might actually be higher than we estimated.

A common forage base and spatiotemporal overlap in habitat use are only two of several conditions necessary for competitive trophic interactions. Link et al.

(2002b) propose four criteria for documenting competition: spatiotemporal co-occurrence, overlap in resource utilization, constraints on resource availability, and "notable population impacts of the interaction". For example, without relative prey abundance estimates, it is impossible to determine whether the diet overlap observed in this study was the result of opportunistic predation on a diverse and abundant forage base (i.e., high predator-prey spatial overlap and high prey abundance; Kempf et al. 2008) or the convergence of trophic niches arising from competition for a limited pool of suitable prey types (Gabler and Amundsen 2009). Either mechanism could explain the similarities in diet between clearnose skate and southern kingfish, yet the implications for individual and population-level dynamics are quite different. Further work is needed to elucidate the interaction between prey availability and prey selection before a more complete understanding of the trophic relationships among these species is possible.

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Chapter 5 Appendix

Appendix Estimates of trophic position based on stomach contents (TP$_{SC}$) gathered

from previous studies for three mesopredator elasmobranchs. Age class, number of

samples (n) and length (mm) of specimens analyzed from each study are provided

where available.

Species	Age class	TP$_{SC}$	n	Length	Study
smooth dogfish	mixed	3.75	64	460-1260[+]	Gelsleichter et al. 1999
	-	3.57	3,806	-	Link et al. 2002
	age-0	3.80	102	300-640	Breder 1921 [a]
	age-0	3.66	100	<410-600	Bowman et al. 2000
	age-0	3.77	85	318-586	Rountree and Able 1996
clearnose skate	-	3.68	651	-	Ebert and Bizzarro 2007 [d]
	-	3.75	38	-	Packer et al. 2003 [b]
	-	3.86	86	-	Packer et al. 2003 [c]
	mixed	4.04	50	310-650	Bowman et al. 2000
bullnose ray	mixed	3.39	15	370-1230	Bowman et al. 2000

[a-c] TP estimate derived from count rather than weight data.

[d] TP estimate derived from meta-analysis of stomach contents data from 3 individual

studies (see Ebert and Bizzaro 2007 for detail).

Chapter 6: Benthic-pelagic Coupling in a Temperate Inner Continental Shelf Demersal Fish Assemblage

Abstract

In temperate latitudes, unstructured areas of the inner continental shelf (ICS, < 20 m) are important nursery and foraging habitats for many finfish species; yet, food web dynamics have received little attention. In this study, the importance of benthic trophic pathways (i.e., detrital-based nutrition sources) for demersal finfish was posited to increase: 1) through ontogeny; 2) with proximity to the ocean floor; and 3) with water column depth. Stomach contents and stable isotope (C, N) data were analyzed for 17 species of finfish and 8 invertebrate groups collected during August and September (2004-2008) from a temperate ICS habitat of the Middle Atlantic Bight (USA). Results showed that species with a high affinity for demersal or epibenthic habitats were more reliant on benthic carbon sources compared to pelagic species. Overall, most species showed a strong tendency to exploit both pelagic and benthic prey sources. Consumers partitioned prey resources along vertical (trophic position) and horizontal (carbon source) gradients rather than as discrete trophic units (e.g., trophic levels). The food web was size-structured and, to a lesser extent, age-structured. Assimilation of benthic carbon sources generally increased with individual size or age. The importance of benthic carbon sources did not vary with water column depth. Overall, there was strong evidence that the demersal assemblage is heavily subsidized by both pelagic and benthic trophic pathways. Future research to extend a comparative analysis to offshore shelf habitats should provide valuable

information on the role of benthic-pelagic coupling at larger spatial scales, particularly for juvenile life stages.

1. Introduction

In continental shelf ecosystems, demersal food webs integrate pelagic and benthic food sources delivered via vertical flux of photosynthesis-driven production from the surface mixed layer (pelagic pathway) or *in situ* detrital-based production (benthic pathway). Water column depth, temperature, euphotic depth, physical mixing, proximity to nutrient sources, primary production, pelagic grazing rates, and the zooplankton and nekton communities all affect the passive sinking or active movement of pelagic material to demersal food webs (Graf 1992; Polis and Strong 1996; Marcus and Boero 1998; Marcogliese 2002). In turn, the relative contribution of pelagic versus benthic pathways influences species composition (Moodley et al. 1998), taxonomic and functional diversity (Gray 2002; Ellingsen et al. 2005), standing biomass (Grebmeier et al. 1988; Ambrose and Renaud 1995), and productivity of demersal communities (Townsend and Cammen 1988). In addition, there is evidence that energy propagates through pelagic pathways faster (i.e., higher production:biomass ratios) than benthic pathways due to differences in interaction strength and life-history characteristics of species that utilize each pathway (Rooney et al. 2006). This has been shown to have a stabilizing effect on consumer populations that couple both trophic pathways (Rooney et al. 2006), but also suggests tighter temporal linkages between pelagic primary production and the availability of planktonic prey for juvenile fish and invertebrates.

Depth, in particular, has been identified as an important physical gradient that modulates the contribution of pelagic versus benthic production pathways to demersal food webs (Duineveld et al. 2000; Giordani et al. 2002; Lampadariou and Tselepides 2006). Inputs of terrigenous, atmospheric, and upwelled nutrients to shallow coastal waters support high pelagic primary production that is readily transferred to the proximal benthic zone (Giles et al. 2007). Benthic production of higher trophic levels is tightly coupled to the quantity and quality of pelagic inputs in these shallow habitats (Rosenberg 2001). In addition, the close proximity of the pelagic zone allows vertically mobile demersal consumers to facultatively forage throughout the water column. In deeper, offshore shelf waters, pelagic primary production becomes decoupled from benthic food webs; organic particulate matter reaching the benthic zone is increasingly refractory due to higher residence times and mineralization processes within the water column. Because of this, offshore benthic food webs are more dependent on microbial mediation, detrital scavenging, and the pulsed deposition of pelagic biomass during bloom and mixing events (Townsend and Cammen 1988).

Cross-shelf turnover of individual species is well documented in demersal finfish assemblages (Hyndes et al. 1999; Steves et al. 2000; Walsh et al. 2006); yet many species persist, often as multiple size or age classes, across a broad spectrum of inner-to-outer continental shelf habitats. It is not clear if these persistent species are functionally dependent upon specific trophic pathways or if they are capable of

opportunistically shifting from one pathway to the other. This is especially true of juvenile life-stages and small-bodied species for which forage availability is constrained by gape limits (Scharf et al. 2000). For such stages and species, a reasonable prediction would be a higher dependence on pelagic trophic pathways, characterized by high turnover rates and small secondary consumers such as copepods and meroplankton. Conversely, larger individuals are not subjected to the same foraging constraints and might be expected to facultatively switch among available prey types, resulting in a diet that more closely recapitulates the average local input of pelagic versus benthic food sources. At higher levels of organization (e.g., assemblage), the gradual decoupling of direct trophic transfers between pelagic and benthic pathways with distance offshore should also result in an identifiable gradient in diet composition within the demersal finfish community.

Here, I compared trophic niches of multiple species and age classes of fish collected from an inner continental shelf habitat (< 20 m) of the mid-Atlantic region in the US Northwestern Atlantic. This analysis includes both directed and descriptive analyses, each focused on the food web structure of the demersal finfish assemblage. Specifically, I hypothesized: 1) juvenile finfish rely more heavily on pelagic versus benthic trophic pathways than larger/older conspecifics; 2) the contribution of pelagic pathways to the diet of juvenile conspecifics will be independent of depth; and 3) the contribution of pelagic pathways to the diet of larger size classes will decline with increasing depth. In addition, I examined niche partitioning and trophic size-

structuring to allow an initial, qualitative description of the food web of the inner continental shelf.

2. Methods

2.1 Site description

The Middle Atlantic Bight (MAB) is the continental margin of the eastern United States, bounded on the north by Cape Cod, MA, and by Cape Hatteras, NC, to the south (Fig 1). Offshore, the continental shelf narrows from a width of 200 km off Cape Cod to 25 km off Cape Hatteras and is characterized by a gently sloping gradient (average declivities < 0.1°) that extends to the continental slope (Milliman 1973). The continental shelf of the MAB can be characterized as a mixture of unconsolidated sediments dominated by sand, although ranging in grain size from gravel to silt and clay (Milliman 1973, Steimle and Zetlin 2000). From north to south, the coastline of the MAB is punctuated by four major estuaries: the Hudson River Estuary (NY), Delaware Bay (DE, NJ), Chesapeake Bay (VA) and Albemarle Sound (NC). The nearshore water mass of the MAB is strongly influenced by the generally southward fluvial outflow from these estuaries as well as interactions with offshore shelf and slope water masses (Mountain 1991). In combination with terrestrial runoff, coastal plume waters create a low salinity water mass along the coast that varies in size and salinity across seasonal and interannual scales (Mountain 1991). Offshore, the surface shelf water mass is predominantly influenced by the tropical Gulf Stream current, being warmer and more saline than the deeper slope water. The

slope water mass is colder and fresher, composed of remnant Labrador Current waters and fluvial outflow from boreal river systems (e.g., St. Lawrence River). Mixing of nearshore, shelf and slope water masses across the continental shelf results in a dynamic, highly productive habitat typified by broad physical gradients and punctuated with seasonal and ephemeral frontal structures (e.g., the annually recurrent slope 'cold pool', estuarine plume frontal zones, Gulf Stream meanders and gyres).

2.2 Field and Laboratory methods

Demersal finfish assemblages were sampled by bottom trawl from the inner continental shelf (ICS: 5–20 m) adjacent to the Delmarva Peninsula. The Delmarva Peninsula is located near the center of the MAB (Fig 1), extending from the southern terminus of Delaware Bay to the northern terminus of Chesapeake Bay. The ICS sampling protocols have been described in detail in Chapters 2–4 and will only be summarized here. Briefly, trawling was conducted along a 22-km section of coastal habitat offshore of Fenwick and Assateague Islands (MD; Fig 1) at roughly bimonthly intervals from June–November 2004–2006 and August 2007–2008. Site selection was randomly stratified between shoal (5–10 m) and deep (10–20 m) strata to ensure equal sampling effort across the available depth gradient. Catch was identified to the species level, sorted, measured (nearest 0.1 cm), and weighed (nearest 0.1 kg for large and 1 g for small species). Finfish were retained for trophic analysis during August 2004–2005 and 2007–2008; specimens destined for stable isotope (SI) and stomach contents (SC) analysis were flash frozen on dry ice immediately following capture.

Fig 1 Site map of Delmarva Peninsula continental shelf habitat (geographic extent of Middle Atlantic Bight inset: Cape Cod, MA −

Cape Hatteras, NC). Study area is identified (left panel) and shown in higher resolution (right panel) with individual trawl locations (n

= 74, Aug-Sept 2004-2008) indicated by solid circles.
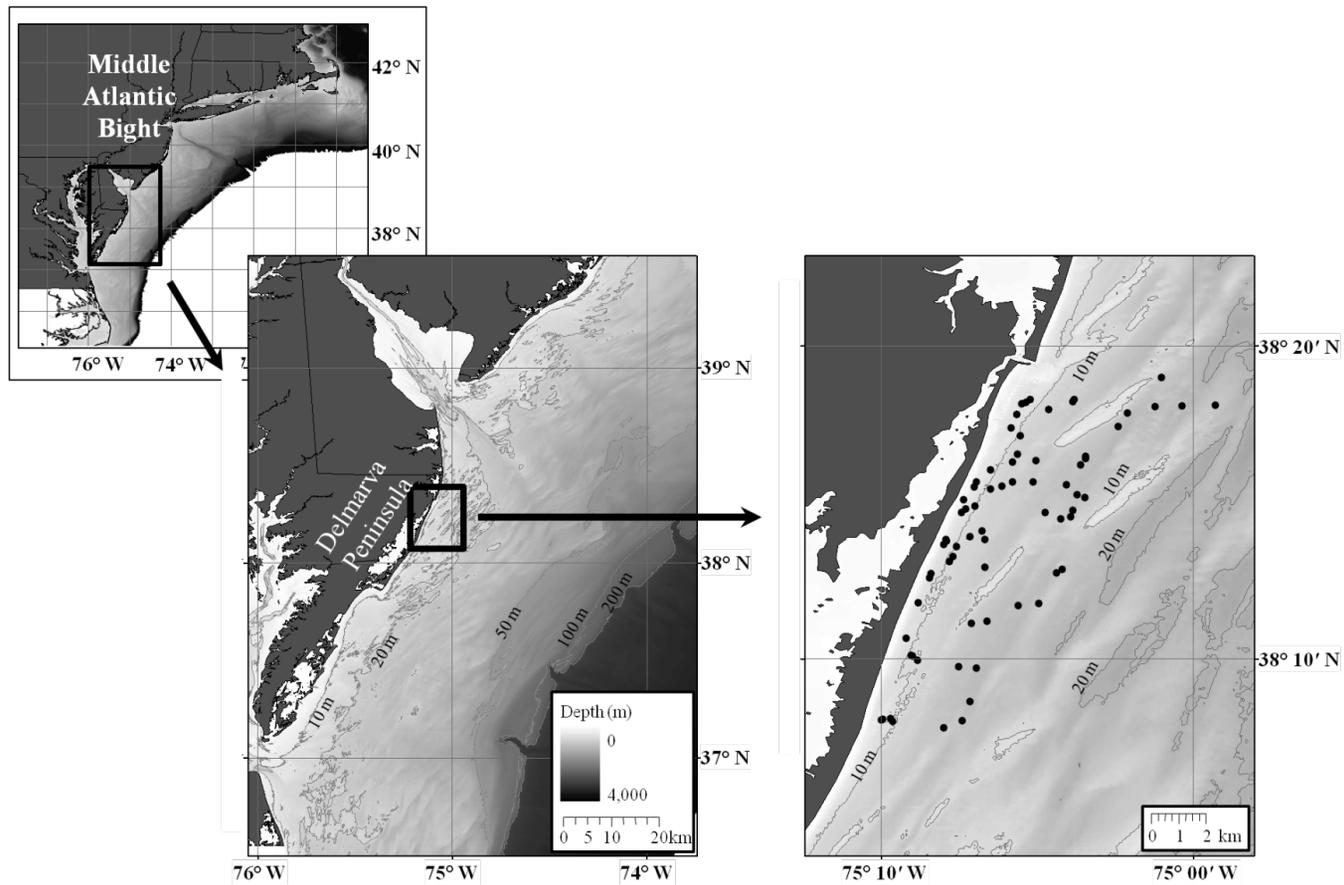
The primary collecting gear for finfish was the demersal otter trawl, although supplemental specimens were taken with a semi-balloon midwater trawl (5.7-m footrope). In 2007 and 2008, lower trophic position invertebrate species or groups were collected to characterize the isotopic structure of the ICS demersal food web. These prey categories were sampled with additional gears including: a 1-m^2 Tucker trawl (280-μm cod-end mesh), 522-cm^2 benthic grab, and depth-integrated zooplankton pump (100-μm sieve, 20-L sample at surface, mid-depth, and near bottom). Benthic macrofauna and zooplankton were transferred to containers of 0.7-μm filtered seawater for 24 hrs to allow evacuation of gut contents prior to freezing. Gear deployments were temporally staggered across the full 24-hr diel period during each August sampling event in 2007-2008.

Specimens from 17 finfish species (Table 1) analyzed for SC and SI data were selected specifically according to age-0 size thresholds (Appendix A). Samples frozen in the field were stored at -20°C until analyzed; at which point samples were partially thawed, stomachs excised from whole specimens, and a fillet of white muscle tissue removed. After thawing, stomachs and contents of 1-181 individuals per species or age class (Table 1) were fixed in a 10% buffered formalin solution. Prey items were identified to the lowest possible taxon, enumerated, blotted dry, and weighed to the nearest milligram.

A random sub-sample of 2-20 individuals per species or age class (Table 1) was selected for SI analysis. White muscle tissue samples were rinsed in de-ionized

Table 1 Sample size for finfish species [a] per analytical approach (SI = stable isotope, SC = stomach contents; subcategories: 0 = age-0, 1 = age-1+, Shoal < 10-m depth, Deep = ≥10-m depth) collected from the Delmarva inner continental shelf August-September 2004-2005, 2006-2007. Vertical habitat group (P = pelagic, D = demersal, E = epibenthic) given for each species.

Order / species	Common name	Group	N_{SC}	N_{SI}	SI 0	SI 1	SC 0	SC 1	Shoal	Deep
Carcharhiniformes										
Mustelus canis	smooth dogfish	D	23	12	12	-	22	1	5	18
Clupeiformes										
Anchoa hepsetus	striped anchovy	P	53	6	3	3	12	41	24	29
Anchoa mitchilli	bay anchovy	P	88	30	20	10	67	21	70	18
Gadiformes										
Urophycis regia	spotted hake	D	20	5	-	5	-	20	1	19
Myliobatiformes										
Myliobatis freminvillei	bullnose ray	E	34	22	11	11	18	16	4	30
Ophidiiformes										
Ophidion marginatum	striped cusk-eel	D	26	5	-	5	-	26	5	21
Perciformes										
Peprilus triacanthus	Atlantic butterfish	P	58	8	3	5	22	36	17	41
Pomatomus saltatrix	bluefish	P	252	24	19	5	181	71	105	14
Cynoscion regalis	weakfish	D	294	10	5	5	126	168	158	13
Leiostomus xanthurus	spot	D	41	7	3	4	1	40	13	28
Menticirrhus americanus	southern kingfish	D	62	7	4	3	14	48	19	43
Menticirrhus saxatilis	northern kingfish	D	25	6	2	4	2	23	1	24
Micropogonias undulatus	Atlantic croaker	D	33	5	-	5	-	33	14	19
Pleuronectiformes										

Etropus microstomus	smallmouth flounder	E	28	5	5	-	4	24	-	28
Paralichthys dentatus	summer flounder	E	80	10	5	5	34	46	23	57
Scophthalmus aquosus	windowpane flounder	E	70	7	4	3	53	17	17	53
Rajiformes										
Raja eglanteria	clearnose skate	E	39	24	14	10	22	17	10	29

[a] SI sample size for invertebrate categories: mixed bivalves (Atlantic nut clam *Nucula proxima*, dwarf tellin *Tellina agilis*, file yoldia *Yoldia limatula*) n = 3, amphipod (*Gammaridae*) n = 1, sand shrimp (*Crangon septemspinosa*) n = 3, inshore longfin squid (*Loligo pealei*) n = 5, mysid shrimp (*Neomysis americana*) n = 5, Shark's eye moon snail (*Neverita duplicata*) n = 6, hermit crab (*Pagurus* sp.) = 3, mixed copepods (primarily Calanoida) n = 5.

water, held at 60°C for ≥ 48 hours until completely dried, then pulverized to a fine

homogeneous powder using a mortar and pestle. Invertebrates were treated similarly.

Muscle tissue was excised from large invertebrates (e.g., moon snails, bivalves) and

analyzed individually for SI analysis. Small invertebrate crustaceans (e.g., mysids,

copepods) were aggregated whole, dried and pulverized, then split into two separate

samples. One sample was acid-fumigated with 1N HCL for 24 hrs within a sealed

desiccator, then redried and sent out for carbon isotope analysis (Bunn et al. 1995).

The second sample, analyzed for nitrogen, was not acidified. Samples were analyzed

for carbon and nitrogen via continuous-flow isotope ratio mass spectrometry coupled

with an elemental analyzer (EA-CFIRMS) at Colorado Plateau Stable Isotope

Laboratory, Northern Arizona University. Stable isotope values are reported as a ratio

in the "δ" notation following established convention in the ecological literature

(Peterson and Fry 1987). All $\delta^{13}C$ values were mathematically normalized using the

C:N ratio of the sample in conjunction with published correction curves (Post et al.

2007).

2.3 Data analysis: Stable isotopes

Two invertebrate species common to the stomach contents of consumer finfish were

selected as representative benthic (shark's eye moon snail *Neverita duplicata*, $\delta^{13}C$ =

-15.383 ‰ ± 0.307) and pelagic (mixed zooplankton, primarily calanoid copepods ~

0.1-1 mm, $\delta^{13}C$ = -20.381 ‰ ± 0.483) isotopic end-members (Fig 2). Moon snails

and zooplankton were assigned average trophic positions (TP) = 3.0 and 2.5,

respectively, based on the predaceous trophic ecology of moon snails (Gosner 1999)

and the diverse trophic ecology of zooplankton (incl. herbivory, carnivory, and omnivory; Kleppel 1993; De Troch et al. 2006). Independent estimates of TP based on $\delta^{15}N$ values of sympatric bivalves (mixed bivalve group: Atlantic nut clam *Nucula proxima*, dwarf tellin *Tellina agilis*, file yoldia *Yoldia limatula*; assumed TP = 2.0) were very similar for these two prey categories: moon snail TP = 2.96, zooplankton TP = 2.40. Carbon SI values of finfish, moon snails, and zooplankton were standardized to TP = 2.0 by assuming C fractionation of 0.5‰ per trophic transfer (Post 2007). This was done to allow for direct comparison of $\delta^{13}C$ values among individuals of different trophic positions. I then used a simple two end-member mixing model:

$$\delta^{13}C_{finfish} = p\delta^{13}C_{benthic} + (1-p)\delta^{13}C_{pelagic}$$

where p is the proportional input of end-members (Kwak and Zedler 1997), to calculate the proportion of C assimilated from benthic versus pelagic (BP$_{SI}$) food webs for individual finfish specimens.

Following a $\sin^{-1}\sqrt{}$ transformation of BP$_{SI}$ values (proportion data, Quinn and Keough 2002), age-dependent changes in BP$_{SI\,was}$ tested with a series of one-tailed t-tests (H$_0$: BP$_{SI}$ of age-0 fish < age-1+) for species with SI data from multiple age classes. Species (or age classes) were also assigned to one of three functional groups based on vertical habitat preference: pelagic, demersal, or epibenthic. One-way ANOVA with Tukey's HSD pair-wise comparison test was used to test the hypothesis that BP$_{SI}$ is ordered according to primary foraging habitat (i.e., pelagic BP$_{SI}$ < demersal BP$_{SI}$ < epibenthic BP$_{SI}$).

Age-0 and age-1+ age classes of bay anchovy (*Anchoa mitchilli*), weakfish (*Cynoscion regalis*), and summer flounder (*Paralichthys dentatus*) were selected for additional SI trophic analysis using the IsoSource software package (Phillips and Gregg 2003, v-1.3.1 downloadable at www.epa.gov). IsoSource is a multiple end-member mixing model that calculates a distribution of possible dietary source contributions to an isotopic mixture when the number of sources exceeds the number of isotope markers. The mixing algorithm examines all possible combinations of source contributions to a mixture in incremental intervals (e.g., 1% intervals); a particular iteration is considered feasible if the contributions sum to the observed mixture within the constraints of a set tolerance (e.g., 0.01‰). Measures of central tendency (e.g., mean, SD) are based on the frequency and range of feasible source contributions (see Phillips and Gregg 2003 for additional information).

Prey categories selected for each species and age class were not exhaustive (i.e., total prey richness > prey categories used in IsoSource), but rather selected to represent dominant prey items identified in SC analysis (Appendix B) and to span the range of pelagic and benthic prey C values (Fig 2). Zooplankton, mysid shrimp (*Neomysis americana*), and sand shrimp (*Crangon septemspinosa*) were chosen as representative prey items in the bay anchovy and weakfish models; whereas mysids, sand shrimp, and age-0 bay anchovy were included as representative prey in the summer flounder models. In addition to the species-specific prey items, moon snails were included as a benthic carbon pathway indicator in all models. Carbon SI values

of consumers (bay anchovy, weakfish, and summer flounder) and prey were supplied to the IsoSource software; N values were not used to avoid influencing model estimates of primary carbon sources. The contribution of prey types were examined for evidence of ontogenetic shifts in the contribution of pelagic vs. benthic pathways within species. Contributions of pelagic and benthic prey were also compared across species to address hypothesized food web dependencies by representative pelagic (bay anchovy), demersal (weakfish) and epibenthic (summer flounder) species.

2.4 Data analysis: Stomach contents

Depth-dependent changes in the relative contribution of benthic versus pelagic food webs to the demersal finfish assemblage were tested with univariate and multivariate approaches. Each prey category was further designated as belonging to either a pelagic or a benthic food web (e.g., Schindler and Scheuerell 2002) and the total biomass of pelagic and benthic prey summed for each individual. The ratio of benthic:pelagic stomach contents biomass (BP_{Diet}) was calculated. Differences in $sin^{-1}\sqrt{BP_{Diet}}$ across depth strata (shoal < 10 m, deep ≥ 10 m) were tested for each species and vertical functional group (one sample t-tests).

Multivariate analysis was used to examine gradients in diet composition across depth strata. Initial, high resolution prey categories (n = 75) were aggregated into lower resolution ecological prey groups. The most important prey categories (by biomass) were maintained at the family-level (e.g., Mysidae). Infrequent prey categories were grouped according to similarities in average body size, body

Fig 2 Average δ^{13}C (±SD) values for representative samples of 17 species of finfish and 8 invertebrate categories from Maryland's ICS (2007-2008). Common name abbreviations (here and elsewhere): striped anchovy = str. anchovy; Atlantic butterfish = Atl. butterfish; Atlantic croaker = Atl. croaker; striped cusk-eel = str. cusk-eel; smooth dogfish = sm. dogfish; spotted hake = spt. hake; southern kingfish = s. kingfish; northern kingfish = n. kingfish; summer flounder = sum. flounder; windowpane flounder = wnpn. flounder; smallmouth flounder = smth. flounder; clearnose skate = clr. skate; bullnose ray = bull. ray.
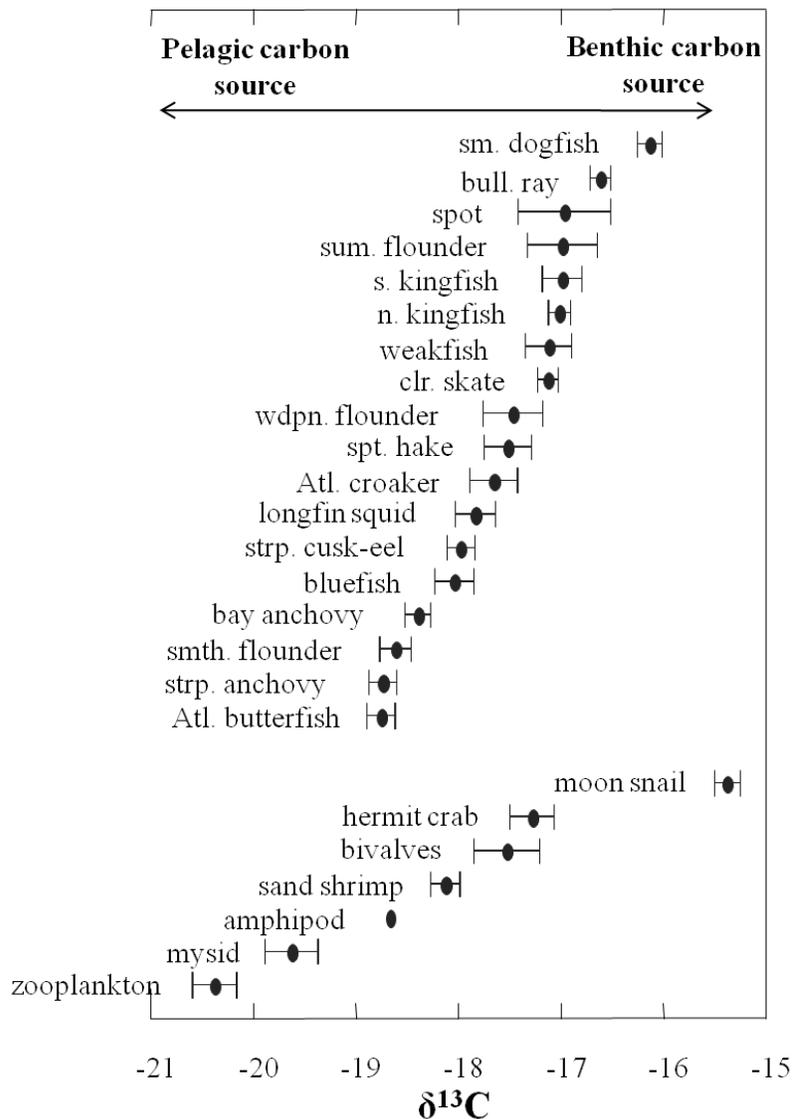
shape, taxonomy and habitat (e.g., pelagic jack-like fishes [incl. Carangidae and Pomatomidae], decapod crabs [incl. Cancridae, Portunidae, Majidae]). The resulting matrix contained 19 aggregate prey groups (Appendix B). A Bray-Curtis similarity matrix was calculated from the SC data and hierarchical agglomerative cluster analysis was used to examine diet composition among species and age classes. I used a permutation-based significance test with species Bray-Curtis similarity profiles (SIMPROF) to identify significant structuring within the dendrogram clusters. Species rank similarities were plotted using non-metric multidimensional scaling (nMDS) to provide a visual means of assessing species diet composition (Clarke 1993). All multivariate analyses were conducted with Primer v-6 software.

3. Results

Stable isotope analysis revealed that species were generally ordered along expected trophic gradients based on probable carbon source and trophic position. As previously noted (see Methods *Stable isotope analysis*), zooplankton were the most $\delta^{13}C$-depleted invertebrate group at -20.381 ‰ ± 0.483 (SD) and moon snails were the most enriched at -15.383 ‰ ± 0.307 (Fig 2). Other invertebrate $\delta^{13}C$ values described a continuum between the moon snail and zooplankton isotopic end-members, indicating an integration of pelagic and benthic pathways among the lower trophic levels. Finfish $\delta^{13}C$ values were arrayed across an interval of approximately 2.5 ‰, half the total range measured among the invertebrates. Two pelagic species, Atlantic butterfish (*Peprilus triacanthus*) and striped anchovy (*Anchoa hepsetus*), were the most $\delta^{13}C$-depleted of the fishes with average $\delta^{13}C$ values of -18.756 ‰ ±

Fig 3 Mean and SD of δ^{15}N values for representative samples of 17 species of finfish and 8 invertebrate categories from Maryland's ICS (2007-2008). See Fig 2 for full species names and Table 1 for invertebrate category composition.
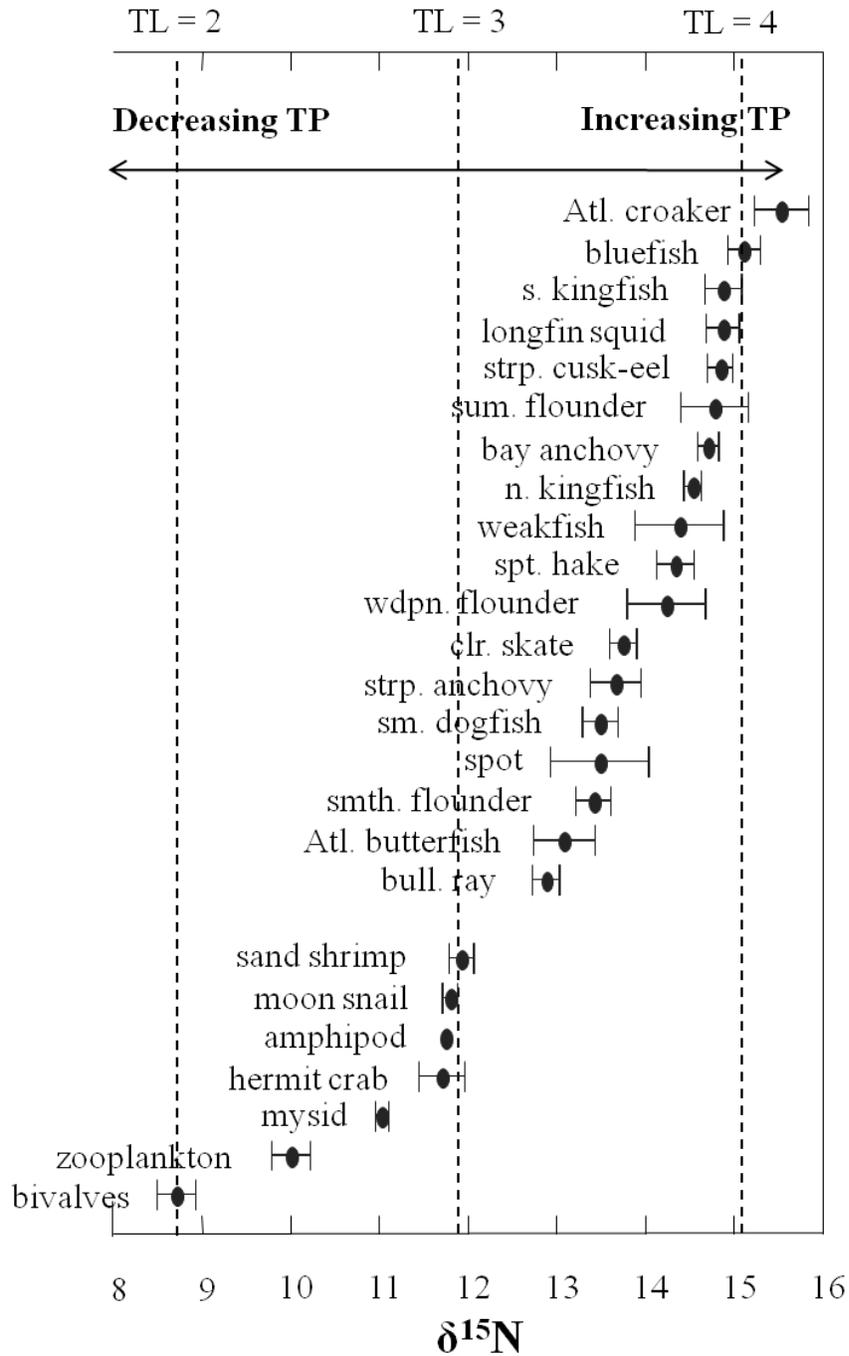
0.390 and -18.739 ‰ ± 0.326, respectively. Conversely, the demersal smooth dogfish (*Mustelus canis*, -16.136 ‰ ± 0.408) and epibenthic bullnose ray (*Myliobatis freminvillii*, -16.616 ‰ ± 0.480) displayed the most enriched finfish δ^{13}C values.

Bivalves, at 8.707 ‰ ± 0.376, were the most δ^{15}N-depleted of all the organisms analyzed; zooplankton followed with an average δ^{15}N = 9.999 ‰ ± 0.476 (Fig 3). Inshore longfin squid (*Loligo pealei*) had the highest δ^{15}N value of the invertebrates at 14.872 ‰ ± 0.423, comparable to many finfish species and commensurate with its predatory trophic ecology (Jacobson 2005). Despite a large body size, bullnose ray had the most depleted-N signature of the finfish at 12.880 ‰ ± 0.718; whereas the much smaller, pelagic anchovy spp. were intermediate at 14.706 ‰ ± 0.665 (bay anchovy) and 13.665 ‰ ± 0.697 (striped anchovy). Atlantic croaker (*Micropogonias undulatus*) and bluefish (*Pomatomus saltatrix*) were the most enriched in δ^{15}N, with δ^{15}N = 15.532 ‰ ± 0.681 and 15.112 ‰ ± 0.889, respectively. Excluding squid, the invertebrates and finfish measured in this study spanned almost exactly 1 trophic position each: from primary to secondary consumers among invertebrates (TP = 2–3), and mid-trophic position secondary consumers to tertiary consumers among the finfish (TP = 3.2–4.2).

Mean δ^{13}C and δ^{15}N values differed significantly among pelagic, demersal, and epi-benthic functional groups (δ^{13}C: $F_{2, 190}$ = 57.84, p < 0.001; δ^{15}N: $F_{2, 190}$ = 13.44, p < 0.001). Delta-^{13}C was significantly more depleted (Tukey HSD, p < 0.001) in the pelagic group (-18.345 ‰ ± 0.094 [SEM]) than the demersal (-17.026

‰ ± 0.107) and epibenthic (-17.087 ‰ ± 0.094) groups. There was no difference

between demersal and epibenthic $\delta^{13}C$ values. Delta-^{15}N did not vary between the

pelagic (14.566 ‰ ± 0.124) and demersal groups (14.298 ‰ ± 0.148), but was

significantly ($p \leq 0.001$) more depleted in the epibenthic group (13.644 ‰ ± 0.128).

There was a significant, positive linear relationship ($r = 0.66$, $F_{1, 191} = 144.46$,

$p < 0.001$) between $\delta^{13}C$ and $\log_{10}$ total length of finfish (Fig 4), indicating an

increasing enriched carbon signature with size. Body lengths ranged from 22 mm

(Atl. butterfish, pelagic) to 1,150 mm (bullnose ray, epibenthic) with mean functional

group lengths of 108 mm, 241 mm, and 376 mm for the pelagic, demersal, and

epibenthic groups respectively. The relationship between $\delta^{15}N$ and $\log_{10}$ length was

dome-shaped, with a quadratic polynomial function ($r = 0.37$, $F_{2, 190} = 16.98$, $p <$

0.001) explaining more variance than simple positive or negative linear models.

Measured $\delta^{13}C$ values ranged from -20.427 ‰ (bay anchovy, pelagic) to -15.118 ‰

(summer flounder, epibenthic) and $\delta^{15}N$ ranged from 16.835 ‰ (bluefish, pelagic) to

11.432 ‰ (bullnose ray, epibenthic).

3.1 Benthic-pelagic coupling

Among pelagic species, pelagic trophic sources were more important to younger (i.e.,

smaller fish) than older and larger individuals. Age-1+ bluefish BP_{SI} (0.75 ± 0.19)

was significantly higher than age-0 bluefish BP_{SI} (0.46 ± 0.13), representing a greater

Fig 4 Measured $\delta^{13}C$ and $\delta^{15}N$ ratios relative to body size (total length mm) for 17 finfish species from the Delmarva inner continental shelf. Species are coded as functional groups defined by vertical habitat preference in the water column. Linear ($\delta^{13}C$) and polynomial ($\delta^{15}N$) functions fit to $\log_{10}$ length data are shown to highlight trends in the data.
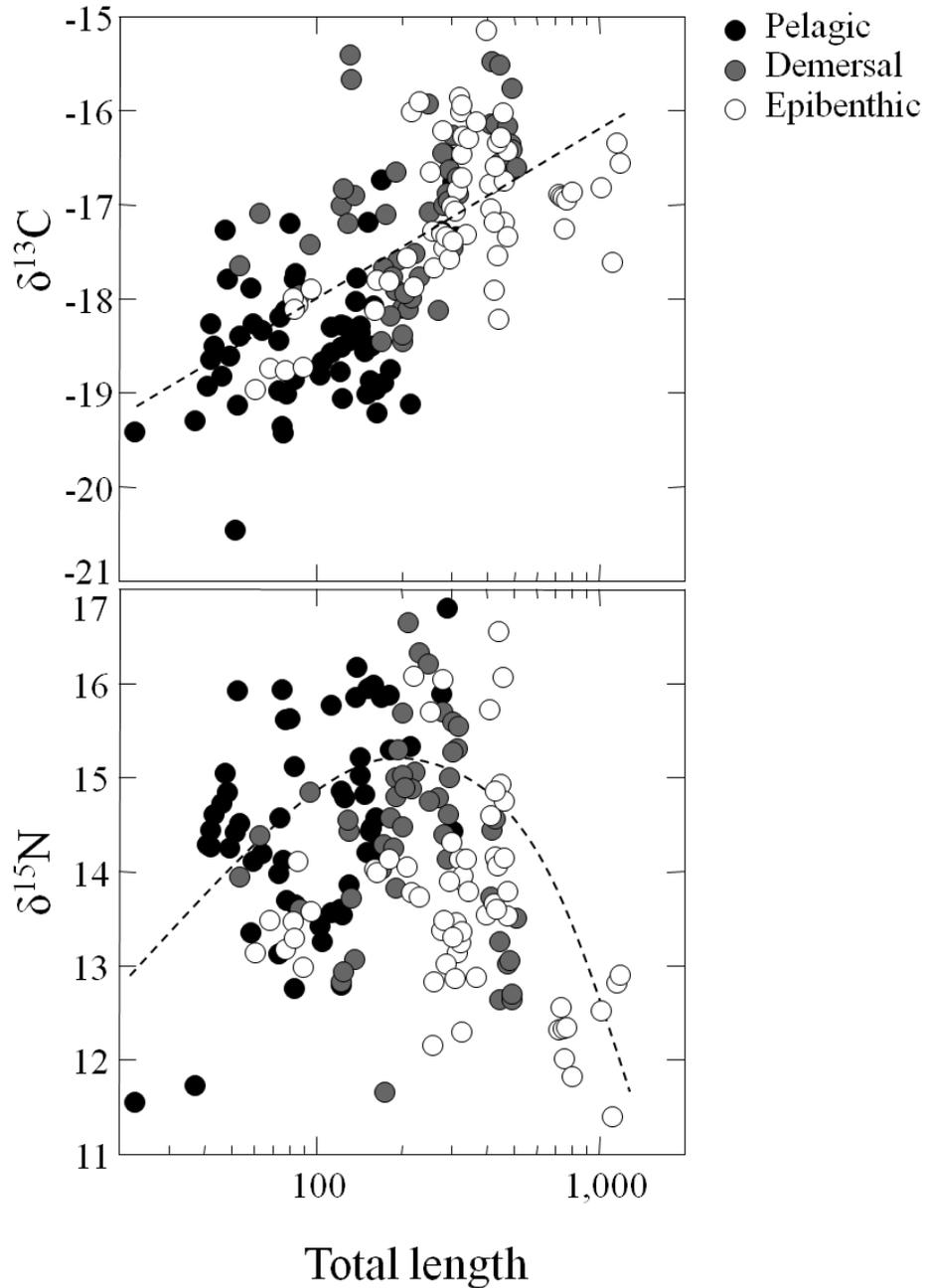
Table 2 Proportion of diet derived from benthic versus pelagic C sources (BP$_{SI}$ [SD]) for each species age class (0 = age-0, 1 = age-1+) from the inner continental shelf. Results of one-sample *t*-tests comparing BP$_{SI}$ among species age classes estimates are shown. Bolded values are significant at $p = 0.05$, * Spot biologically significant at $p = 0.06$. See Fig 2 for full species names.

Habitat	Species	BP$_{SI}$ 0	1	*t*	*df*	*p*
Pelagic	str. anchovy	0.34 (0.02)	0.41 (0.08)	1.45	2.18	0.27
	bay anchovy	0.43 (0.14)	0.48 (0.14)	0.83	20.30	0.42
	Atl. butterfish	0.33 (0.13)	0.40 (0.03)	0.91	2.09	0.45
	bluefish	**0.46 (0.13)**	**0.75 (0.19)**	**2.62**	**4.49**	**0.05**
Demersal	Atl. croaker	-	0.59 (0.10)	-	-	-
	str. cusk-eel	-	0.53 (0.06)	-	-	-
	sm. dogfish	0.90 (0.08)	-	-	-	-
	spot	0.94 (0.15)	0.58 (0.16)	-2.90	2.97	0.06*
	spt. hake	-	0.62 (0.10)	-	-	-
	weakfish	0.70 (0.10)	0.70 (0.19)	0.31	5.45	0.77
	s. kingfish	**0.65 (0.05)**	**0.83 (0.05)**	**4.69**	**5.00**	**0.005**
	n. kingfish	0.69 (0.10)	0.74 (0.02)	0.55	1.03	0.68
Epibenthic	sum. flounder	0.63 (0.17)	0.83 (0.23)	1.46	7.82	0.18
	wnpn. flounder	0.53 (0.02)	0.77 (0.14)	2.72	2.04	0.11
	smth. flounder	0.40 (0.07)	-	-	-	-
	clr. skate	0.68 (0.09)	0.73 (0.10)	0.87	21.35	0.39
	bull. ray	**0.86 (0.09)**	**0.75 (0.07)**	**-3.23**	**16.09**	**0.005**

contribution of relatively enriched C to the diet of older bluefish (Table 2). There were no significant differences in BP_{SI} between age classes of striped anchovy or Atlantic butterfish. Among demersal species, age-dependent changes in BP_{SI} varied in direction. Spot BP_{SI} declined from 0.94 (0.15) to 0.58 (0.16) from age-0 to age-1+ ($p = 0.06$); whereas southern kingfish BP_{SI} increased from 0.65 (0.05) to 0.83 (0.05) with age (Table 2). With the exception of bullnose ray, which decreased in BP_{SI} with age (Table 2), the contribution of benthic pathways generally increased or remained stable with increased age and size of epibenthic species.

The strength of benthic-pelagic coupling was significantly different ($F_{2,190}$ = 46.91, $p < 0.001$) across functional groups. Post hoc pair-wise comparisons identified the pelagic group as a significant minimum (pelagic < demersal = epibenthic groups, Tukey HSD, $p < 0.001$), with $BP_{SI} = 0.46 \pm 0.16$ (SD). The contribution of benthic trophic pathways increased to 0.72 ± 0.16 and 0.71 ± 0.16 (BP_{SI}) for demersal and epibenthic functional groups. Pair-wise tests between demersal and epibenthic groups were not significant.

IsoSource models indicated that the contribution of benthic carbon sources increased from age-0 to age-1+ for bay anchovy, weakfish and summer flounder (Fig 5). All models were successfully run with a proportion increment change of 1% and final convergence tolerance of 0.01 ‰. For bay anchovy, feasible contributions of benthic prey sources, as represented by sand shrimp and moon snails, contributed slightly more than pelagic prey (i.e., zooplankton, mysids) to both age classes

Fig 5 IsoSource estimated feasible average prey contributions to consumer species (bay anchovy, weakfish, summer flounder [sum. flounder]) $\delta^{13}C$ values from the inner continental shelf. Representative prey categories are labeled as follows: Zoo = zooplankton, Mys = mysid shrimp, Shr = sand shrimp, Sna = moon snails, B-0 = age-0 bay anchovy. Prey species for each consumer age class are ordered from left to right in terms of their association with pelagic versus benthic food webs. Error bars are -1 SD.
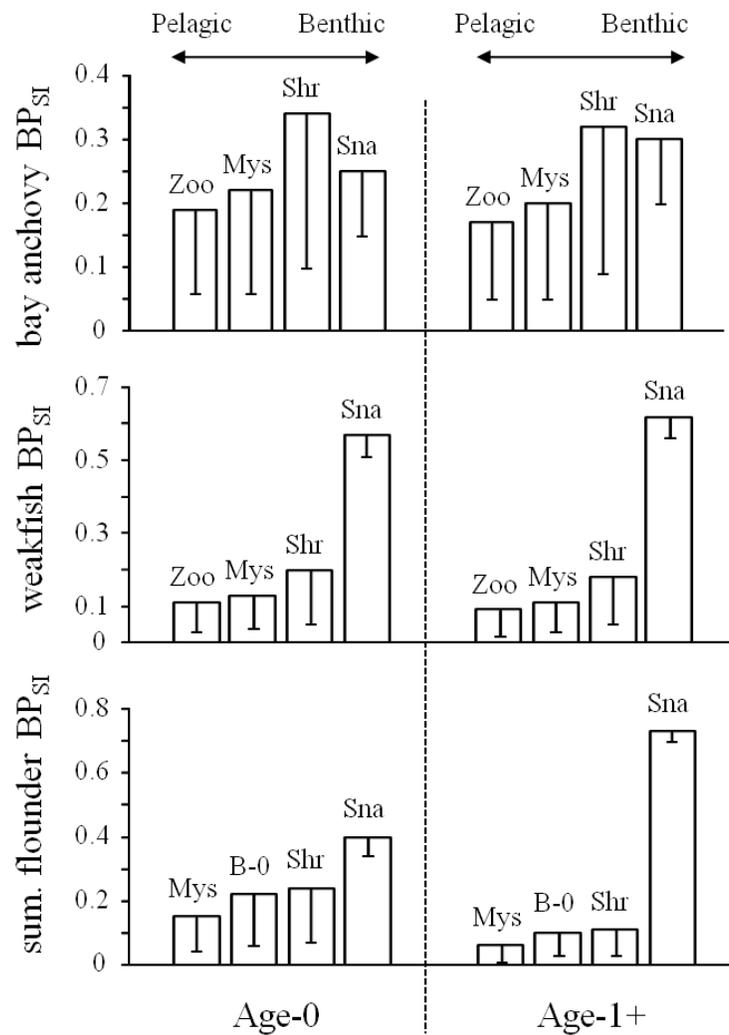
(proportion benthic contribution: age-0 = 0.56 ± 0.02 [SEM]; age-1+ = 0.60 ± 0.02). A significant increase in the proportional contribution of moon snails (age-0 = 0.22 ± 0.14, age-1+ = 0.28 ± 0.09, Bonferroni-adjusted p = 0.03) suggests greater benthic influence in age-1+ bay anchovy. Weakfish and summer flounder models showed very similar trends; average prey contributions to age-0 fish of both species were generally evenly distributed among pelagic and benthic sources. The average contribution of benthic C, as indexed by the proportion contributed by moon snails, increased dramatically for older weakfish (age-0 = 0.20 ± 0.10, age-1+ = 0.57 ± 0.05, Bonferroni-adjusted p < 0.001) and summer flounder (age-0 = 0.33 ± 0.08, age-1+ = 0.67 ± 0.04, Bonferroni-adjusted p < 0.001), while the average estimated contributions of other prey sources show consistent declines (Fig 5).

Benthic prey contribution to diet composition was highly variable among individuals and only a single species showed significant trends in BP_{Diet} between depth strata (Table 3). Qualitatively, BP_{Diet} of pelagic species increased (anchovy spp., Atlantic butterfish) or remained stable (bluefish) with increased depth. Diet of the demersal group also showed a general increase in the proportion of benthic prey biomass in deep habitats; spot BP_{Diet} in particular increased from 0.42 ± 0.32 (SD) to 0.93 ± 0.23 (Table 3). Conversely, BP_{Diet} among species in the epibenthic group declined, with a qualitative reduction in group-level. This pattern was most apparent in summer and windowpane flounder, which declined in average BP_{Diet} from 0.40 to 0.27, and 0.10 to 0.01, respectively.

3.2 Multivariate diet analysis

Cluster analysis identified six significant (SIMPROF, $\alpha = 0.05$) multispecies clusters. An nMDS ordination of the species similarities illustrated the partitioning of species and age classes based on a continuum of pelagic and benthic prey resources (Fig 6). Atlantic butterfish, bay anchovy, striped anchovy, age-0 weakfish and age-1+ spot occupied a zooplankton/benthivore cluster with zooplankton contributing 54%, mysids 19%, and macrobenthos (e.g., amphipods [incl. gammarid and tubiculous spp.], sandshrimp) 9% of the total within cluster Bray-Curtis similarity (Sim_{BC}). Windowpane flounder, age-0 summer flounder, and age-1+ weakfish formed a second group that also relied heavily on pelagic food webs consisting of mysid ($Sim_{BC} = 87\%$) and pelagic forage fish prey (incl. *Anchoa* spp., Atherinidae, and Clupeidae; $Sim_{BC} = 5\%$). The final pelagic cluster included both age classes of the highly piscivorous bluefish, which foraged heavily on pelagic forage fish ($Sim_{BC} = 86\%$) and other fish prey (unID fish; $Sim_{BC} = 8\%$).

The remaining three species clusters were characterized by benthic diet compositions. Smallmouth flounder, Atlantic croaker, spotted hake, southern kingfish, and northern kingfish diets were composed primarily of macrobenthos ($Sim_{BC} = 48\%$), worm-like prey (e.g., polychaetes, nemerteans; $Sim_{BC} = 34\%$), and molluscs (incl. bivalves and gastropods; $Sim_{BC} = 10\%$). The remaining two species clusters were composed of the three elasmobranchs included in the analysis. Clearnose skate and smooth dogfish formed one cluster, with diets dominated by decapod crabs, molluscs, and demersal fish (incl. Gadidae, Sciaenidae, and Triglidae;

Fig 6 Non-metric multidimensional scaling plot of species diet composition by age

class. Species are coded according to significant cluster membership (clusters 1-6) as

follows: open triangles (cluster 1) = age-0/ age-1+ bay and striped anchovy, age-

0/age-1+ Atl. butterfish, age-0 weakfish, age-1+ spot; shaded triangles (cluster 2) =

age-0/age-1+ windowpane flounder, age-0 summer flounder, age-1 weakfish; solid

circles (cluster 3) = age-0/age-1+ bluefish; solid squares = age-0/age-1+ smallmouth

flounder, age-0/age-1+ southern and northern kingfish, age-1+ Atl. croaker, age-1+

spotted hake; shaded diamonds (cluster 5) = subadult/adult clearnose skate, age-0

smooth dogfish; open circles (cluster 6) = age-0/age-1+ bullnose ray.
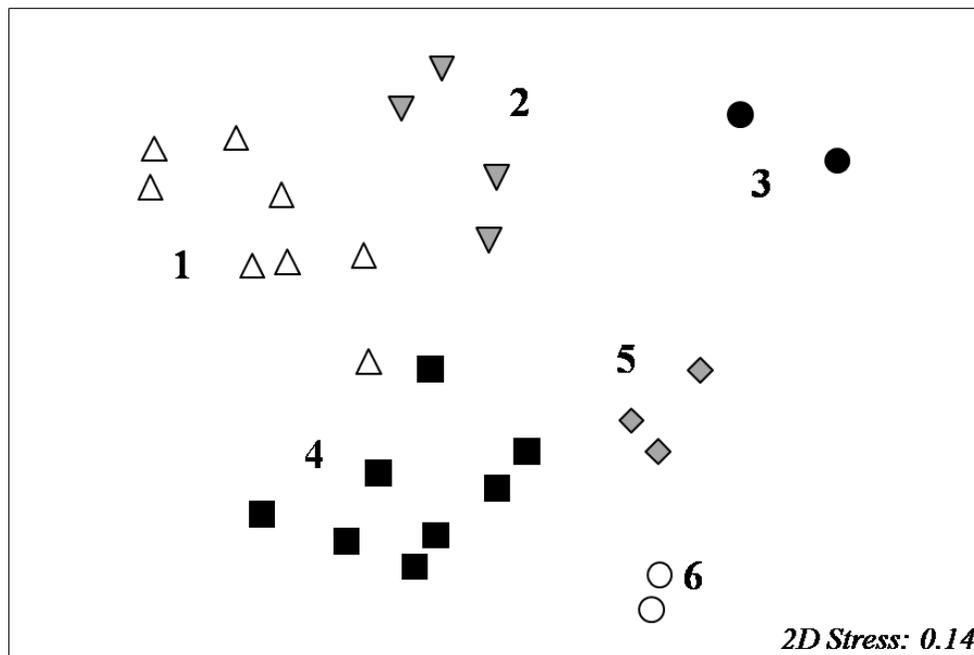
Table 3 Proportion of diet derived from benthic versus pelagic prey sources (BP$_{Diet}$) for each species (mean [SD]) and functional group (mean [SEM]) from shoal (< 10 m) and deep (≥ 10 m) depth strata from the inner continental shelf. Bolded values are significantly different at $p = 0.05$ (two-sample t-tests). See Fig 2 for full species names.

Habitat	Species	Depth	
		Shoal	Deep
Pelagic	str. anchovy	0.26 (0.31)	0.39 (0.25)
	bay anchovy	0.22 (0.32)	0.30 (0.31)
	Atl. butterfish	0.12 (0.34)	0.27 (0.47)
	Bluefish	0.06 (0.22)	0.05 (0.22)
Demersal	Atl. croaker	1.00 (0)	0.95 (0.13)
	str. cusk-eel	0.93 (0.15)	1.00 (0)
	sm. dogfish	0.99 (0.04)	1.00 (0)
	Spot	**0.42 (0.32)**	**0.93 (0.23)**
	spt. Hake	0.75 (0.42)	-
	Weakfish	0.29 (0.40)	0.34 (0.42)
	s. kingfish	0.98 (0.04)	1.00 (<0.01)
	n. kingfish	1.00 (<0.01)	-
Epibenthic	sum. flounder	0.40 (0.49)	0.27 (0.41)
	wnpn. flounder	0.10 (0.30)	0.01 (0.03)
	smth. flounder	1.00 (0)	-
	clr. Skate	1.00 (0.01)	0.95 (0.14)
	bull. Ray	1.00 (0)	1.00 (0)
Group	Pelagic	0.17 (0.05)	0.25 (0.02)
	Demersal	0.80 (0.10)	0.87 (0.11)
	Epibenthic	0.70 (0.19)	0.56 (0.25)

Sim_{BC} = 51, 48, and 10%, respectively). Finally, both age classes of bullnose ray were almost exclusively molluscivores – the mollusc prey category contributed 99% of Sim_{BC}.

4. Discussion

4.1 Benthic-pelagic coupling

The strength of trophic coupling was closely linked to trophic position; species or age classes displaying enriched $\delta^{15}N$ (i.e., higher trophic position; Post 2002) also exhibited intermediate $\delta^{13}C$ values ($r = 0.66$, $F_{2,14} = 5.47$, $p = 0.02$; Fig 7). Similar structuring has been observed in lacustrine fish assemblages (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002). Rooney et al. (2006) recently proposed the phenomenon as an inherent structure in estuarine, marine, and terrestrial food webs; whereby upper trophic level consumers convey stability to food webs by coupling trophic pathways that respond to environmental variability at different rates (viz. fast [pelagic] and slow [benthic] energy channels; sensu Rooney et al. 2006). This pattern was consistent across functional groups in the ICS; yet it is interesting to note that specific groups contributed differently to the form of the relationship (Fig 7). Demersal consumer species (e.g., Atl. croaker, striped cusk-eel *Ophidion marginatum*, kingfish spp.) predominated near the center of the curve, suggesting the production dynamics of these species are intimately linked to the integration of pelagic and benthic trophic pathways. If true, perturbations in the dynamics of this particular functional group could disproportionately influence

Fig 7 Two end-member model estimates of the proportion of benthic to pelagic C in muscle tissue (primary x-axis: BP_{SI}; secondary x-axis: $\delta^{13}C$ values) and $\delta^{15}N$ for 17 finfish species from the Delmarva inner continental shelf. Species are coded as functional groups defined by vertical habitat preference in the water column. See Fig 2 for full species names. Least-squares fit of polynomial function to BP_{SI}-$\delta^{15}N$ data provided to highlight trend in the data.
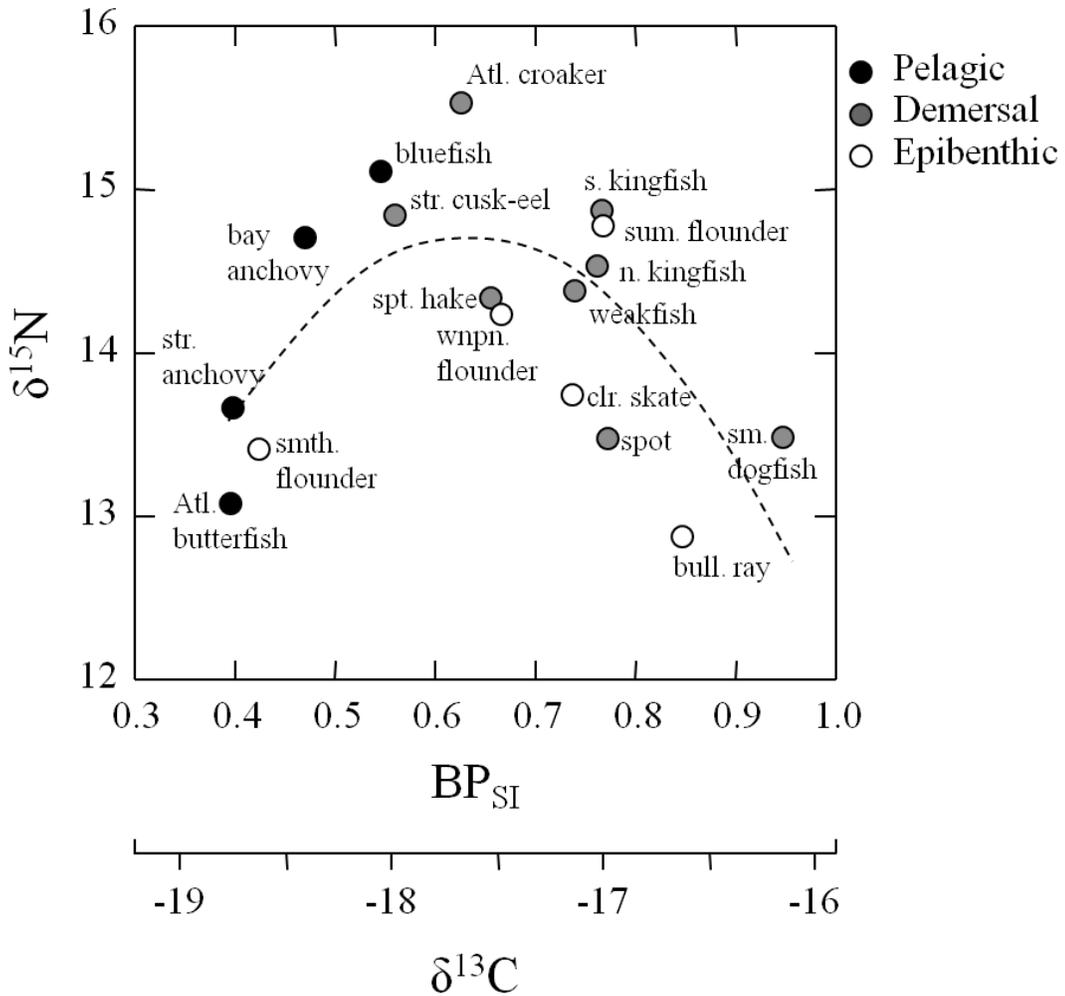
energy flow among other food web compartments by altering the strength of benthic-pelagic coupling (Vander Zanden and Vadeboncoeur 2002).

Evidence from SI data confirmed that all species included in this study relied on pelagic production pathways to some extent. This was true even of species such as clearnose skate and bullnose ray that are morphologically constrained to feeding at or below the sediment-water interface. The water column of the ICS is typically well-mixed despite episodic stratification (Fig 8, and see Epifanio and Garvine 2001) and the sedimentation of relatively undegraded phytoplankton has been shown to be high in similar habitats (Koseff et al. 1993) due to advective deposition via vertical mixing and the absence of a strong pycnocline hindering sinking rates. These physical attributes lead to benthic secondary production that derives a large fraction of its carbon directly from autotrophic pelagic sources, yielding an indirect pelagic-linkage for benthivorous consumers such as skates and rays. This process is evident in the intermediate δ^{13}C values of bivalves (Fig 2), which reflects carbon assimilation from both pelagic (suspension feeding) and benthic (deposit feeding) pathways.

Conversely, benthic food webs contributed an average of 48% of the carbon assimilated by pelagic species. Diet analysis substantiated the isotopic evidence; stomach contents of pelagic species included a benthic trophic component composed of prey such as amphipods, sand shrimp, mysids, and harpacticoid copepods. In coastal habitats, a substantial fraction of the benthic macro- and meiofauna exhibit diel vertical migration (DVM; Forward 1988; Garland et al. 2002) resulting in a large

Fig 8 Density profiles measured by CTD at representative shoal (<10m) and deep (>10m) trawl sites on the Delmarva inner continental shelf during August 2004-2005 and 2007-2008. Sharp density gradients and increased density at depth for shoal stations in 2007 & 2008 are evidence of episodic system stratification in response to climatic forcing (e.g., upwelling event in 2008, see 2008 conditions reported in Table 3, Chapter 5).
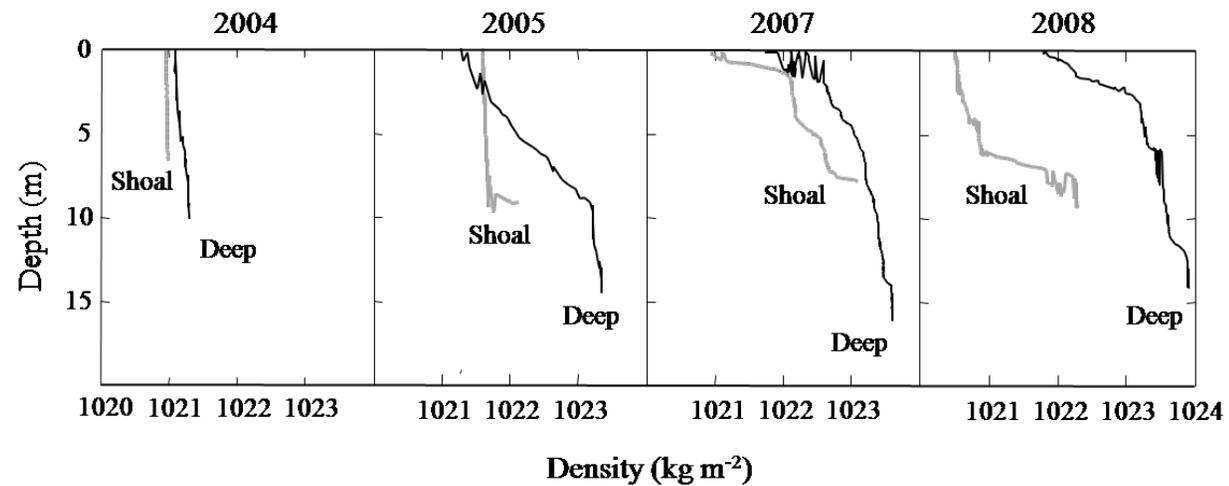
daily pulse of zoobenthic biomass to the pelagic realm. In addition, all of the pelagic

species included in this study associate with demersal habitats to some extent (i.e.,

because they were sampled by bottom trawl), providing an opportunity for

opportunistic foraging at or near the sediment surface. While the relative importance

of these feeding behaviors (i.e., DVM vs. bottom feeding forays) will vary by species,

both likely play a role in the delivery of benthic carbon to the pelagic consumer food

web.

Results from the diet analysis show mysid shrimp represent a dominant vector

for benthic-pelagic coupling in this food web. Data from ancillary sampling of lower

trophic levels during the course of this study indicate that *Neomysis americana*, the

most abundant mysid species in the study area (Williams et al. 1974), displays strong

DVM (Fig 9). Several recent reviews have argued that mysids act as important

modulators of nutrient and biomass flux between pelagic and benthic food webs

(Macquartmoulin and Maycas 1995; Jumars 2007), principally through daily forays

into the watercolumn to feed on suspended particulate matter followed by a return to

benthic refugia. Here, in addition to its importance to the diets of several demersal

and pelagic species, mysids formed a substantial fraction of the stomach contents

biomass of small flatfishes such as smallmouth, windowpane, and age-0 summer

flounder. For species such as flounder, vertically migrating and hyperbenthic mysids

presumably represent a primary pelagic carbon source for these otherwise

benthically-oriented predators. Other studies have noted the importance of mysids to

the diet of small flatfish (e.g., Burke 1995; Link et al. 2002; Latour et al. 2008) and

Fig 9 Total catch (N, primary y-axis) and density (secondary y-axis) of the mysid *Neomysis americana* as discretely sampled in the upper 50% and lower 50% water column (wc) by 1-m^2 Tucker trawl on Delmarva inner continental shelf during August 2007.
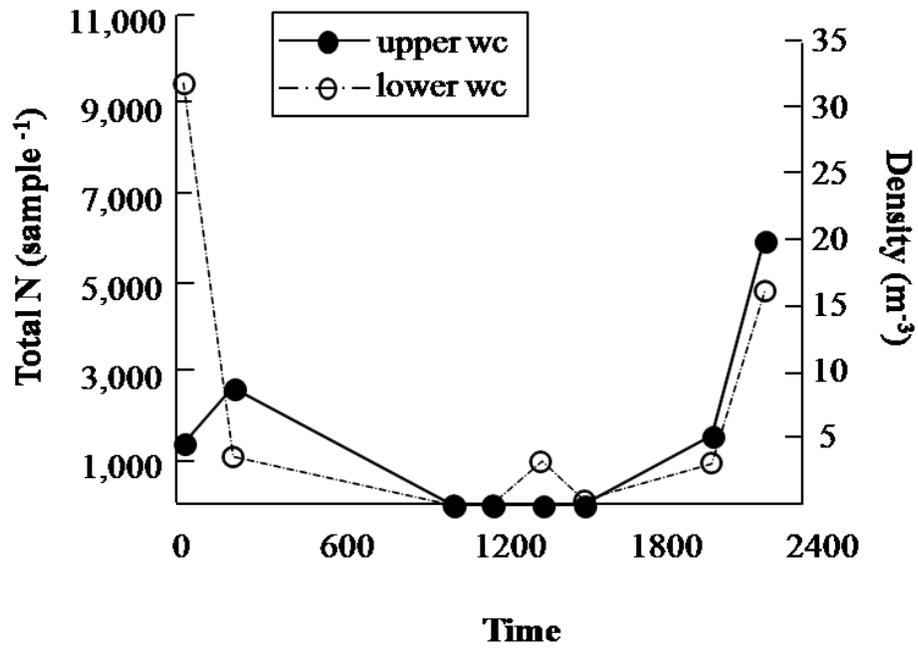
other finfishes (e.g., Link and Almeida 2000; Hartman et al. 2004; Nemerson and Able 2004; Marancik and Hare 2007) in proximal shelf and estuarine habitats. Many invertebrates (e.g., decapod shrimp, cephalopods, sand shrimp; Vovk 1985; Jumars 2007) also feed on mysids and it is likely that mysids play a pivotal role in ICS food web dynamics given the prevalence and biomass of these species observed in finfish stomachs. Quantification of mysid stock biomass in the ICS appears to be an important prerequisite to the creation of an accurate, representative food web model. A rigorous assessment of diel changes in mysid density and contemporaneous contribution to finfish diet is also needed to evaluate the availability of mysids relative to other prey, the electivity of consumer species, and the role of mysids in the production of economically valuable fishery species.

Results from this study are used to draw inferences regarding the trophic niche of some fishes that typically inhabitat the pelagic zone. However, the primary sampling gear used in this analysis was a large, demersal trawl. Because the demersal gear would have only captured those pelagic species when they were at or near the bottom (with the exception of the brief deployment and haul-back periods), it is possible that the collection method was a source of bias in determining trophic niche of pelagic species. Individuals of pelagic species vulnerable to the gear were those found near bottom. As a consequence the trophic niche of these particular pelagic individuals might have a benthic signal unlike the rest of the population. However, it is unlikely that there was a significant bias for several reasons. First, the BP coupling ratios were supported by stable isotope as well as stomach contents data, two metrics

that integrate diet over very different temporal scales. For a gear-bias in trophic niche estimate to occur, the pelagic individuals selected for analysis would need to display spatial foraging behavior that: 1) deviated from the species norm; and 2) was consistent over a sufficient period to allow isotopic equilibrium to the 'benthic-influenced' diet. In addition, there was no evidence of intra-specific niche partitioning within the ICS (stomach contents – this study) as has been observed in some fish species in lentic habitats (e.g., lake trout *Salvelinus namaycush*, threespine sticklebacks *Gasterosteus aculeatus*). Finally, pelagic species composed a substantial fraction of the total catch (Chapter 3, Appendix A). This suggests that a sizeable fraction of these species' populations were vulnerable to the trawl, possibly due to the 3.0-3.5 m height of the trawl headrope above the bottom (Chapter 2).

4.2 Ontogenetic and size-dependent patterns

Body size had an observable effect on the demersal food web structure: there was a tendency, albeit not statistically significant, for older age classes to incorporate a larger proportion of benthic carbon in their diet. This was true of pelagic, demersal, and epibenthic species, although the increase was not significant for most species. For several species, the lack of significance is likely due to small sample size. For example, estimates of mean BP_{SI} for summer and windowpane flounder suggest a >20% increase in benthic C assimilation; yet sample size was 3 per age class for these two species. If the observed patterns represent true ontogenetic niche shifts, increasing sample size should provide the statistical power to identify biologically significant differences between ages. Other species, such as weakfish, displayed

stable BP_{SI} between age classes despite changes in diet. This conservative isotopic response could result if the new prey were functionally equivalent integrators of pelagic and benthic carbon sources or if carbon fractionation dynamics were different for the new diet (McCutchan et al. 2003).

In this study, age-0 individuals substantially exceeded size-at-settlement (Able and Fahay 1998); therefore, observed isotopic and diet metrics should reflect an adopted juvenile foraging strategy rather than planktonic larval feeding. Among pelagic and some demersal species, older age classes appear to approach a trophic equilibrium in which equal amounts of carbon are assimilated from pelagic and benthic food webs. A potential mechanism underlying this pattern is ontogenetic or "life-history" (sensu Polis and Strong 1996) omnivory, which describes a developmental shift in trophic niche with omnivory defined as feeding at multiple trophic levels (Diehl 1993; Shurin et al. 2006). Juvenile fish are constrained to feed on prey within the scope set by gape dimensions (Gerking 1994; Scharf et al. 2000), detection and capture distances, and behavioral choices (e.g., predation-risk taking, Biro et al. 2003). In this habitat, these constraints appear to effectively limit the primary prey field to small zoobenthic organisms, many of which are directly subsidized by pelagic production (e.g., amphipods, mysids, sand shrimp; see above). Conversely, older (and bigger) fish are capable of exploiting larger, detritivorous prey such as penaeid shrimp, brachyuran crabs, and hermit crabs in addition to the smaller, vertically mobile crustaceans. The expansion of foraging opportunities for larger

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individuals enhances feeding across the trophic spectrum (Polis and Strong 1996) and promotes integration of multiple trophic pathways.

The dome-shaped response of δ^{15}N to body size was unexpected given that N fractionates by approximately 2-5‰ per trophic transfer (Pinnegar and Polunin 1999; Post 2002; McCutchan et al. 2003) and trophic position generally positively covaries with size (Cohen et al. 2003; Brose et al. 2006) although exceptions occur (e.g., basking and whale sharks). Bullnose ray and smooth dogfish were the largest species analyzed and also had two of the lowest average δ^{15}N signatures. This was particularly evident among age-1+ bullnose ray. The ontogenetic shift in isotopic niche of bullnose ray coincided with a transition from a diet heavily skewed toward carnivorous gastropods among age-0 fish, to a diet composed primarily of bivalves in the older age classes. This size-dependent progression from epibenthic to infaunal diet composition may reflect one or more of the following: 1) increased effective excavation depth with larger buccal volume (Higham et al. 2006); 2) ontogenetic 'tuning' of ampullary electrosensory systems from predator avoidance to prey detection (Tricas and Sisneros 2004); or 3) a shift in foraging habitat coinciding with higher bivalve densities. Older age classes of smooth dogfish were not available for a similar comparison but stomach contents of larger smooth dogfish (c. 860-1,250 mm) taken from the Virginia ICS (Gelsleichter et al. 1999) suggests a relatively unchanging trophic niche with increased size. Although several species of coastal and pelagic sharks were captured during the trawl survey, these were released and not available for SI or SC analysis. Had large piscivores such as sand tiger *Carcharias*

taurus, Atlantic sharpnose *Rhizoprionodon terraenovae*, sandbar *Carcharhinus plumbeus* and angel shark *Squatina dumeril* been included in this study, there likely would have been an increase in trophic position with size.

It is worth noting the high δ^{15}N of Atl. croaker, a species commonly associated with estuaries during the summer months, particularly as age-0 juveniles and yearlings (Hare and Able 2007). Despite the excavating foraging behavior often associated with this species, recent evidence has shown that larval and juvenile-stage fish can form a substantial portion of the diet of Atl. croaker in Chesapeake Bay (Nye 2008). The relatively high N signature of this species may also reflect recent foraging histories in proximal coastal lagoons or estuaries, habitats typified by enriched biogeochemistry relative to depleted coastal ocean conditions (Fry 2002). Emigration from local estuaries may also explain the relatively high observed δ^{15}N of the zooplanktivorous bay anchovy relative to known piscivores.

4.3 Depth and the inshore-offshore gradient

I found no significant evidence of pelagic and benthic decoupling across the depth gradient available in this study. Results were suggestive of a shift to benthic trophic pathways, yet the relatively narrow range of depths considered and horizontal (i.e., longitudinal) proximity of the shoal and deep strata likely factored into the non-significance of this analysis. Garrison and Link (2000) recently analyzed the trophic guild structure of the demersal finfish assemblage(s) spanning the contiguous Northeast US continental shelf ecosystem (Nova Scotia–Cape Hatteras, NC), and

reported size-structured guild membership for several species identified in this study. For example, they identified weakfish < 260 mm and summer flounder 210-400 mm as occupying a piscivorous niche on the continental shelf; yet these size classes overlapped the age-0 and age-1+ length ranges used in my study. This difference in size classification hinders direct comparisons between the Garrison and Link study and my results that show age-0 individuals for both species feed primarily on mysids prior to an ontogenetic niche shift to piscivory at older ages (Appendix B). In addition to size-based differences, broad geographic area, long temporal integration (30+ years), and aggregation of samples across the width of the continental shelf make direct comparisons of my results to those of previous studies difficult. Still, global evidence from continental shelf habitats supports the initial hypothesis that particulate rain is increasingly composed of refractory carbonaceous material of low nutrient value with depth (e.g., Danovaro et al. 1998). This pattern is consistent with a dampening of direct energy/biomass transfers between pelagic and benthic trophic pathways (i.e., unmediated by microbial mineralization) and the inclusion of a wider depth or longitudinal gradient will potentially clarify the patterns suggested in this study.

In partially-mixed or salt-wedge estuaries, circulation dynamics and climatological forcings modulate the seasonal strength (or presence) of vertical stratification (Brown et al. 2006) and facilitate the dominance of certain phytoplankton communities (e.g., Chesapeake Bay: winter – diatom, summer – dinoflagellate/nano-/picoplankton; Patten et al. 1963, Harding et al. 1999). During

summer months, stratification of these estuaries is enhanced, phytoplankton

sedimentation inhibited (e.g., Gerritsen et al. 1994), and the overall availability of

non-degraded phytoplankton biomass to demersal food webs declines. The seasonal

shift from diatom to smaller-bodied phytoplankton assemblages would further reduce

sedimentation of viable primary producers due to the greater motility of many

phytoplankton relative to diatoms (e.g., dinoflagellates, Kamykowski et al. 1992) and

slower sinking rates of smaller particulates (Johnson and Smith 1986). The

synergistic effects of seasonal stratification, phytoplankton assemblage phenologies,

and other factors (e.g., zooplankton grazing activity, Malone et al. 1988) are

responsible for the predominant summer flux of organic detritus (instead of viable

phytoplankton cells) from pelagic to demersal food webs (Malone et al. 1988).

Additionally, sharp discontinuities in watercolumn salinity can inhibit diel vertical

migration in zooplankton (Grindley 1966), potentially shifting primary nutrition

sources of vertically mobile zooplankton away from viable phytoplankton and

disrupting the delivery of pelagic productivity to demersal food webs. All these

processes, physical, biological and ecological, would serve to reduce the summertime

importance of pelagic food webs to estuarine demersal fish assemblages relative to

ICS assemblages.

4.4 Conclusions and Future directions

The Delmarva ICS is an important nursery habitat and foraging ground for a diverse

assemblage of seasonally transient, temperate finfish species (Chapter 2); the current

analysis provides strong evidence that the demersal component of the ICS assemblage

is heavily subsidized by the productivity of the overlying pelagic food web. Through a combination of stable isotope and stomach contents analysis, I have shown that the relative importance of pelagic pathways varies depending on ontogenetic stage, species and vertical niche within the water column. There was equivocal evidence of increased decoupling of pelagic and benthic food webs with increasing depth, potentially due to the narrow depth gradient currently available for analysis. Across species, there was evidence of trophic size-structuring and partitioning of prey resources although similarities in prey consumed did not necessarily follow the vertical habitat affinities of consumers. While it is clear that pelagic food webs play an important role in demersal finfish trophodynamics in the ICS, future efforts to extend this analysis to offshore shelf habitats will provide valuable information on the spatial dynamics of benthic-pelagic coupling, particularly for juvenile life stages.

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Chapter 6 Appendices

Appendix A Size-range (total length mm) of species age classes for inner continental shelf stable isotope and diet composition analysis (SI = stable isotope, SC = stomach contents; subcategories: 0 = age-0, 1 = age-1+, S = shoal [< 10-m depth], D = deep [≥10-m depth]).

Order / species	Common name	SI data		SC data			
		0	1	0	1	S	D
Carcharhiniformes							
Mustelus canis	smooth dogfish	400-494	-	419-519	1,092	465-494	419-1,092
Clupeiformes							
Anchoa mitchilli	bay anchovy	40-58	62-109	36-68	70-109	36-109	48-85
Anchoa hepsetus	striped anchovy	71-81	120-127	40-86	92-136	40-128	71-136
Gadiformes							
Urophycis regia	spotted hake	-	168-200	-	141-218	171	141-218
Myliobatiformes							
Myliobatis freminvillei	bullnose ray	305-356	701-1,150	305-497	515-1,150	315-721	305-1,150
Ophidiiformes							
Ophidion marginatum	striped cusk-eel	-	177-211	-	120-230	129-151	120-230
Perciformes							
Peprilus triacanthus	Atlantic butterfish	22-41	100-119	22-81	91-200	41-182	22-200
Pomatomus saltatrix	bluefish	119-208	270-303	42-245	250-347	50-347	42-336
Cynoscion regalis	weakfish	85-133	217-271	38-149	150-297	38-271	51-297
Leiostomus xanthurus	spot	121-129	164-195	119	121-211	121-211	119-205
Menticirrhus americanus	southern kingfish	52-92	288-305	52-197	201-345	52-345	120-319
Menticirrhus saxatilis	northern kingfish	125-125	244-284	125	215-296	284-284	125-296

Micropogonias undulatus	Atlantic croaker	-	185-309	-	185-334	185-334	205-309
Pleuronectiformes							
Etropus microstomus	smallmouth flounder	59-87	-	59-76	81-147	-	59-147
Paralichthys dentatus	summer flounder	156-215	386-459	134-260	272-569	134-565	151-569
Scophthalmus aquosus	windowpane flounder	80-93	203-271	54-189	190-291	72-291	54-268
Rajiformes							
Raja eglanteria	clearnose skate	224-330	401-460	270-398	401-471	296-449	270-471

Appendix B Total biomass (g) per prey category [a] per species and age class from stomach contents analysis conducted on species captured during Aug-Sept 2004-2008 from the Delmarva inner continental shelf. Species at the bottom of the table for which Latin names alone are provided were analyzed in the laboratory but not included in statistical analyses due to small sample size.

Species / Age	Vertebrate prey					Invertebrate prey													Algae
	CarFi	DemFi	FlaFi	PelFi	unFis	Amphi	Cepha	Cteno	DecCr	DecSh	HerCr	MacCr	MacOt	Mollu	Mysid	Plank	Worm	Arthr	MacAl
striped anchovy																			
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	<0.01	0.02	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0.07	0	0	0.11	0.11	0	0.02	0
bay anchovy																			
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0.12	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.04	0.01	0	0.02	0
weakfish																			
0	0.02	0.15	0.03	0.64	0.02	0	0	0	0	0	0	0.87	0	0	1.76	0.7	0	0.08	0
1	0	0.71	0.11	23.47	1.02	0	0	0	0.01	0.32	0	0.8	0	0.05	9.21	0.14	1.16	0.99	0
smallmouth flounder																			
0	0	0	0	0	0	0.01	0	0	0	0	0	0.02	0	0	0	0	0.01	0	0
1	0	0	0	0	0	0.05	0	0	0.03	0	0.15	0.4	0	0.05	0	0	0.28	0	0
spot																			
1	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0.41	0.28	0.29	0.3	0	0.01
southern kingfish																			
0	0	0	0	0	0	0	0	0	0	0	0	1.21	0	0.2	0	0	1.15	0	0
1	0	0	0.05	0.21	0	0.37	0	0	1.98	5.32	2.18	2.52	0.27	5.27	0.01	0.01	4.26	0.03	0

Species / Age	CarFi	DemFi	FlaFi	PelFi	unFis	Amphi	Cepha	Cteno	DecCr	DecSh	HerCr	MacCr	MacOt	Mollu	Mysid	Plank	Worm	Arthr	MacAl
Atlantic croaker																			
1	0	0	0	0	0	0	0.93	0	1.61	0	0.04	0.34	0	12.48	0.08	0	0.74	0.19	0
smooth dogfish																			
0	0	7.65	0.02	0.04	0.4	0	0.2	0	26.28	4.79	13.09	0.2	0	8.69	0	0	2.5	12.11	0.54
1	0	0	0	0	0	0	0	0	33.75	0	0	0	0	0	0	0	0	0.88	0
bullnose ray																			
0	0	0	0	0	0.01	0	0	0	0	0	0.12	0.01	0	210.99	0	0	0	0.01	0.06
1	0	12.38	0	0	0	0	0	0	0.59	0	0	0	0	186.05	0	0	0.65	0	0.29
striped cusk-eel																			
1	0	0.01	0.1	0.17	0.02	0	0	0	0.21	0.62	0	1.47	0	0.26	0.04	0	0	0.01	0
summer flounder																			
0	0	0	0	3.07	0	0	0	0	0.03	0.78	0	0.08	0	0	6.87	0.07	0	0	0
1	3.66	29.1	2.39	4.6	0.52	0	41.01	0	6.5	0.41	0	0	0	0	0.24	0	0	0	0
Atlantic butterfish																			
0	0	0	0	0	0	0	0	0.04	0	0	0	0	0	0	0	0.01	0	0.01	0
1	0	0	0	0	0	0	0	0.22	0	0	0	0	0	0	0	0.01	0	0.11	0
bluefish																			
0	0	1.63	0	166.95	5.28	0	3.1	0	0	0	0	0	0	0	0.01	0	0	0.01	0.01
1	4.7	23.1	0	139.15	7.29	0	3.04	0	0	0	0	0	0	0	0	0	0	0	0
clearnose skate																			
0	0	18.64	0	0.25	0.18	0.17	0	0	34.78	0.68	5.74	0.69	0	6.31	0.02	0	0.42	1.26	0
1	0	39.92	1.53	2.6	1.5	0	0	0	21.06	1.99	0.47	0	0	2.15	0	0	0.29	1.51	0

Species / Age																		
windowpane flounder																		
0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0	7.08	2.08	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.71	0	0	0	0

Species / Age	CarFi	DemFi	FlaFi	PelFi	unFis	Amphi	Cepha	Cteno	DecCr	DecSh	HerCr	MacCr	MacOt	Mollu	Mysid	Plank	Worm	Arthr	MacAl
spotted hake																			
1	0	0	0	0	0	0	0	0	0	0	0.24	2.21	0	0.5	0.87	0	0.04	0.01	0
Astroscopus guttatus	0	40.34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chilomycterus schoepfi	0	0	0	0	0	0	0	0	1.96	0	0.22	0	0	1.53	0	0	0	0	0
Dasyatis americana	0	0	0	0	0	0.61	0	0	0	0	0	0.82	0	0	0	0	0	0	0
Dasyatis centroura	0	0	0	0	0	0	0	0	2.12	0	0.29	0.31	0	0.21	0	0	21.39	0.14	0
Dasyatis sayi	0	0	0	2.93	0	0	0	0	0	0	0	1.07	0	0	0	0	10.76	0	0
Gymnura altavela	0	3.3	0	0	0.11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnura micrura	0	0	0	0	0.15	0	0	0	0	0	0	0	0	0.01	0	0	0.01	0	0
Rhinoptera bonasus	0	0	0	0	0	0	0	0	0	0	0	0	0	2.06	0	0	0	0	0

[a] Prey categories

MacC = Macrobenthic crustaceans: sand shrimp *Crangon septemspinosa*, gammarid-like amphipod (incl. *Gammarus* spp., *Haustorius* spp., unID Gammaridae) tubiculous amphipod *Corophium* and similar spp., isopod unID Isopoda, unID Decapoda

Worm = Worm-like spp.: clam worms *Nereis* and *Platynereis* spp., blood worms *Glycera* spp., opal worm *Arabella iricolor*, thread worms unID Lumbrineridae, cage worms unID Flabelligeridae, unID Opheliidae, unID Orbiniidae, unID Syllidae, unID Annelida, nemertean unID Nemertea

PelFi = Pelagic forage fish: Atlantic silverside *Menidia menidia*, bay anchovy *Anchoa mitchilli*, striped anchovy *A. hepsetus*, Atlantic butterfish *Peprilus triacanthus*, round herring *Etrumeus teres*, unID Clupeidae

Mollu = Molluscs: shark's eye moon snail Neverita duplicata, whelk *Busycon* spp., unID Gastropoda, blue mussel *Mytilus edulis*, common razor clam *Ensis directus*, soft-shelled clam *Mya arenaria*, unID Bivalva

Amphi = Amphioxus *Branchiostoma* sp.

DecCr = Decapod crabs: Atlantic rock crab *Cancer irroratus*, lady crab *Ovalipes ocellatus*, common spider crab *Libinia emarginata*, commensal crab *Pinnixia* sp., unID Brachyura

Cepha = Cephalopods: longfin inshore squid *Loligo pealei*, unID Cephalopoda

Plank = Zoo/Meroplankton: Copepoda (incl. Calanoida, Harpacticoida, Cyclopoida), arrow worm Chaetognatha, cumacean Cumacea, unID larval fish, larval Crustacea (incl. decapod zoeae and megalopae. mysis-stage mysid shrimp)

Arthr = Arthropod: unID Arthropoda, unID Crustacea

Cteno = Ctenophores: comb jelly *Mnemiopsis leidyi*, unID gelatinous zooplankton

DecSh = Decapod shrimp and similar spp.: mantis shrimp *Squilla empusa*, flat-browed mud shrimp *Upogebia affinis*, *Penaeus* sp.

MacOt = Macrobenthos-other: sea cucumber unID Holothuridae, barnacles unID Cirripedia, sponge unID Porifera

MacAl = Macroalgae: unID macroalgae

Mysid = mysid shrimp *Neomysis americana*

DemFi = Demersal fish: scup *Orthopristis chrysoptera*, spot *Leiostomus xanthurus*, striped cusk-eel *Ophidion marginatum*, weakfish *Cynoscion regalis*, searobin *Prionotus* sp. unID Sciaenidae

HerCr = Hermit crabs: long-clawed hermit crab *Pagurus longicarpus*, flat-clawed hermit crab *Pagurus pollicaris*, *Pagurus* sp.

FlaFi = Flatfish: smallmouth flounder *Etropus microstomus*, windowpane flounder *Scophthalmus aquosus*, unID flatfish

CarFi = Carangiform fish: bluefish *Pomatomus saltatrix*, unID Carangidae

unFis = unID fish prey

Chapter 7: Synthesis and future studies

1. Summary

I evaluated several sources of evidence in support of the hypothesis that inner

continental shelf (ICS) habitats of the Middle Atlantic Bight serve an important

nursery function for temperate marine finfish that also use estuarine nurseries.

Through a series of comparative analyses, I marked correspondence in the

composition and seasonal structure of the juvenile finfish assemblages from the

Delmarva Peninsula ICS and lower mainstem Chesapeake Bay (estuary). This

demographic similarity was also present at the species level, as indicated by

similarities in growth rate, abundance, and trophic ecology in juveniles of several key

species that are abundant in both the ICS and estuary habitat. Juvenile and adult

finfish using demersal habitats of the ICS relied on both benthic and pelagic food

webs for nourishment, indicating a complex trophic structure that spans the full water

column. Within the ICS, juvenile finfish exhibited a variety of trophic roles that

ranged from planktivore to piscivore. Despite evidence of niche overlap, the largely

generalist diet composition of most species suggests both stochastic (i.e.,

environmental) and deterministic (i.e., community composition) processes are likely

to influence assemblage structure.

2. Principal findings and management implications

The most important finding of this dissertation was the multifaceted evidence that the

inner continental shelf (ICS) of the US Middle Atlantic Bight (MAB) is capable of

functioning interchangeably with polyhaline estuary areas as nursery habitat for a

diverse group of marine finfish. This functional similarity between ICS and estuary

habitats was evident at multiple biological scales, ranging from the community- to the

species-level and spanning both demographic and ecological properties. These

findings are not unprecedented (faunal similarities have long been noted between ICS

and estuarine habitats; see Able 2005 for a review); yet, this dissertation provides a

rare, direct comparison of gear-calibrated catch data from independent juvenile

finfish surveys of each habitat. Additional findings of significance include: 1) the

trophic coupling of pelagic and benthic food webs by juvenile-stage finfish in ICS

habitats; 2) evidence of habitat specific differences in trophic niche by conspecifics;

and 3) and the statistical support of size-dependent gear-calibration models from a

low-replicate paired trawl experiment.

2.1 Nursery role of the Middle Atlantic Bight ICS

There is compelling scientific evidence that coastal ocean habitats of the MAB (and

elsewhere: e.g., Australia, Lenanton 1982; Blaber and Blaber 1980; South Africa,

Bennet 1989; Central America, Yanez-Arancibia et al. 1980) serve a nursery function

for many marine finfish species that also use estuarine nurseries. This body of

knowledge has cummulated over the past half-century (McHugh 1967, Lenanton

1982, Bennet 1989; Blaber et al. 1995, Able et al. 2006); yet there has been

surprisingly little effort to extend fisheries-independent surveys to shallow coastal

ocean habitats of the MAB – particularly from the Delmarva Peninsula to Cape

Hatteras, NC. This oversight was recently addressed with the inception of the

Northeast Area Monitoring and Assessment Program (NEAMAP; Bonzek et al. 2009)

although data from this nascent survey has yet to be operationally included in species stock assessments (e.g., SARC 2009).

The use of ICS nursery habitats by marine finfish has several clear implications for fisheries management. Perhaps most importantly, indices of age 0 abundance based solely on estuarine surveys will significantly underestimate actual age-0 abundance. For example, the most recent population models of weakfish *Cynoscion regalis* and summer flounder *Paralichthys dentatus* do not include a marine juvenile survey component in the MAB region (weakfish, SARC 2009; summer flounder, Terceiro 2009). When extrapolated to the Delmarva Peninsula ICS and lower mainstem Chesapeake Bay, estimated juvenile abundances of these species in the two habitats were within 1 order of magnitude (see Chapter 3). This simple scaling exercise illustrates the potential for inaccuracies in population models that do not consider ICS habitats when deriving annual juvenile abundance indices.

Similarly, describing and forecasting recruitment dynamics such as spawner-recruit relationships or environment-recruitment correlates requires unbiased indices of juvenile abundance and (in the case of environmental conditions) knowledge of juvenile habitat use (e.g., Kempf et al. 2009; Hare et al. 2010). A recent study by Kempf et al. (2009) for example, examined the role of biotic (spawning stock biomass, predator-prey overlap) and abiotic (sea surface temperature) conditions on annual recruitment strength of North Sea cod *Gadus morhua* and Norway pout *Trisopterus esmarkii*. By restricting these explanatory variables to known nursery

habitats, they reported that spring SST and the abundance of co-occurring predators

explained 88% of the interannual recruitment variability of cod and 66% for Norway

pout (Kempf et al. 2009). Without spatially-explicit knowledge of nursery habitats,

studies that attempt to link environmental conditions to recruitment success could

lack the precision necessary to successfully identify significant patterns and

processes. Our understanding of the biotic and abiotic processes driving annual

juvenile production patterns for many marine finfish of the MAB will remain

incomplete until the spatial scope of potential nurseries is expanded to include ICS

habitats.

The ability to facultatively exploit marine and estuarine nursery habitats could

constitute an advantage at evolutionary time scales and explain the apparent

commonality of this life history strategy in present-day coastal marine finfish

assemblages. In recent geological time (i.e., <0.5 my), estuaries on the US East Coast

have been cyclically ephemeral – ocean waters intruding into fluvial flood plains

during interglacial periods and then retreating again with the initiation of the next

glacial period (e.g., Chesapeake Bay has 'reformed' at least 3 times in the last 0.5 my;

Colman et al. 1990). During glaciations, estuarine-dependent taxa would be forced to

depend on radically reduced nursery habitat availability. Conversely, populations of

ecologically flexible species, capable of using either marine or estuarine nursery

habitats, could potentially rely more heavily on coastal ocean production of juveniles.

The shift from estuary-favorable to shelf-favorable nursery conditions probably led to

marked changes in the coastal fish assemblages during the glaciation cycle as the

assemblage structure shifted to reflect the relative dominance of those species most suited to estuarine conditions under the current glacial stage.

2.2 Trophic structuring with the ICS

It has been suggested that there is a causal relationship between the timing and magnitude of the vernal phytoplankton bloom in mid- to high latitude or shallow ocean habitats and the annual carrying capacity of those habitats for juvenile demersal finfish (Townsend and Cammen 1988). This hypothesis is predicated on the notion that detritus from the spent bloom sets the annual 'scope' for secondary benthic production during the spring and summer, providing the primary nutrition source for juveniles following settlement. This indirect linkage between vernal bloom dynamics and juvenile finfish production may not be as strong in the Middle Atlantic Bight as in other areas – juvenile finfish recruiting to ICS demersal habitats appear to derive a substantial fraction of their assimilated carbon directly via pelagic trophic pathways. The relative contribution of each trophic pathway varied by species, but even foraging conditions for epibenthic species such as smallmouth flounder *Etropus microstomus*, windowpane flounder *Scophthalmus aquosus*, and summer flounder are unlikely to respond directly to annual bloom dynamics. Additional factors that drive stratification (e.g., upwelling events, along-shore current, estuarine plume dynamics, precipitation) may be as, or more, important than the timing and size of vernal blooms in driving trophic conditions and influencing annual year-class strength of demersal finfish in the ICS of the MAB.

The management implications of this integrative food web role are not clear although it seems likely that the shallow ICS nursery habitats offer relatively stable foraging conditions due to availability of prey to demersal fish from all levels of the water column. If foraging conditions for juvenile finfish in ICS habitats are buffered from the interannual variability of springtime bloom conditions, ICS food webs may be intrinsically more resilient to changes in the seasonal phenology of bloom dynamics than estuarine food webs. Still, persistent alterations in oceanic conditions from global climate change are unlikely to be limited to shifts in the timing or strength of seasonal blooms. As discussed in the previous paragraph, changes in climatic forcing conditions leading to increased stratification of the water column as well as any negative environmental influence on vertically mobile prey sources (e.g., reduced calcification rates among calcifying prey populations due to anthropogenic acidification; Fabry et al. 2008) could serve to reduce the strength of benthic-pelagic coupling and disrupt the trophic niche of juvenile finfish. Correlative studies between environmental factors and juvenile density (or abundance) in ICS habitats are needed before more resolved models of recruitment dynamics (e.g., individual-based models) can be parameterized and used to enhance understanding of the linkages between juvenile production and current or future coastal conditions.

2.3 Role of small-scale gear-calibration studies

As a prerequisite to the direct comparison of ICS and estuary finfish survey data, a small scale gear-calibration experiment was conducted to support size-dependent modeling of relative catchability (q_r) of juvenile-stage ecomorphological groups of

fish species between two bottom trawls. In conjunction with information theoretic

model selection criteria, the SELECT method (as described in Millar 1992; also see

Chapter 2 - Methods) was the modeling approach used to construct and fit gear-

calibration models for 13 species of age-0 marine fish and one marine invertebrate.

The objective of this analysis was to derive statistically supported gear-calibration

models appropriate for ecological hypothesis testing. Based on this objective, the n =

8 paired hauls of the gear-calibration experiment were sufficient to identify size-

dependent changes in q_r despite prevalent overdispersion in the data.

Many published gear-calibration studies evaluate the effects of gear changes

on regional fisheries or seek to reconcile historical catch patterns with those generated

using a new gear configuration (e.g., Pelletier 1998; Wilderbruer et al. 1998; King et

al. 2004; Kingsley et al. 2008). Such studies are generally composed of >50 replicate

hauls (Pelletier 1998); high replication reflecting the need for precise gear conversion

estimators given the potential risk of fishery mismanagement and historical

investment in long-term surveys. Conversely, there is often little financial support for

ad hoc gear-calibration experiments to compare aspects of species catch between

disparate sampling surveys (e.g., Walsh 1984; Stokesbury et al. 1999; Powell et al.

2006; Tyson et al. 2006); yet meaningful incorporation of catch data from multiple

extant surveys is a necessary component in numerous critical research areas (e.g.,

defining nursery habitat, deriving habitat suitability indices, investigating effects of

climate change, evaluating pollution-mediated effects). To this end, limited-scope

gear comparisons can yield information on spatial or temporal catch patterns that are

vital to formulating topical ecological hypotheses despite levels of model variance

that may be inadequate in other scientific or management settings (Millar and Fryer

1999). Based on results from this study, even small-scale gear-calibration

experiments can yield sufficient information to support modeling of size-dependent

q_r.

3. Future studies

Of the myriad follow-up studies that could be addressed using data generated during

my field and laboratory research, two avenues of future analysis stand out as natural

extensions of my dissertation research. The first is a modeling approach aimed at

describing the trophic structure of the Delmarva ICS relative to adjacent habitats. A

natural modeling platform for this approach is Ecopath (www.ecopath.org), a

formalized mass-balance model of system throughput that has been used to represent

a variety of aquatic and marine ecosystems. The second research approach is a

spatial extension of the benthic-pelagic coupling analysis to the offshore mid- and

outer continental shelf. This would increase the spatial scale for drawing inferences

regarding the role of depth in the integration of benthic and pelagic food webs, but

would also allow examination of 'distance from shore' as a potentially important

factor influencing benthic-pelagic coupling.

The strength and scientific impact of these analyses depend heavily on placing

them within a comparative framework that allows direct hypothesis testing. A

potential limitation of food-web modeling is that the final product can become an

isolated case study, with structural characteristics and attributes highly influenced by the unique parameterization of that particular model. Models parameterized on a per case basis do not allow robust comparisons between systems – differences in initial parameterization (e.g., level of taxonomic resolution, basal system inputs and outputs) can obscure or over-emphasize ecological (dis)similarities. Similarly, using diet composition to estimate the strength of benthic-pelagic coupling relies on the level of taxonomic (or functional) resolution of prey categories, the assignment of individual prey categories to benthic or pelagic production pathways, and the measure of dietary importance used to calculate the benthic:pelagic ratio (e.g., total biomass, index of relative importance). Methodological differences in any of these decisions will influence final estimates and inferences. Simultaneous model construction within Ecopath, defining the resolution and scope of the models in parallel, can allow one to explore the assumptions and limitations of food-web case studies across habitats on a standardized basis.

Future research could thus directly compare food web structure and the spatial dynamics of benthic-pelagic coupling within the demersal finfish community that spans the continental shelf from the Delmarva ICS habitat and the shelf break. These extended analyses could incorporate material within the body of my dissertation, but also would rely on external data from the Autumn Bottom Trawl Survey conducted annually by the Northeast Fisheries Science Center (www.nefsc.noaa.gov). Sampling protocols for the NEFSC Autumn Bottom Trawl Survey are described in detail in several publications (e.g., Desprespatanjo et al. 1988; Link and Almeida 2000). The

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NEFSC sampling area relevant to this proposed analysis is offshore of the Delmarva Peninsula (roughly 39° N – 35.5° N) with trawl sites selected each year based on an area-weighted sampling allocation scheme (approximately one station per 690 km^2) stratified by depth and latitude. The survey collects species catch and biomass data, as well diet data for a subset of species.

In conjunction with the diet and demographic NEFSC trawl data, reports and previous Ecopath models (available at: www.ecopath.org) could be used to construct three Ecopath food web models, one of Chesapeake Bay, one of the inner continental shelf and the third of the mid-outer shelf habitats. By using standardized species groupings, size thresholds, lower trophic level categories, and contemporaneous seasonal data collected with similar sampling platforms (estuary survey: 9-m demersal bottom trawl, ICS survey: 28-m footrope Yankee bottom trawl, NEFSC survey: 27-m footrope Yankee bottom trawl), I believe that models could be developed that have sufficient underlying similarity to allow direct comparisons of food-web structure between these three habitats. Both of these proposed studies address a natural question that arises from my dissertation: Having established both similarities and differences between the ICS and proximal estuarine habitat, how different then are the ICS and estuary from adjacent shelf habitats (i.e., how far does the coastal continuum extend in this continental shelf system)? The simultaneous construction of Ecopath models for the estuary, ICS and offshore shelf ecosystem, in tandem with a focused study on the spatial dynamics of benthic-pelagic coupling along the inshore-offshore gradient, would provide a significant step toward

answering this question and contributing to understanding the ecological

interdependencies that link these habitats across the coastal continuum.

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