Trophic Resource Overlap Between Small Elasmobranchs and Sympatric Teleosts in Mid-Atlantic Bight Nearshore Habitats

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Abstract Small, abundant elasmobranchs use shallow marine areas (<20 m depth) of the US 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 km², 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 with 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.

Keywords Stomach contents · Elasmobranch mesopredators · Stable isotope · Carbon · Nitrogen · Diet

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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 US 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 US Middle Atlantic coast. We focus on the trophic status of three 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 inter-

actions 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).

Materials and Methods

Field and Laboratory Methods

Trawling was conducted roughly bimonthly from June to November 2004–2006, and in August of 2007 and 2008 on the ICS (5–20 m) along the southern edge of the northeastern US 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
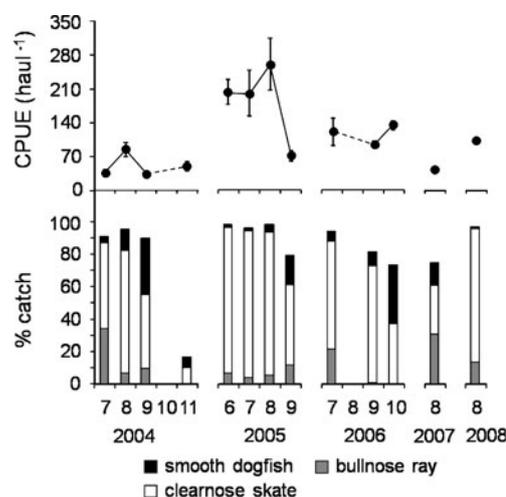

Fig. 1 Monthly catch-per-unit-effort (CPUE=catch haul^{-1}±SE) of small elasmobranchs (*upper panel*) from a 30-m footrope demersal trawl survey of Maryland's inner continental shelf from 2004–2008 and percent contribution to the total catch of elasmobranchs (% catch, *lower panel*) by smooth dogfish (*filled bars*), clearnose skate (*empty bars*), and bullnose ray (*shaded bars*). Additional small elasmobranchs from the 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*

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 ($n=8$)
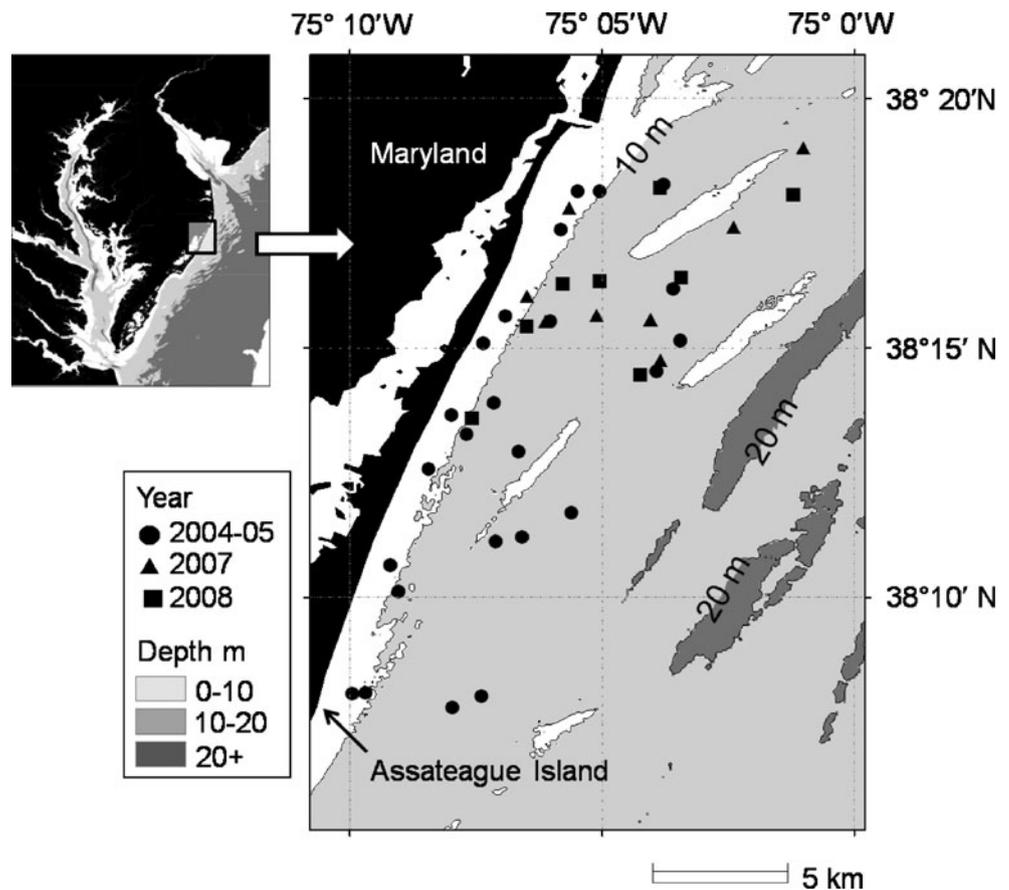
was a demersal Yankee otter trawl with 30-m foot-rope and 6.4-mm cod-end mesh. Samples collected with this gear were also supplemented with a few specimens (bullnose ray [$n=1$], bluefish [$n=2$], weakfish [$n=9$]) taken in a smaller semi-balloon mid-water trawl (5.7-m foot-rope, 6.4-mm cod-end mesh) 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 three 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-s intervals (6-min total tow duration). During each cruise, gear deployments were temporally staggered over 2 to 3 days 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 h 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 published correction curves (Post et al. 2007). Mathematical lipid normalization (as compared with 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).

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 to 2008 were pooled for all subsequent analyses. Stable isotope data from 2007 to 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 two-stage weighting approach to account for autocorrelation in diet among individuals captured from the same site (Buckel et al. 1999a, b). 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).

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 one-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 nonempty 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).

Niche Overlap Hypothesis

Potential niche overlap between elasmobranchs and teleosts was evaluated using multivariate and univariate approaches. Firstly, 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, $\alpha = 0.05$) 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's 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 (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., 00:00–05:59 hours, 06:00–11:59 hours), and then the stomach fullness index and CPUE was calculated for each 6-h period. Temporal patterns were visually and statistically (1-way analysis of variance [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

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

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 with 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 $\alpha = 0.05$.

Results

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). Con-

Table 1 Detailed stomach contents by total weight (g) of three small elasmobranchs collected from Maryland's inner continental shelf during August 2007–2008

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	–	–

All smooth dogfish=age-0, clearnose skate and bullnose ray=mixed age-classes

versely, 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

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

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	-	-	-
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

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

[a] Unidentifiable or inorganic stomach contents were present in all species but were not included in Table 2

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.

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
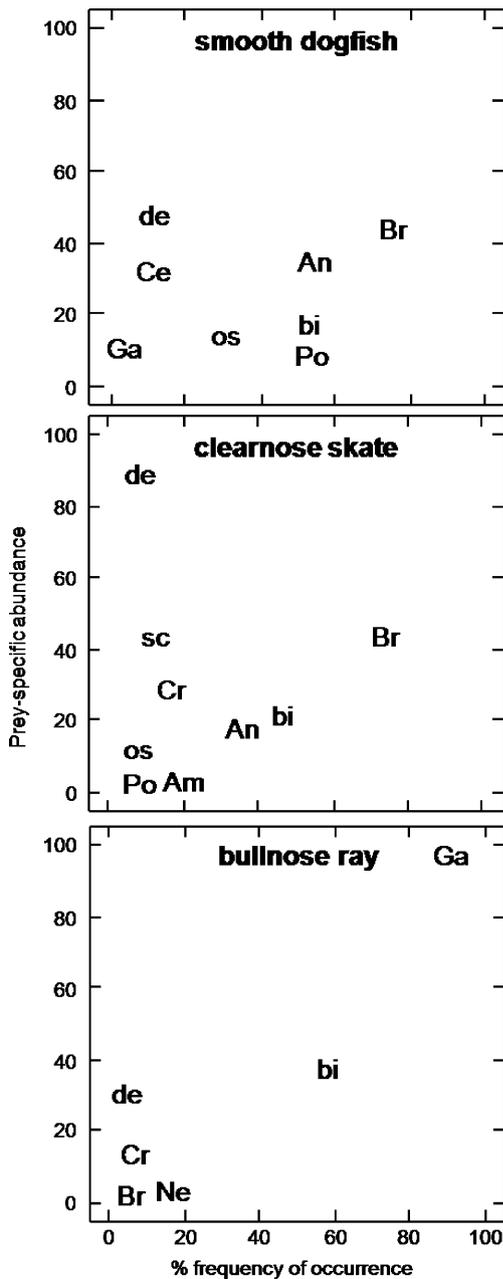
Fig. 3 Prey-specific biomass plotted against percent frequency of occurrence for 12 primary prey categories identified within stomachs of smooth dogfish, clearnose skate, and bullnose ray from Maryland's inner continental shelf during August 2007–2008. Prey categories are coded as: *Am* Amphipoda, *An* 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

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.

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
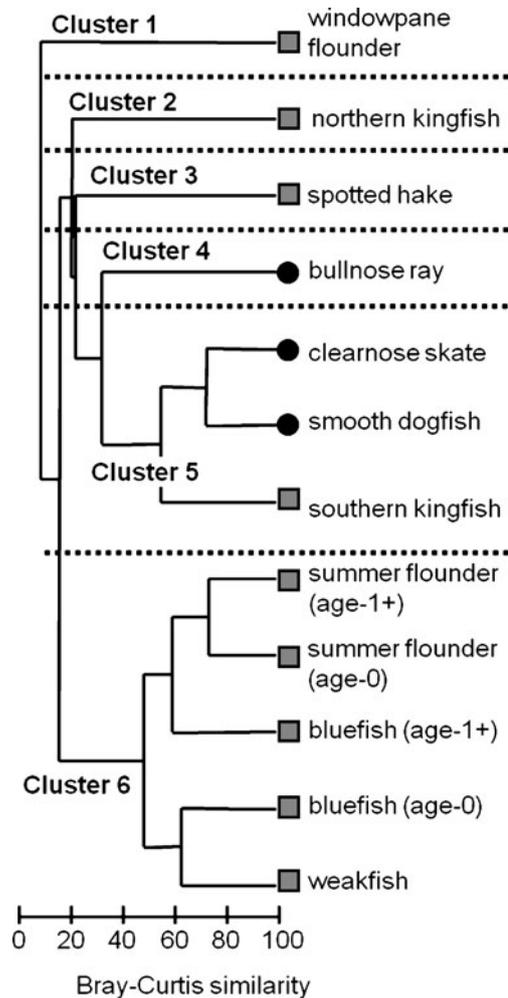

Fig. 4 Dendrogram of diet similarity among elasmobranch (*filled circles*) and teleost (*shaded squares*) species from Maryland's inner continental shelf during August 2007–2008. Species clusters (*separated by dotted lines*) are significantly different at $\alpha \leq 0.05$ (permutation test)

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 2004-05 and 2007-08

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)
Overall mean	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

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).

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 4-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≥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
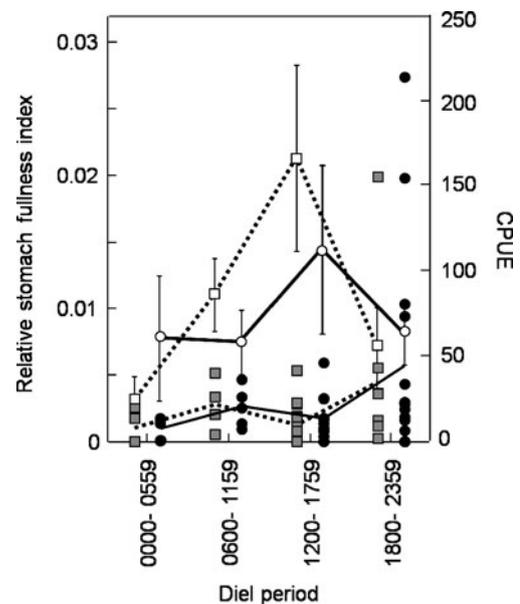

Fig. 5 Diel patterns in an index of relative stomach fullness (primary y-axis: clearnose skate, *filled circles*; southern kingfish, *gray-filled squares*) and catch-per-unit-effort (CPUE haul^{-1} ±1 SE, secondary y-axis: clearnose skate, *empty circles*; southern kingfish, *empty squares*) for two species. *Solid* (clearnose skate) and *dotted* (southern kingfish) *lines* indicate average stomach fullness and CPUE per 6-h period
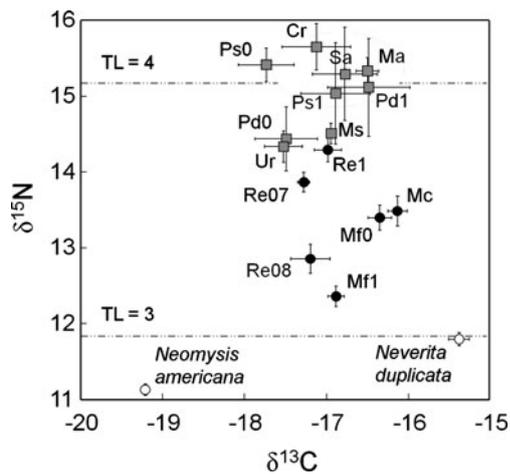
Fig. 6 $\delta^{13}C$ and $\delta^{15}N$ signatures (±1 SE) from elasmobranch (*filled circles*), teleost (*gray-filled squares*), and isotopic baseline (*empty circles*) species from Maryland's inner continental shelf during August 2007–2008. Abbreviations are based on Latin names as follows, Species: *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). $\delta^{15}N$ signatures corresponding to trophic levels (TL) 3 (secondary consumer) and 4 (tertiary consumer) are plotted for reference (*dot-dot-dashed lines*)

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 ($F\le1.60$, $p\ge0.21$) and stomach fullness ($F\le1.76$, $p\ge0.17$) across 6-

h periods were not statistically significant for either species although visual examination of the data indicated similar temporal trends. Average CPUE peaked between the hours of 1,200–1,759 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 (18:00–23:59 hrs: clearnose skate=0.005±0.002 SE, southern kingfish=0.007±0.002 SE).

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, $p\le0.05$) in TP between estimation methods occurred for six of the 12 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

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

Entries in italics 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 $\alpha=0.05$ (Tukey's 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	*4.1*	*3.50*	
	Adult		3.73	B, C, D, E
	Subadult (2007)		3.61	B, C, D
	Subadult (2008)		3.3	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+	*3.3*	*3.8*	C, D, E
Summer flounder	Age-0	*4.22*	*3.8*	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+	*3.6*	*4.07*	E
Weakfish	Age-1+	4.12	4.16	E

skate and age-1+ bullnose ray occupied a significantly lower TP_{SI} than all the teleost species and age-classes (Tukey's 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 and summer flounder. Conversely, TP_{SI} of age-0 bullnose ray and bluefish was higher than that of older conspecifics.

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 (460–1,260+ 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 (MacNeill 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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