

Seasonality and Ontogenetic Habitat Partitioning of Cownose Rays in the Northern Gulf of Mexico

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Abstract The seasonal and spatial heterogeneity of highly mobile mesopredators may play a large structuring role in estuarine dynamics. With a hypothesized relaxation of predation pressure from large sharks, growing populations of cownose rays (*Rhinoptera bonasus*) have been implicated in negatively affecting shellfish beds across multiple estuaries of the Atlantic coast; however, the pervasiveness of these potential impacts remains poorly understood elsewhere due to a lack of information on cownose ray distribution and seasonality across the species' range. To better predict cownose ray dynamics in estuaries of the northern Gulf of Mexico, we conducted a multi-scale study using a combination of aerial and gillnet surveys. Cownose ray abundance was highly seasonal along the Mississippi-Alabama shelf, and a significant along-shelf gradient (west-east) in nearshore ray density was observed. This trend was best explained by changes in salinity, with higher abundances best correlated with more estuarine (i.e., lower salinity) conditions in nearshore areas. From north-south across the Alabama shelf, cownose rays displayed strong spatial and seasonal distributional patterns with ontogeny: adults (in particular, females) were primarily restricted to

barrier islands and Gulf waters, whereas juveniles and young-of-the-year (YOY) exploited fresher waters of inshore bays protected from large predators. Among inshore locales, cownose ray catch was lowest over oyster habitats and only consisted of YOY rays, suggesting that foraging impacts may be reduced in these structurally complex substrates.

Keywords Cownose ray · Elasmobranch · Mobile bay · Gulf of Mexico

Introduction

Understanding the distribution and habitat use of predatory fishes is central to discerning the role of top-down control and connectivity in marine ecosystems. Yet, the ecology of many predatory species still remains poorly examined due to the difficulty in monitoring the dynamic nature of their presence (Estes and Peterson 2000). Recent studies have shown that even predators with limited residence in coastal ecosystems (i.e., highly migratory species) can have impacts on prey communities. One such species is the cownose ray, *Rhinoptera bonasus*, which has been implicated in shellfish declines due to their patch-depleting foraging behavior along fall migration corridors of the Atlantic coast (Fegley et al. 2009; Myers et al. 2007; Peterson et al. 2001). Cownose rays are encountered in temperate to subtropical waters throughout the central West Atlantic, including the Gulf of Mexico (Bigelow and Schroeder 1953; McEachran and de Carvalho 2002). While the life history of the cownose ray (Neer 2005; Neer and Thompson 2005), outmigration patterns (Ajemian and Powers 2014), and summer shelf use (Craig et al. 2010) have all been described from the northern Gulf of Mexico, the year-round dynamics in distribution and abundance of this species remain poorly examined. Such data gaps limit our

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ability to estimate potential interactions of cownose rays with shellfish restoration programs as well as develop conservation plans for this “near-threatened” species (Barker 2006).

It has been hypothesized that Gulf of Mexico cownose rays comprise a single population that migrates in a clockwise fashion beginning in Mexico during winter, the northern Gulf during spring, and southwest Florida in the fall (Schwartz 1990); however, this hypothesis has been challenged by multiple studies. Rogers et al. (1990) examined cownose ray distribution throughout the Gulf of Mexico from aerial surveys and found seasonality in densities, but did not notice an eastward expansion along the northern Gulf of Mexico as suggested by Schwartz (1990). Moreover, in southwest Florida, acoustic monitoring studies found cownose rays were year-round residents that did not migrate seasonally, though it was suggested that rays from the northern Gulf of Mexico could exhibit these behaviors (Collins et al. 2008; Collins et al. 2007b). Unfortunately, few studies have implemented year-round fishery-independent surveys to characterize this seasonality.

There are also few studies that have examined cownose ray use of inshore structural habitat. Structural complexity may decrease the foraging efficiency of benthic predators (Peterson 1982; Sponaugle and Lawton 1990) and may thus provide refuge for some prey (e.g., bivalves) consumed by cownose rays (Collins et al. 2007a; Powers and Gaskill 2003; Smith and Merriner 1985). While previous studies have shown cownose rays utilize and forage in eelgrass (*Zostera marina*) meadows across the temperate Atlantic coast (Orth 1975; Peterson et al. 2001; Powers and Gaskill 2003), it is likely that this highly mobile species utilizes several other substrate types widely available in the northern Gulf of Mexico (e.g., oyster and non-*Zostera* seagrass beds, sand flats, mud banks). Understanding the relative abundance of cownose rays in these various benthic habitats may help better guide restoration of shellfish by identifying substrates that are most vulnerable to these mollusk predators. Further, though use of dynamic habitat (temperature, salinity, dissolved oxygen) has been well documented for cownose rays (Collins et al. 2008; Craig et al. 2010; Goodman et al. 2010; Smith and Merriner 1987), no studies have examined how these physical parameters affect the distribution of various life stages, which may also affect restoration as rays may have differential impacts depending on size (Kolmann et al. 2015).

In this study, we integrated two survey techniques (aerial and gillnet) to examine cownose ray seasonality, distribution, and habitat use on multiple spatial scales (10s–100s of kilometers) in the northern Gulf of Mexico. Furthermore, because gillnet surveys captured all life stages of cownose rays, we used these data to examine how this species ontogenetically partitioned habitat across the inshore region. Based on previous studies, we predicted a seasonal ingress of cownose rays concurrent with water temperatures rising above 16 °C and a seasonal departure as temperatures dropped to 20 °C (Smith

and Merriner 1987). Moreover, we hypothesized that rays preferred structured habitats that supported high densities of mollusk prey over unstructured bottom due to their demonstrated association with these substrate types elsewhere (Orth 1975; Peterson et al. 2001; Powers and Gaskill 2003).

Methods

Aerial Surveys

The utility of aerial surveys has been well demonstrated in locating schools of cownose rays (Blaylock 1993; Powers and Gaskill 2003; Rogers et al. 1990; Smith and Merriner 1987). Our goal was to use the aerial surveys to map occurrence and large-scale distribution of cownose rays along the Mississippi-Alabama shelf. On a complete aerial survey day ($n = 12$ days), 12 north-south line transects were flown between Pensacola, Florida, and Biloxi, Mississippi. Depending on region, line-transects were flown between 40 and 100 km in length and covered the coastal shelf waters out to approximately 60 m depth (Fig. 1). While the initial intent was to fly surveys year-round between July 2008 and March 2010, weather conditions (high winds, sea surface state) limited winter and spring flights. All surveys were conducted from a twin-engine fixed-wing aircraft (Piper Geronimo) at an altitude of 200 m and at a speed of 200 km/h. Surveys were flown between 0900 and 1500 on clear and sunny days with relatively calm seas (Beaufort scale <3). During flight, two trained observers (one on each side of the plane) constantly scanned an area from directly below the aircraft window to the wing (85°) for surface schools of cownose rays. When a ray(s) was observed, it was marked with a waypoint in a handheld GPS unit and enumerated by the observer. When groups were too large to be enumerated while flying along the survey path, photographs were taken and later geo-referenced from the synchronized timestamp between the camera and GPS unit.

Geo-referenced count data were plotted in ArcGIS to examine the spatiotemporal behavior of school size and ray distribution. For a given survey day and transect, both sighting and ray densities were quantified by calculating the number of sightings and individuals observed per square kilometer of transect. Environmental data (bottom depth, sea surface temperature, sea surface salinity, chlorophyll-a) were derived from each survey and sighting using the Marine Geospatial Ecology toolbox (Duke University) in ArcGIS 10.0 (ESRI, Inc.). Specifically, the HYCOM consortium model was used to extract fine-scale (0.25 km² cell) temperature and salinity data while NASA's Ocean color was used to extract chlorophyll-a for each sighting and leg of the transect. Data from all environmental parameters were downloaded from satellite passes conducted on the same day of the aerial survey. Multiple linear regressions were run on both sighting and ray

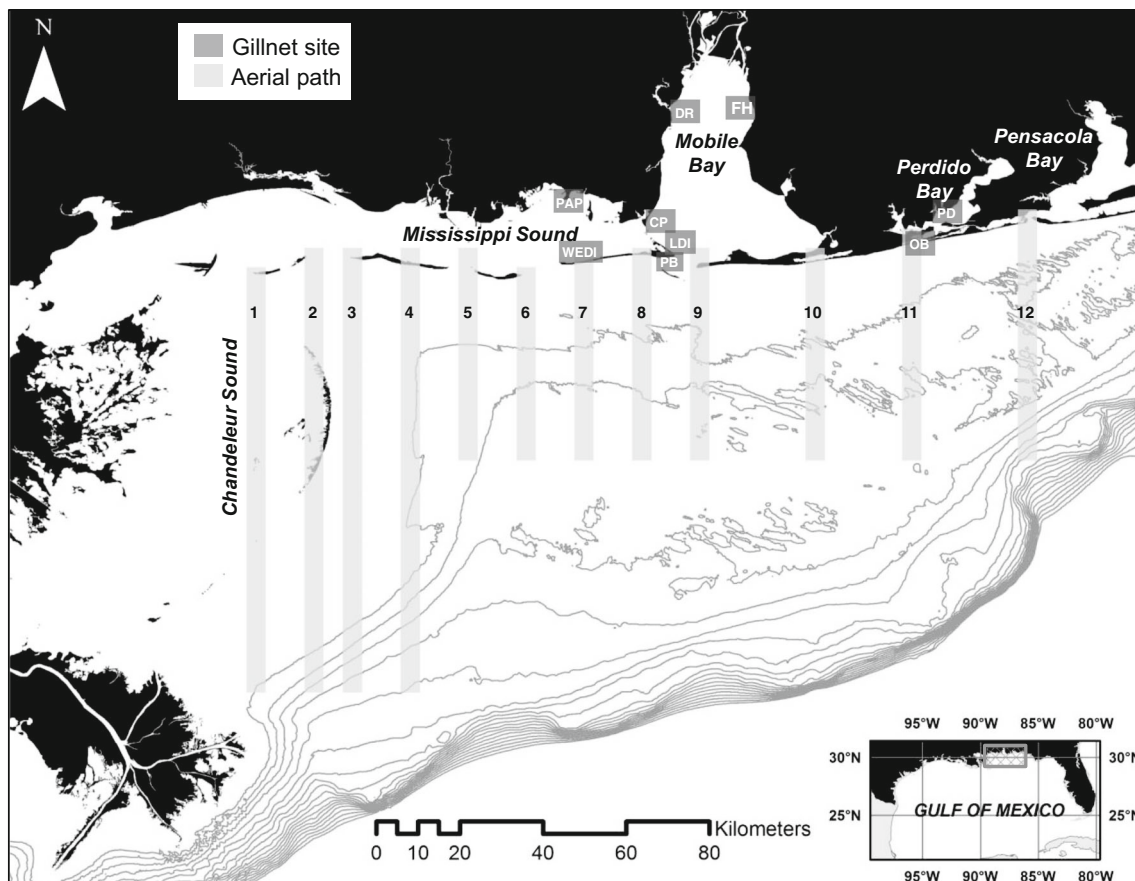


Fig. 1 Map of aerial survey route across the Mississippi-Alabama shelf and inshore gillnet survey sites along the coast of Alabama. Bathymetry is shown in 10-m increments from 20- to 200-m isobaths. Transect numbers are overlain on aerial paths. Abbreviations for gillnet sites: *DR* Dog River,

FH Fairhope, *PAP* Point Aux Pins, *CP* Cedar Point, *LDI* Little Dauphin Island, *PD* Perdido Bay, *WEDI* West End Dauphin Island, *PB* Pelican Bay, *OB* Orange Beach

density data to determine the abiotic factors (including Julian day) most responsible for along-shelf distribution trends. Given our interest in the stochasticity of ray sightings (presence/absence) and violations of the assumptions of linear models, we also examined the impact of these factors on the probability of having a single sighting with multiple logistic regression modeling. All regression models and curve fitting were run in SigmaPlot 12.0 (Systat Software, Inc.).

Gillnet Survey

In fall 2007, monthly gillnet surveys were initiated at the Dauphin Island Sea Lab (DISL) to estimate cownose ray seasonality and abundance within inshore waters of the northern Gulf of Mexico. The DISL surveys sampled nine sites along coastal Alabama and encompassed Mississippi Sound, Mobile Bay, and Perdido Bay estuarine systems (Fig. 1). Each block consisted of paired 0.3×1.0 km rectangular grids, one for a “shallow” (1.0–2.9 m) and one for a “deep” (3.0–4.9 m) set. One set was made in each of the shallow and deep grids of each block for every month of the year through December 2009. The start location of the set was randomly chosen within the grid

using Hawth’s tools in ArcMap 9.2 (ESRI, Inc.). The gillnets utilized for the survey were 300 m in length (3.0 m depth) with alternating 50 m panels of 10.16 and 15.24 cm monofilament mesh (stretch length). Panels were strung together and fished as a single gear perpendicular to shoreline. Dominant benthic substrate (seagrass, oyster, sand, or mud) was classified for each set, and mid-water environmental parameters (temperature, salinity, dissolved oxygen, and turbidity) were recorded with a YSI-85 and Secchi disk. All rays caught by this method were sexed, measured for straight disk width (DW, ventral distance between pectoral fins) and disk length (DL; ventral distance between snout and cloaca), and weighed to the nearest 0.1 kg. In addition, maturity level for all captured individuals was assessed following Neer (2005). Catch per unit effort (CPUE) for each gillnet set was defined as the number of animals caught divided by the soak time of the net (the time from when the gear first entered the water until all gear was fully retrieved).

To complement our understanding of cownose ray inshore distribution, we also obtained year-round inshore gillnet survey data from the Alabama Department of Marine Resources (ALMRD) from 2004 to 2009. However, data from the ALMRD survey were only used to examine qualitative spatial

trends. Thus, CPUE data were only statistically analyzed from the DISL survey and were modeled using delta-lognormal generalized linear models (dGLM). These models were chosen due to the high frequency of no catch occurrences (i.e., zero-inflated) in our survey and the need to develop interpretable indices of abundance for analyzing the distribution of cownose rays in both space and time. To standardize CPUE, the delta-lognormal index of relative abundance (I_f) as described by Lo et al. (1992) and Ingram et al. (2010) was estimated as $I_i = c_i p_i$, where c_i is the estimate of mean CPUE for positive catches only for factor i , and p_i is the estimate of mean probability of occurrence within factor i (Ingram et al., 2010; Lo et al. 1992). Both c_i and p_i were estimated using generalized linear models. Data used to estimate abundance for positive catches (c) and probability of occurrence (p) were assumed to have lognormal and binomial distributions, respectively. The final index was the product of the back-transformed effects of factor f from the two abovementioned GLMs. Response variables included overall cownose ray abundance and adult, juvenile, and young-of-the-year (YOY) abundances. The standard error and coefficient of variation were estimated using a jackknife routine on factors with greater than two positive observations per level. Because no post hoc tests are available for delta lognormal GLM, comparisons were made between various levels of a factor by visually inspecting the overlap of standard error bars from bar plots. All models were run using the statistical package R (2.12.1). Standardized CPUE was compared for the three life stages across month, site, and benthic habitat.

Multivariate Analyses

Cownose ray life stage partitioning was assessed using multivariate techniques. In this analysis, we treated abundance per life stage (YOY = <50 cm DW, juvenile = 50–70 cm DW, and adult = >70 cm DW) as three separate dependent variables, following Bethea et al. (2014). Catch per unit effort indices for gillnet sets with positive cownose ray catch ($n = 86$) were imported into PRIMER, fourth-root transformed, and used to develop a Bray-Curtis similarity matrix. Two-way crossed permutational multivariate analysis of variance (PERMANOVA) examined the effects of region (Estuary vs. Barrier Island; sensu Ajemian and Powers 2012) and season (winter = December–February, spring = March–May, summer = June–August, fall = September–November) on the catch composition. The PERMANOVA used a population-wide dissimilarity metric to evaluate differences in cownose ray catch composition among the various regions and seasons (Anderson 2001). All tests were permuted 999 times under a reduced model (Anderson 2001). Significant factors were further analyzed using PERMANOVA pairwise comparisons, and similarity percentage (SIMPER) analysis was employed to examine the life stages most responsible for the separation among factors (Clarke 1993). We accompanied our analysis with a distance-

based test for homogeneity of multivariate dispersions (PERMDISP) to determine possible reasons for the rejection of the null hypothesis (no differences life stage composition) by PERMANOVA as this test is known to be sensitive to sample dispersion (Anderson et al. 2006).

Because our data set included samples from a wide range of environmental regimes across the northern and eastern Gulf of Mexico, we followed our PERMANOVA and SIMPER with additional analyses to identify potential dynamic habitat drivers in the variation of cownose ray life stages. For these analyses, we used data from gillnet sets where all five environmental parameters (temperature, salinity, turbidity, depth, and dissolved oxygen) were recorded ($n = 359$). Environmental data were normalized and used to build a Euclidean distance-based resemblance matrix. These data were exposed to a non-parametric form of a Mantel test, RELATE, to assess agreement in the multivariate pattern between the biological and environmental resemblance matrices using a suite of random permutations. The biological resemblance matrix was comprised of CPUE data from all sets of the gillnet survey, with a dummy variable (1) added to all sets without catch. Following RELATE, we then used a BEST analysis (i.e., Bio-env) to find the best match between multivariate among sample patterns of cownose ray assemblages and the environmental data recorded with gillnet sets. Finally, principal components analysis (PCA) was conducted on the environmental data to visually assess sample dispersion and environmental drivers of catch by life stage. All community and multivariate analyses were conducted using PRIMER 6.1.16 and PERMANOVA+ 1.0.6 statistical package (PRIMER-E, Ltd.)

Results

Aerial Surveys

Cownose rays were sighted in all aerial surveys conducted during spring, summer, and fall months, but were absent from the single winter sampling survey (Table 1). Cownose ray sighting densities were highest during spring and summer and generally increased from northeast to southwest in the survey area (Fig. 2). Approximately 90 % of sightings occurred in nearshore waters at depths <20 m (56 % of survey track). Transects 1–4 recorded the highest mean ray densities and were also characterized by the largest estimated school sizes of cownose rays (max = 589 individuals). Ray densities and school sizes were somewhat reduced in the central block (transects 5–9) and noticeably low in the eastern block (transects 10–12). Though ray school sizes reached >100 individuals in spring, summer, and fall surveys, schools of >200 individuals were only observed in the summer months and appeared associated with waters straddling the 20-m isobath (Fig. 2). Despite an overt trend in ray schools becoming

Table 1 Summary of cownose ray (CNR) sightings form all aerial surveys conducted from 2008 to 2010

Date	Season	% Transects completed	CNR sightings	Total CNR	Mean group size
July 15, 2008	Summer	100	9	48	5
August 19, 2008	Summer	100	31	2060	66
September 25, 2008	Fall	100	1	130	130
October 17, 2008	Fall	50	5	254	51
October 30, 2008	Fall	100	3	95	32
November 11, 2008	Fall	100	1	114	114
April 28, 2009	Spring	100	5	47	9
June 16, 2009	Summer	100	72	547	8
July 21, 2009	Summer	100	46	2432	53
August 26, 2009	Summer	100	21	1793	85
September 25, 2009	Fall	100	17	69	4
November 24, 2009	Fall	100	42	129	3
February 18, 2010	Winter	100	0	0	0
March 19, 2010	Spring	100	189	1655	9
		Sum	442	9373	

denser offshore during summer months, no along-shore seasonal pattern was detectable from aerial surveys.

The relative impacts of various factors on cownose ray presence/absence, sighting, and ray densities largely depended

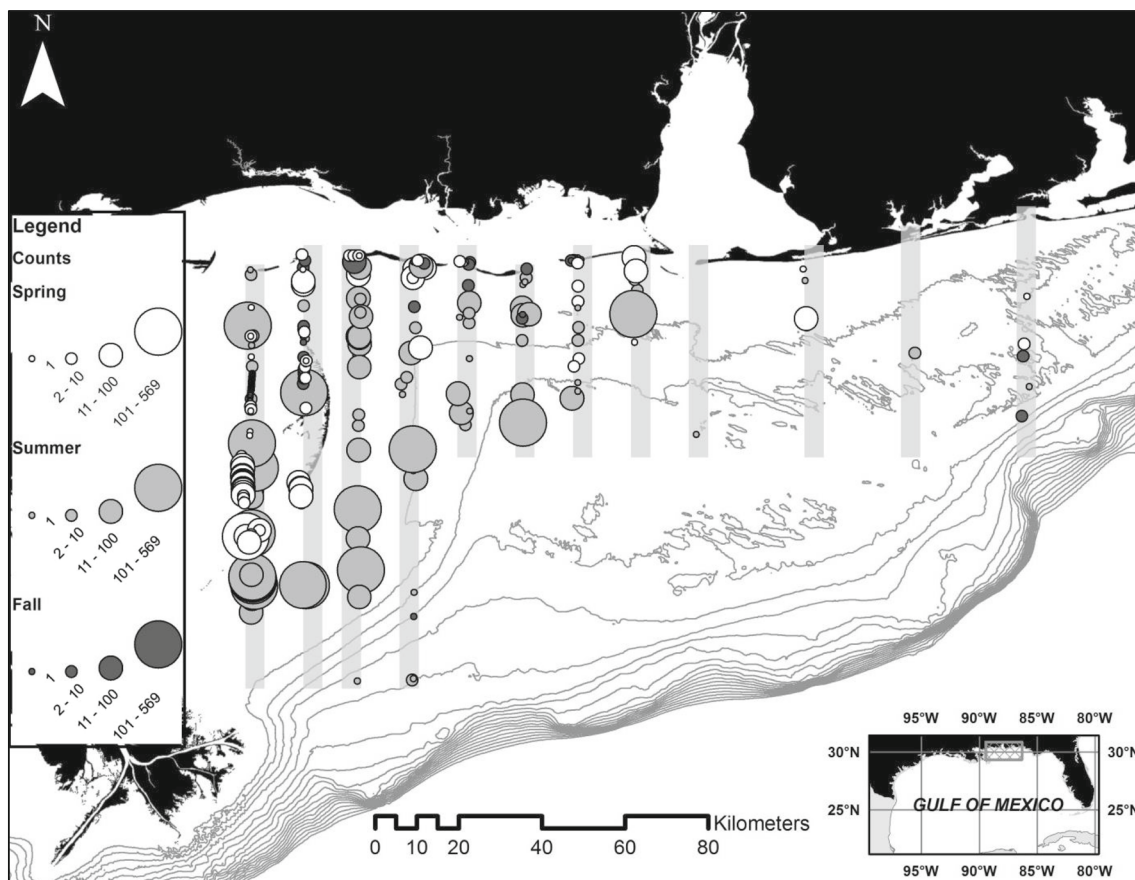


Fig. 2 Bubble plot of cownose ray distribution and school sizes from aerial surveys (2008–2010). Time of year is represented by color (*white* = spring, *medium gray* = summer, and *dark gray* = fall). No rays were

observed during winter flights. Note: the size of circles does not scale to ray school size. *Light gray bars* represent north-south transect lines

on the response variable examined (Table 2). Multiple logistic regression analysis found a statistically significant overall fit of cownose ray presence/absence and the independent variables (likelihood ratio test statistic = 19.568; $P = 0.002$). However, of the five variables tested, only salinity influenced the probability of sighting at least one cownose ray school (Wald statistic = 4.64; $P < 0.05$). A scatter plot of the predicted values indicated a negative relationship between the probability of sighting a cownose ray school and salinity (Fig. 3a) with an inflection point around 33 psu. Multiple linear regressions on positive (i.e., presence only) data found that mean SST was the only significant factor that could predict sighting density ($t = -2.126$; $P = 0.039$), with reduced numbers of sightings as SST increased (Fig. 3b), while bottom depth (i.e., proportion of habitat <20 m) was the sole factor explaining variability in ray density ($t = 2.966$; $P = 0.005$). Ray densities were highest in regions with the greatest amount of shallow habitat (Fig. 3c).

Gillnet Surveys

From 2007 to 2009, the DISL survey captured 453 total cownose rays while the ALMRD data set provided information on 53 rays. Both gillnet surveys captured individuals from all three life stages but were similarly dominated by YOY followed by adults and lastly juveniles (Table 3). The influence of ontogeny on cownose ray spatial distribution was evident in both data sets. Adults were rarely captured in the upper region of Mobile Bay and appeared in highest abundances along coastal barrier islands (Figs. 4, 5). Juveniles were distributed throughout the upper bay, lower bay, and across the gulf barrier islands. YOY individuals were also captured throughout the estuary but were observed in highest abundances in Mississippi Sound (e.g., Point Aux Pins) and Perdido Bay sites (Figs. 4, 5b).

Cownose ray catch rates and life stage depended on season. Rays were generally absent from gillnet surveys in the months of December and January but otherwise were captured in all other months of the year (Fig. 5a). A surge in abundance was noted during February and March along coastal barrier islands where catch was mainly comprised of adult rays. These abundance peaks were prevalent at both the West End and Pelican Bay and to a lesser degree at Orange Beach (Fig. 5b). Adult ray abundance decreased and shifted from barrier islands to inshore estuaries during April and May as temperatures neared 20 °C and became low throughout the summer months (water temperature >30 °C) as higher proportions of juvenile and young-of-the-year dominated the catch (Fig. 5a). During this warmer period, high abundances of YOY were observed at sites within the estuary (e.g., Point Aux Pins, Perdido Bay) and upper portions of Mobile Bay (e.g., Dog River) (Figs. 4, 5). Adult rays reappeared along barrier islands during October and November as average water temperatures cooled below

25 °C (Fig. 5a). Juvenile rays rarely dominated the catch across all sites or seasons, but were present from February to November.

Benthic habitat use varied ontogenetically; YOY rays were more common over mud bottom habitats than other life stages, whereas adults appeared to prefer sandy and seagrass habitats. Similar to adults, juvenile catch was highest over sandy bottom, but was comparatively low in seagrass. Catch rates were lowest over oyster habitat, where juveniles and adults were completely absent and only YOY rays were observed (Fig. 5c).

Sex ratios varied across region and season (Fig. 6). At barrier island locations, females consistently outnumbered males across all seasons. At estuarine sites, males dominated the catch, although ratios were closer to 1 in summer and fall. Bay sites had equal numbers of males and females in the two seasons that cownose rays were present in this region (summer and fall).

Multivariate Analyses

The PERMDISP test indicated that there was no heterogeneity in multivariate dispersion patterns for both region and season. Permutational multivariate analyses of variance (PERMANOVA) found that both region (pseudo- $F_{1,87} = 7.3087$; $P = 0.002$) and season (pseudo- $F_{3,87} = 3.7348$; $P = 0.005$) significantly affected cownose ray ontogenetic composition, but there was no significant interaction between the two factors (pseudo- $F_{3,187} = 0.3413$; $P = 0.861$; Table 4). Subsequent pairwise comparisons found that cownose ray assemblages differed between estuary sites and barrier island sites ($t = 2.7035$; $P = 0.006$). SIMPER analyses indicated that the differences among regions were explained by higher contributions of YOY at estuary sites when compared to barrier island sites, which were dominated by higher catches of adults. Seasonally, the summer assemblages were significantly different from both winter ($t = 1.8154$, $P = 0.05$) and spring ($t = 2.8092$, $P = 0.006$), but not different from fall ($t = 1.0997$, $P = 0.289$). Fall assemblages were also different than spring assemblages ($t = 2.5058$, $P = 0.004$), but were similar to winter assemblages ($t = 1.2425$, $P = 0.216$). SIMPER analyses suggested the main driver in these seasonal differences was higher contributions of YOY in summer and fall catch as well as strong adult contributions to winter and spring catch.

Resemblance matrices between environmental data and the corresponding cownose ray composition exhibited weak yet statistically significant agreement (RELATE test; $\rho = 0.066$; $P = 0.021$). A subsequent BIO-ENV test identified temperature as the factor producing the highest Spearman rank correlation value ($\rho = 0.121$) among the possible combination of the five environmental factors. While the correlation values were relatively low (0.071–0.121), temperature was the sole variable retained in the top 10 combinations of variables

Table 2 Results from various regression analyses of aerial survey data. *Asterisks* are placed adjacent to independent variables that appeared to account for the ability to predict response variables (i.e., $P < 0.05$)

Response variable	Regression type	N	Likelihood ratio test statistic	P value	Independent variable	Coefficient	Standard error	Wald statistic	P value	VIF	Odds ratio
Ray presence/absence	Multiple logistic	176	19,568	0.002	Constant	26.755	13.719	3.803	0.051		4.16548E + 11
					MeanSST	0.065	0.048	1.828	0.176	1.781	1.067
					MeanSal*	-0.874	0.406	4.640	0.031	3.441	0.417
					Prop < 20 m	-0.553	1.112	0.247	0.619	2.314	0.575
					ChlA	-0.009	0.088	0.011	0.918	2.405	0.991
					JulianDay	-0.002	0.004	0.224	0.636	3.146	0.998
Positive sighting density	Multiple linear	53	2.613	0.036	Constant	0.525	0.994	<i>t</i>	<i>P</i> value	VIF	
					MeanSST*	-0.007	0.003	-2.126	0.039	2.344	
					MeanSal	-0.012	0.030	-0.401	0.690	3.968	
					Prop < 20 m	0.116	0.062	1.877	0.067	1.977	
					ChlA	-0.002	0.004	-0.554	0.582	1.566	
					JulianDay	0.000	0.000	0.566	0.574	3.509	
Positive ray density	Multiple linear	53	3.143	0.016	Constant	-1.597	17.539	<i>t</i>	<i>P</i> value	VIF	
					MeanSST	0.011	0.060	0.179	0.859	2.344	
					MeanSal	0.026	0.522	0.050	0.960	3.968	
					Prop < 20 m*	3.244	1.094	2.966	0.005	1.977	
					ChlA	-0.042	0.071	-0.587	0.560	1.566	
					JulianDay	-0.001	0.005	-0.278	0.783	3.509	

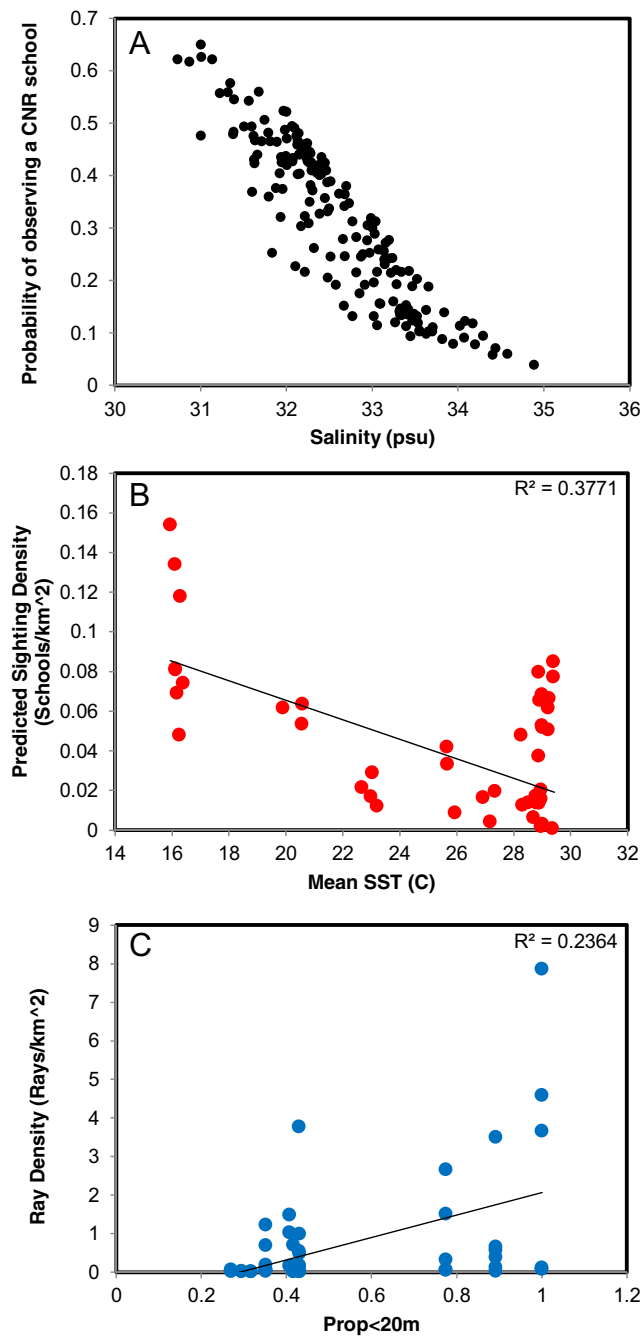


Fig. 3 Scatterplot of predicted values (generated by regressions) for a probability of sighting a cownose ray (CNR) school along the Mississippi-Alabama shelf with salinity, **b** predicted sighting density from mean sea surface temperature (SST), and **c** ray densities with the proportion of transects (Prop) under 20 m (m)

(Table 5). PCA qualitatively confirmed these results as catch by life stage varied more greatly along the temperature vector than any other independent variables (Fig. 7). Adults were observed at the lowest average, minimum, and maximum temperatures (mean = 21.8 ± 0.9 °C; range 13.8–30.1 °C), followed by juveniles (mean = 23.7 ± 0.8 °C; 14.0–32.0 °C), and YOY (mean = 26.7 ± 0.6 °C; 16.1–33.3 °C).

Discussion

Seasonality

Both aerial and gillnet survey data indicate cownose rays are seasonal to nearshore waters of the northern Gulf of Mexico. While only a single winter aerial survey could be conducted and did not report any sightings, cownose rays were observed on all other surveys (Table 1), suggesting there may only be a short-term departure from coastal waters of this region. Both aerial and gillnet surveys also suggest adult abundance is highest along barrier islands in spring and shifts to the near-shore shelf regions during summer months when rays form the largest schools. Rays are present along coastal barrier islands again in fall before departing in early winter. No massive migration was observed from aerial surveys in fall, suggesting ray emigration in this region is not synchronized as in other locations off the Atlantic coast.

Unlike Chesapeake Bay, where rays arrive at 16 °C and depart as water temperatures drop below 20 °C (Smith and Merriner 1987), rays in the northern Gulf of Mexico appear to exhibit both ingress and egress behaviors at 16 °C. These different outmigration patterns may be explained by a considerably larger travel distances to Florida overwintering grounds in east coast cownose rays (Grusha 2005; R.A. Fisher, unpublished data) compared to the northern Gulf of Mexico population that likely overwinters on the nearby shelf (Ajemian and Powers 2014). Our findings of seasonal use of inshore habitats contrast with work in Charlotte Harbor estuary (eastern Gulf of Mexico), where rays are apparently resident year-round (Collins et al. 2007b; Poulakis 2013). It is likely that the colder temperatures associated with the northern Gulf of Mexico trigger emigration from this region during late-fall and winter. Southwest Florida estuarine temperatures rarely fall below 14 °C (Collins et al. 2008; Collins et al.

Table 3 Description of gillnet survey gear types used in the study and the catch composition (by percent) of various life stages

Survey	Start year	End year	Mesh (cm)	Net length (m)	Net depth (m)	Total sets	Total rays	% ADU	% JUV	% YOY
DISL	2007	2009	10.16, 15.24	300.0	3.0	385	453	35	20	45
ALMRD	2004	2009	5.08–15.24	228.6	2.4	1286	53	39	11	50

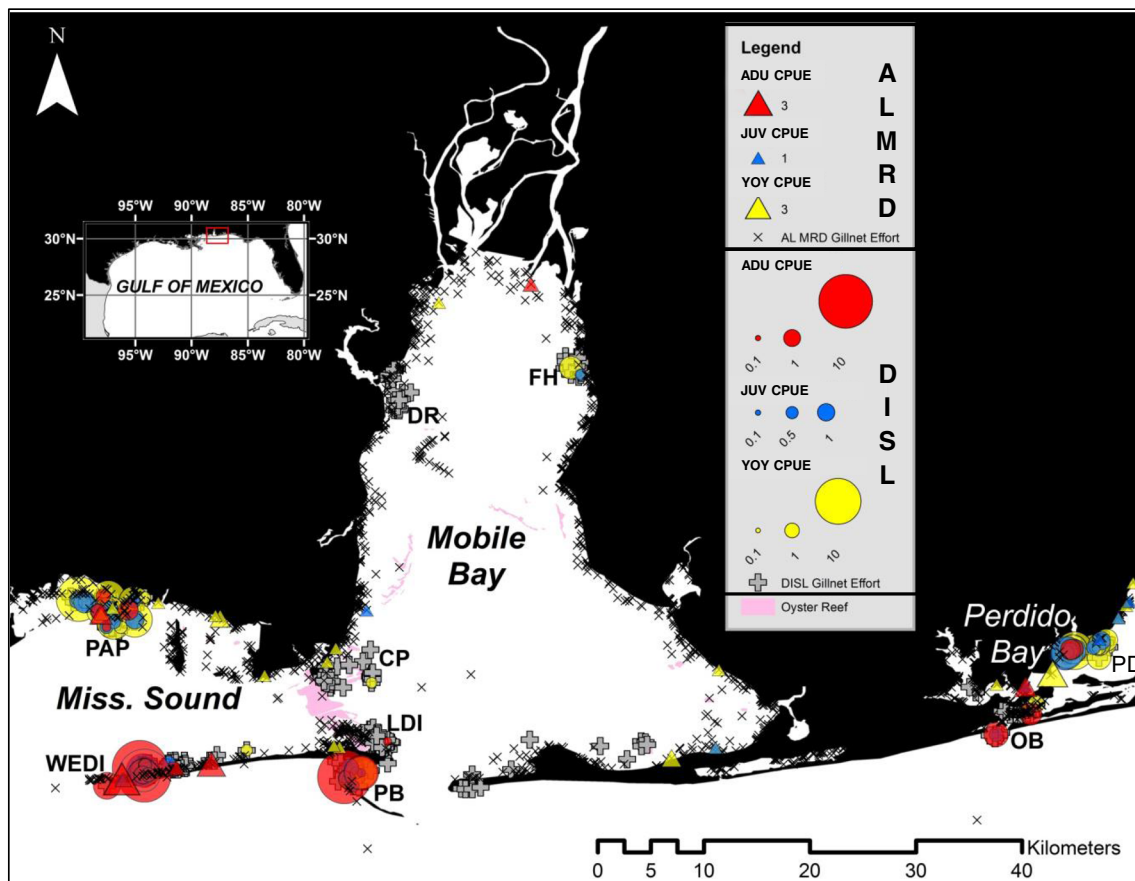


Fig. 4 Catch distribution and abundance map of cownose rays across coastal Alabama. Nominal catch per unit effort (CPUE, rays/net/h) is shown for three different life stages (yellow = YOY, blue = juvenile, and red = adult) for both the ALMRD (2004–2009) and DISL (2007–

2009) gillnet surveys. Black “X” marks and white circles represent locations where no rays were captured during ALMRD or DISL sampling, respectively. Pink polygons represent oyster reefs

2007b) whereas temperatures across coastal Alabama in this study were recorded well below 12 °C, the hypothesized lethal minimum temperature for cownose rays (Schwartz 1964).

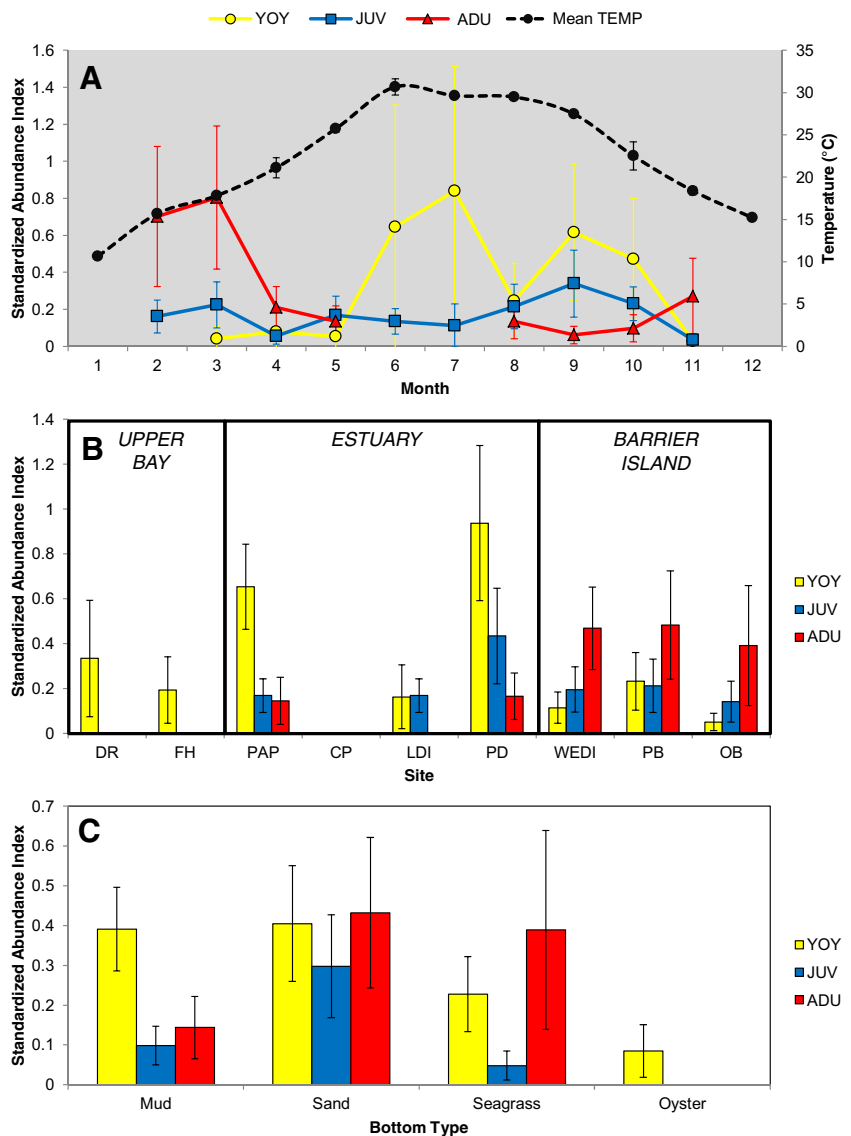
Support for massive aggregations of cownose rays is well documented in the literature. In lower Chesapeake Bay, surface schools of cownose rays have been estimated as large as 5×10^6 individuals (Blaylock 1989). Rogers et al. (1990) observed large surface schooling behavior in the northern Gulf of Mexico and estimated schools of >10,000 rays in the Chandeleur and Mississippi Sounds. The maximum surface school size we estimated from aerial surveys in this same region was 589 individuals, though this was likely an underestimate as cownose rays are known to stack atop one another when schooling (Schwartz 1990). School sizes of several hundreds of individuals were frequently reported in Chesapeake Bay (Blaylock 1993) and recently in Pamlico Sound (Goodman et al. 2010). While it is possible that previous school sizes were overestimated, the generally smaller sizes of schools observed in the northern Gulf of Mexico compared to the Atlantic coast may also be indicative of a lack of coordinated migratory behavior in this more subtropical large marine ecosystem (Schwartz 1990). Additionally, ray school

sizes and densities may be limited by heavier nearshore trawling activities in the northern Gulf of Mexico which routinely capture these animals as bycatch (Shepherd and Meyers 2005).

Along-Shelf Distribution

Along-shelf distribution of cownose ray schools in the northern Gulf of Mexico appears correlated with multiple environmental variables. Aerial survey data showed that relatively high densities of rays were observed adjacent to regions of large estuarine outflow, generally west of Mobile Bay. These regions are characterized by relatively lower salinities than regions to the east as they receive freshwater input from the Mississippi, Pascagoula, and Mobile-Tensaw rivers. Despite water clarity being poorer in these regions, the probability of observing a cownose ray school was highly elevated in shelf areas adjacent to these outputs, as were overall school sizes and sighting densities. These outflows are advected to the west as they leave these estuaries from north to south and are likely associated with higher productivity of benthic

Fig. 5 Standardized abundance indices of all life stages of cownose rays captured in the DISL gillnet survey (2007–2009) plotted against three factors: month (a), site/region (b), and bottom type (c). Error bars in all graphs represent jackknifed standard error values from delta-lognormal GLM. Abbreviations for sites: DR Dog River, FH Fairhope, PAP Point Aux Pins, CP Cedar Point, LDI Little Dauphin Island, PD Perdido Bay, WEDI West End Dauphin Island, PB Pelican Bay, OB Orange Beach. Within-region (b upper bay, estuarine, barrier island) sites are listed from west to east



invertebrates (Heip et al. 1995) that are consumed by cownose rays along this region (Ajemian and Powers 2012).

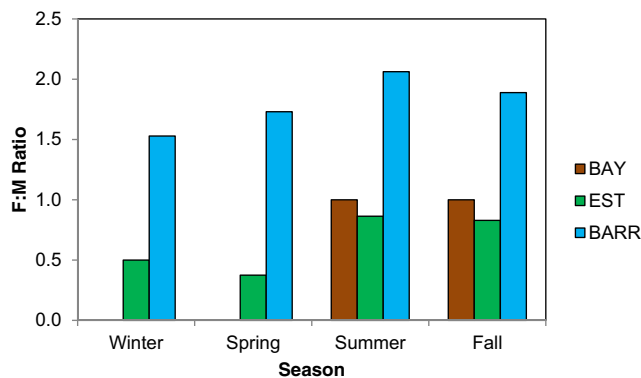


Fig. 6 Spatiotemporal variation in sex ratios of cownose rays based on gillnet survey data (2007–2009)

While the association of cownose rays with lower-saline waters has been demonstrated across numerous estuaries of the Atlantic coast, including Chesapeake Bay (Smith and Merriner 1987), Pamlico Sound (Goodman et al. 2010; Peterson et al. 2001), and various regions in the Gulf of Mexico (Collins et al. 2008; Craig et al. 2010), this study demonstrated that the probability of observing nearshore schools of cownose rays decreased with increasing nearshore salinities. Nearshore ray schools may avoid higher-saline regions (i.e., >33 psu) as an antipredator strategy since larger sharks are known to inhabit these waters (Drymon 2010). However, evidence for this remains weak as concurrent long-line survey data indicate most potential predatory shark species (bull: *Carcharhinus leucas*, great hammerhead: *Sphyrna mokarran*, sandbar: *Carcharhinus plumbeus*, scalloped hammerhead: *Sphyrna lewini*, spinner: *Carcharhinus brevipinna*, and tiger: *Galeocerdo cuvier*) have little to no pattern in along-

Table 4 Results from two-way crossed permutational analysis of variance on cownose ray life stage composition from DISL gillnet data

Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)	Unique perms
Region	1	13,749	13,749	7.3087	0.002	999
Season	3	21,077	7025.8	3.7348	0.005	999
Region × season	3	1926.1	642.04	0.3413	0.861	998
Res	80	1.51E + 05	1881.2			
Total	87	2.04E + 05				

shelf distribution in this region (Drymon 2010). Like adult cownose rays, both blacktip (*Carcharhinus limbatus*) and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks decrease in abundance from west to east along the Mississippi-Alabama shelf and are positively correlated with crustacean biomass and chlorophyll-a, respectively (Drymon et al. 2013). Thus, the along-shelf correlation observed between abundances of these smaller coastal sharks and cownose rays could indicate similar resource needs in these elasmobranch mesopredators.

A previous study in the region demonstrated coupling between cownose ray schools and high levels of chlorophyll-a (Craig et al. 2010). Despite the known association between this parameter and other predatory elasmobranchs (Sims et al. 2003; Weng et al. 2008), chlorophyll-a was not a significant driver of nearshore ray presence/absence or densities in our study. This contrasting finding may be due to differences in the sampling period between the two studies (summer vs. year-round) or inconsistencies in survey gears (aerial vs. trawl/aerial). Further analyses are needed to understand the impact of primary productivity on the distribution and abundance of these benthopelagic elasmobranchs.

While salinity best predicted the stochastic nature of cownose ray schools along the shelf, temperature and depth were most explanatory for sighting and ray density, respectively. Thus, while salinity may drive the broad-scale distribution of cownose rays, temperature and depth appear to control

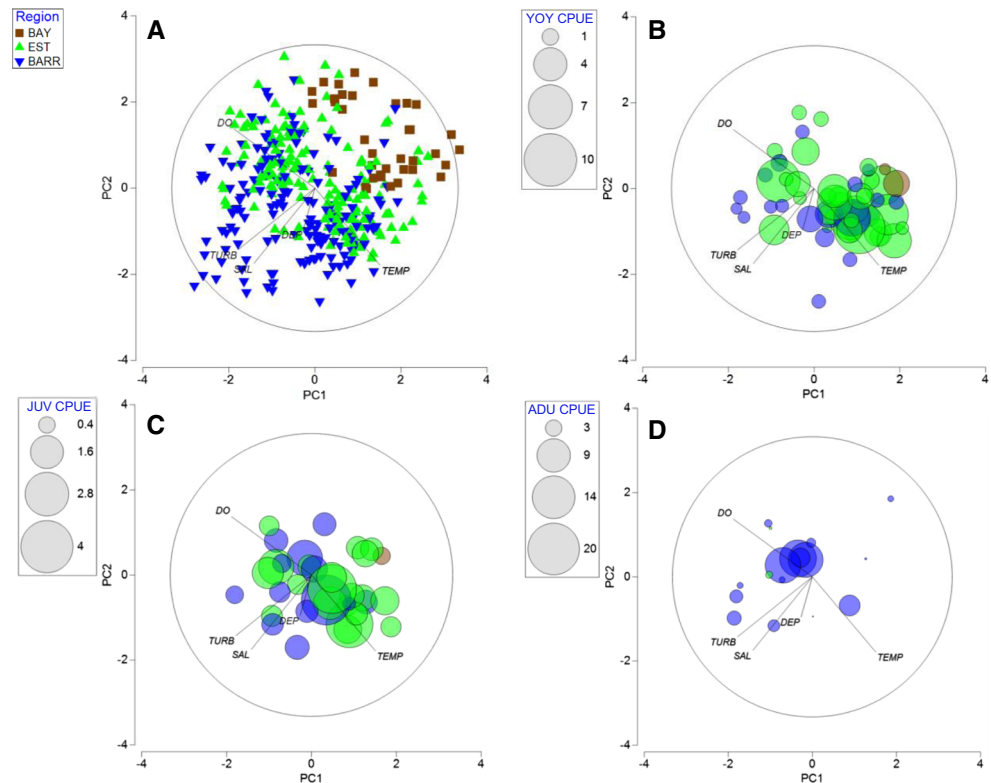
densities within those preferred salinity regimes. Our observations of maximal sighting densities during our spring survey (mean SST = 16 °C) is indicative of cownose ray ingress to coastal estuaries as demonstrated in more temperate areas of the Atlantic (Goodman et al. 2010; Smith and Merriner 1987). As waters warm through summer, nearshore ray schools become denser, but patchier. Large but spatially segregated aggregations during summer months along shallow shelf-regions could indicate that adults leave the inshore region after parturition for offshore reproductive activities.

We do caution that the depth effect on ray densities may be influenced by higher bottom contrast associated with shallower areas (<20 m), which may enhance the aerial observer's ability to sight rays. However, work by Craig et al. (2010) confirms the use of these shelf habitats during summer months. Taken together, these studies indicate that cownose rays are highly dependent on the nearshore region of the Gulf of Mexico. Unfortunately, we were unable to measure dissolved oxygen levels along the shelf, which are known to be inversely correlated with temperature and thus may have an impact on localized ray densities (Craig et al. 2010). Authors have suggested that hypoxic bottom waters make prey more available to these benthic foraging rays (Craig et al. 2010). Indeed, the locations of the large summer schools of cownose rays in the north-central Gulf of Mexico overlapped with regions of historical coastal hypoxia in the Mississippi Bight (Brunner et al. 2006), suggesting there may be a link between

Table 5 Results of BIO-ENV test identifying the independent variables that were best correlated with a Bray-Curtis similarity matrix of cownose ray life stage composition

Number of variables	Spearman correlation (ρ)	Variables selected
1	0.121	Temperature
2	0.111	Temperature Depth
3	0.107	Temperature Depth Turbidity
2	0.098	Temperature Turbidity
4	0.097	Temperature Salinity Depth Turbidity
3	0.096	Temperature Salinity Depth
2	0.094	Temperature Salinity
3	0.085	Temperature Salinity Turbidity
3	0.072	Temperature Depth Dissolved oxygen
4	0.071	Temperature Depth Turbidity Dissolved oxygen

Fig. 7 Principal component plots of normalized environmental data from DISL gillnet surveys (2007–2009). Plots are shown for PCs 1 and 2 (58.9 % variation explained) color-coded by region (bay = brown, estuary = green, and barrier island = blue) and shown for environmental conditions (a), and with overlays of nominal CPUE (scaled to size of bubbles) for three different life stages: young-of-the-year (b), juvenile (c), and adult (d). Trajectories of the five normalized variables (temperature, depth, salinity, turbidity, and dissolved oxygen) are also overlain for each plot. Note *bubbles* for each life stage are scaled differently relative to highest CPUE and represent 10, 40, 70, and 100 % intervals



cownose rays and overlying waters of low dissolved oxygen environments. However, given the timing of these aggregations and gillnet survey data from inshore locales, we suggest that these aggregations may also form for copulation purposes, as suggested for other benthopelagic batoids (Le Port et al. 2012; Notarbartolo-di-Sciaria and Hillyer 1989). Targeted capture, tagging, and environmental monitoring at these offshore sites could help further elucidate the roles of hypoxia and water temperature in cownose ray distribution and aggregation behavior.

Across-Shelf Distribution and Ontogenetic Partitioning

Our work demonstrated ontogenetic partitioning of habitat by cownose rays along inshore locales. Multivariate analyses suggest that temperature is an important abiotic driver of life stage partitioning. Young-of-the-year cownose rays were found at higher abundances in warmer, shallower, fresher, and more turbid inshore environments when compared to adults. This finding supports life history strategies found in several species of sharks (Grubbs 2010). Young-of-the-year (inclusive of neonates) abundance peaked in June and July and is likely associated with post-parturition. The highest abundances of YOY were observed at Point Aux Pins and Perdido Bay and were also observed at upper bay sites of Mobile Bay. These sites are characterized by muddy estuarine habitat and abundant benthic shellfish (Flemer et al. 1999),

and likely protect YOY from predators found along lower reaches of the estuary (Drymon 2010). As such, the regions of Mississippi Sound, Mobile Bay, and Perdido Bay may function as nurseries for cownose rays. Further tagging work (e.g., acoustic telemetry) is warranted to better assess the nursery potential (sensu Heupel et al. 2007) of these habitats.

Unlike many species of bony fishes, which generally switch from a benthic crustacean to bony fish diet with ontogeny (Mittlebach and Perrson 1998), all life stages of batoids (with the exception of filter-feeding mobulids) are morphologically restricted to feeding on the seabed (Dean et al. 2007). Despite this shared feeding location among life stages, we found evidence of variable benthic habitat use with ontogeny; YOY rays were more common over mud bottom habitats than other life stages, whereas adults appeared to prefer sandy bottom. The variability observed in bottom habitat use, which may be a simple correlation of where these benthic habitats are located across the estuary, suggests differential abilities of adults and YOY in sediment excavation for feeding. Larger and more powerful adult rays may be more adept at manipulating coarse sand and seagrass rhizomes (Orth 1975), whereas smaller individuals may only be capable of excavating finer mud and silt bottoms. A previous study in the region also showed that dietary differences existed among cownose ray life stages, with YOY consuming thin-shelled bivalves (e.g., *Mulinia lateralis*) associated with inshore waters, while adults preyed upon larger bivalves and gastropods along barrier

islands and the nearshore region (Ajemian and Powers 2012). As bite force scales with ontogeny in this species (Kolmann et al. 2015), it is possible that cownose ray ontogenetic distribution patterns could be an adaptation to inshore-offshore gradients in benthic prey size and shell thickness as well.

Young-of-the-year and juvenile cownose rays have reduced mobility compared to adult rays (Collins et al. 2007b), and may be unable to compete with larger individuals that are known to school and heavily exploit benthic resources to extinction (Peterson et al. 2001). Thus, the ontogenetic partitioning we observed may lastly be an adaptation to reduce intraspecific competition among life stages. In sum, the across-shelf partitioning observed in cownose ray ontogenetic composition likely maximizes food availability and reduces predation risk (Lima and Dill 1990). The causal mechanisms that explain the distribution patterns of this species over ontogeny need further experimentation. Future studies should attempt to stratify surveys by benthic habitat to better resolve ontogenetic partitioning of cownose ray substrate use.

Sexual Segregation

Sexual segregation has been noted for several species of coastal sharks in the northern Gulf of Mexico, where males generally outnumber females along inshore regions (Bethea et al. 2014). Habitat use differences between sexes may be linked to variation in temperature preference, foraging grounds, and/or reproductive behaviors (Wearmouth and Sims 2008). For many species of sharks, adult females utilize shallower and more turbid inshore environments as these represent productive and protected pupping areas for their newborns (Heithaus 2007). Our gillnet survey data do not support this paradigm as adult females dominated barrier island habitats fringing the Gulf of Mexico, whereas males dominated habitats further upstream in the estuary. This trend may be due to the more nomadic behavior of males, which may be more broadly distributed and thus lead to lower overall densities across habitats.

Near even sex ratios in the upper bay sites and estuarine regions in summer and fall are likely indicative of post-parturition as the catch in these areas was dominated by YOY. The consistently higher ratio of females at barrier islands across all seasons may indicate that these individuals prefer to remain in these habitats. This finding also suggests that parturition may occur along these barrier islands, and neonates follow cues to lower-saline regions of estuaries. This statement is supported by a single capture of 10 neonates (open umbilical scars; 30–37 cm DW) along with a female-dominated (90 %) group of 17 adults in Pelican Bay on June 9, 2009. While the capture of neonates adjacent to open waters of the Gulf of Mexico is somewhat surprising due to potential predator presence (Drymon 2010), salinity at the time of capture was 22.1 ppt and turbidity was relatively low at 70 cm. As

such, the dynamic habitat in this instance resembled estuarine conditions typically associated with pupping in elasmobranchs (Heithaus 2007). Adult female cownose rays may therefore aggregate around inlets during this period as they await suitable conditions for pupping. Further work is clearly needed on identifying the environmental conditions associated with parturition in cownose rays.

Oyster Restoration Impacts

Shellfish managers in the northern Gulf of Mexico must consider the strong spatiotemporal dynamics in cownose ray distribution and abundance in restoration planning. Due to habitat partitioning by life stage and, thus, varied gape and bite forces (Fisher et al. 2011; Kolmann et al. 2015), the risk of commercial bivalves to predation by cownose rays will vary spatially and seasonally in this region. Larger shellfish have the highest risk of being consumed late winter through spring and again in late fall, when the highest densities of adult rays are evident along inshore barrier island habitats and the lower reaches of the Mobile Bay estuary. However, few shellfish restoration projects currently exist in these areas, as they are generally situated further upstream in this system or along existing oyster reefs that do not appear to support high cownose ray densities. Thus, in concert with other recent studies of cownose ray feeding ecology along coastal Alabama (Ajemian and Powers 2012, Ajemian and Powers 2013), we consider the potential impacts of this species on shellfish restoration to be very limited in this region.

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