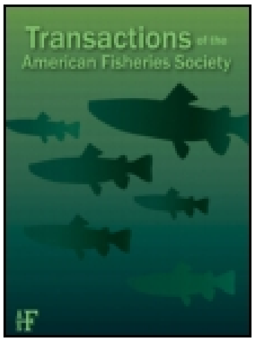

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ARTICLE

Recruitment of Juvenile Gags in the Eastern Gulf of Mexico and Factors Contributing to Observed Spatial and Temporal Patterns of Estuarine Occupancy

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Abstract

We conducted a comprehensive examination of long-term (10 + years) fisheries-independent data to characterize the spatial and temporal patterns of habitat selection and recruitment of juvenile gags *Mycteroperca microlepis* in four eastern Gulf of Mexico estuaries in Florida: Apalachicola Bay, Cedar Key, Tampa Bay, and Charlotte Harbor. Results from generalized linear modeling and habitat suitability analyses indicated that juvenile gags selected euhaline or polyhaline habitats with sloping bottoms and extensive coverage of submerged aquatic vegetation; the observed patterns were similar among estuaries. Latitudinal differences in the timing and duration of estuarine occupancy by juvenile gags were evident, with individuals appearing earlier and remaining later in more southerly estuaries. Significant interannual variability in recruitment of juvenile gags was evident within all estuaries, with high juvenile recruitment evident every 2 to 4 years. Continued efforts toward characterizing year-class strength through the development of a regional index of juvenile gag recruitment may be useful in forecasting fisheries productivity, although such efforts would benefit greatly from an increased understanding of the relative contribution of presumed estuarine nurseries to nearshore populations.

Gags *Mycteroperca microlepis* support extensive commercial and recreational fisheries in the eastern Gulf of Mexico. From 1986 to 2008, commercial landings of gags in the Gulf averaged approximately 800,000 kg annually, while annual recreational landings averaged approximately 1.2 million kg (National Marine Fisheries Service, Fisheries Statistics Division, personal communication). Despite the productivity of commercial and recreational gag fisheries, a 2009 stock assessment update indicated that gags in the Gulf are currently overfished and continue to undergo overfishing (SEDAR 2009). Gags are especially susceptible to the effects of overfishing due to unique life history characteristics such as size- and sex-specific depth and habitat preferences, longevity, slow maturation, and the tendency to form spawning aggregations (Coleman et al. 1996, 1999; Morris et al. 2000). Accordingly, traditional management practices such as restrictive size and bag limits have proven to be problematic for gag management due to the high probability of discard mortality for undersized individuals (Bartholomew and Bohnsack 2005) as well as the tendency to harvest proportionally more males from this protogynous hermaphrodite species. Overfishing of gags may be manifested in a variety of population-level responses, including declining abundance, reduced size, and a skewed sex ratio (Coleman et al. 1996, 2000; McGovern et al. 1998). These responses have led some to believe that gags are at an elevated risk of extinction (Musick et al. 2000).

In light of the status of the gag in the eastern Gulf of Mexico, it is especially important to improve understanding of its juvenile recruitment processes. As fishing effort increases, the quantity of biomass available to the fishery is increasingly linked to the strength of recruitment and survival of early life history stages (Smith 1993). Accordingly, accurate estimation and prediction

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of juvenile recruitment is critical to the effective assessment and management of at-risk fisheries (Smith 1993; Koenig and Coleman 1998; Coleman et al. 1999). Gags spawn along deep (50–120-m) shelf-edge reefs from late winter through early spring (McErlean 1963; Hood and Schlieder 1992; Coleman et al. 1996; Collins et al. 1998) and have a planktonic larval duration of 35–45 d before ingress and settlement in estuarine nurseries at approximately 15 mm standard length (SL) (Keener et al. 1988; Ross and Moser 1995; Fitzhugh et al. 2005). Juvenile gags generally occupy structured polyhaline habitats such as seagrass beds and oyster reefs for several months before emigrating to nearshore reefs in autumn (Ross and Moser 1995; Koenig and Coleman 1998; Levin and Hay 2003; Renán et al. 2006; Casey et al. 2007). The reliance of gags on estuarine nurseries, combined with a relatively brief period of estuarine occupancy, greatly facilitates the accurate characterization of the relative strength of juvenile recruitment.

Several field studies examining various aspects of habitat use by juvenile gags in the Gulf of Mexico have been published (Koenig and Coleman 1998; Fitzhugh et al. 2005; Renán et al. 2006; Casey et al. 2007); however, these studies have generally either been restricted to specific habitat features (e.g., shoal grass *Halodule wrightii*, turtle grass *Thalassia testudinum*, and manatee grass *Syringodium filiforme*) or focused on relatively limited temporal and spatial scales. To effectively characterize the recruitment of juvenile gags requires a comprehensive examination of multiyear data collected at the regional scale. Accordingly, we conducted a series of retrospective analyses of long-term (10 + years) monitoring data collected in four eastern Gulf of Mexico estuaries to (1) examine regional variability in the strength and timing of juvenile gag recruitment and (2) characterize the relative importance of various environmental factors in structuring observed patterns of distribution and abundance of juvenile gags. These analyses not only will enhance our understanding of recruitment processes for juvenile gags in the eastern Gulf but also will provide valuable insight into observed patterns of habitat use and the relative importance of various habitat types.

METHODS

Study area.—We investigated patterns of habitat use by gags in four estuarine systems—Apalachicola Bay, Cedar Key, Tampa Bay, and Charlotte Harbor—extending from the Florida Panhandle to midpeninsular Florida (Figure 1). These estuaries are proximate to the West Florida Shelf, a broad expanse of ocean bottom containing much of the natural hard-bottom habitat of the Gulf of Mexico (Briggs 1958; McEachran and Fechhelm 1998) as well as the principal shelf-edge spawning habitat for gags in the region (Moe 1963; Coleman et al. 1996; Koenig et al. 2000). The broad geographic expanse of the overall study area encompasses two distinct climatic regions that are reflected in fundamental latitudinal differences in aquatic floral (Sherrod and McMillan 1985) and ichthyofaunal (Smith 1976) communities.

Apalachicola Bay and Cedar Key, the two most northerly estuaries included in the present study, differ markedly with respect to geomorphological characteristics. Apalachicola Bay is a shallow, semi-enclosed estuary bounded by a barrier island complex. Freshwater flow into Apalachicola Bay originates from the Apalachicola River and, to a lesser extent, the Carabelle River (Livingston 1983). Cedar Key, the only open coastal system sampled in this study, includes the Suwannee River estuary to the north. Although freshwater flow into Cedar Key is dominated by the Suwannee River, additional freshwater input originates from numerous fringing marsh tidal creeks (Lindberg et al. 1992). Shoreline vegetation within both systems consists largely of salt marsh habitat (primarily smooth cordgrass *Spartina alterniflora* and black needlerush *Juncus roemerianus*). Both systems contain seagrass meadows (mainly shoal grass, turtle grass, and manatee grass) that are restricted essentially to the outer regions of each estuary.

Tampa Bay and Charlotte Harbor, the two most southerly estuaries sampled during the present study, have historically been viewed as drowned-river estuaries (Galperin et al. 1991; Sheng 1998), although recent evidence brings this conclusion into question for Tampa Bay (Suthard et al. 2010). Both Tampa Bay and Charlotte Harbor are bounded by barrier islands and connected to the Gulf of Mexico by several main channels and smaller passes. Freshwater flow into Tampa Bay originates primarily from the Alafia, Hillsborough, Manatee, and Little Manatee rivers, all of which have numerous smaller tributaries (Schmidt and Luther 2002). Freshwater flow into Charlotte Harbor comes principally from the Peace, Caloosahatchee, and Myakka rivers. Shoreline vegetation for both systems consists largely of fringing mangroves (predominantly red mangrove *Rhizophora mangle* and black mangrove *Avicennia germinans*). Seagrasses (predominantly turtle grass and shoal grass) are widely distributed throughout the shallow regions of both estuaries.

Field methods.—Monthly stratified-random sampling of shoreline habitats was initiated in January 1997 in Tampa Bay and Charlotte Harbor, in January 1998 in Cedar Key, and in January 1999 in Apalachicola Bay; the results presented here include data collected through December 2009 for all four estuarine systems. Monthly sampling effort was allocated among spatial zones defined by geographic and logistic criteria that defined areas of biological and hydrological homogeneity. In Tampa Bay and Charlotte Harbor, sampling locations were further stratified based on the presence or absence of overhanging shoreline vegetation. Monthly sampling effort within each stratum for each estuary was proportional to the total number of potential sampling sites available. All sampling sites were selected randomly without replacement each month. For additional survey design details, see Winner et al. (2010).

Samples were collected by using a 183-m × 2.5-m center-bag haul seine with nylon netting of 38-mm stretched mesh that was deployed by boat, set in a rectangular shape along the shoreline (approximately 40 × 103 m, or 4,120 m^2), and retrieved

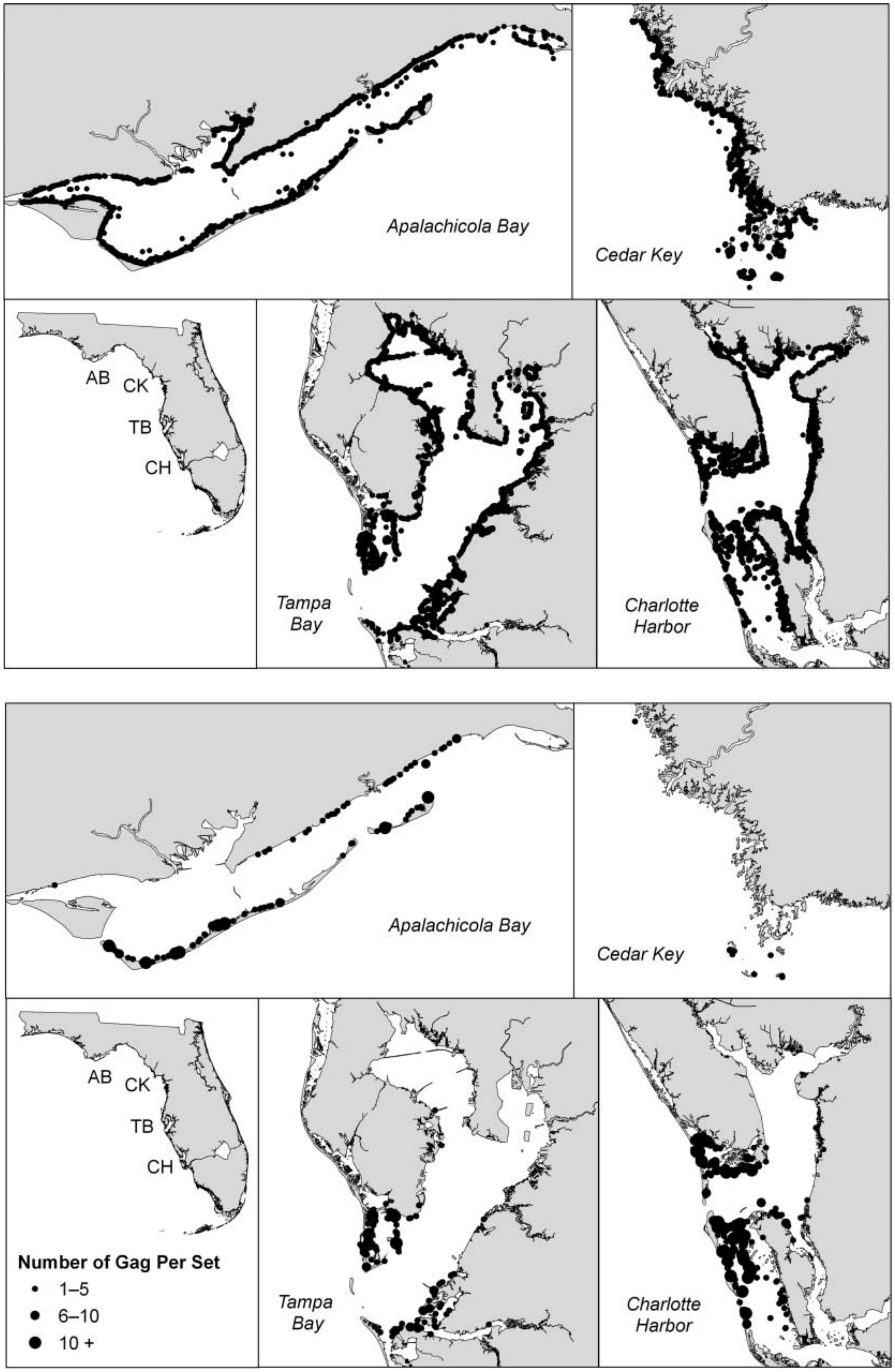

FIGURE 1. Maps of the four estuarine systems in the eastern Gulf of Mexico within which monthly stratified-random sampling of nekton abundance was conducted (AB: Apalachicola Bay, 1999–2009; CK: Cedar Key, 1998–2009; TB: Tampa Bay, 1997–2009; CH: Charlotte Harbor, 1997–2009). In the upper set of panels, the circles represent the locations at which samples were collected. In the lower set of panels, the circles represent the locations at which gags were collected; the size of each circle represents the total number of gags within that set.

by hand. All gags collected in each sample were identified and enumerated, and as many as 40 individuals per sample were measured to the nearest millimeter SL. Location, date, time, and water depth along the shoreline (wing depth) and at the bag of the net (bag depth) were recorded at each sampling site; wing depth was then subtracted from bag depth to calculate a proxy for bottom slope for the area sampled by the haul seine. Temperature (°C) and salinity (practical salinity units [psu]) were recorded at the surface, at 1.0-m depth intervals, and near the bottom (~0.2 m); temperature and salinity values were averaged for each sample. Estimated distance from the net to the land–water interface (distance to shore in meters) and percentage coverage of submerged aquatic vegetation (SAV cover) were recorded at the time of sampling for each net set. Primary components of bottom type were identified in the field and were used to characterize bottom type at each sampling location as mud, mud–sand, sand, and shell (oysters and shell hash present).

Analytical methods.—Initially, total effort and catch data were summarized for all gags collected within each estuarine system. Locations at which samples were taken, as well as those at which gags were collected, were plotted for each estuary in a geographic information system to explore spatial patterns of catch and effort. In addition, length-frequency histograms were constructed monthly to explore variability among the four estuarine systems with respect to the timing of juvenile recruitment as well as the duration of estuarine occupancy for young of the year (age-0) gags. Due to our interest in examining the nursery function of estuarine habitat for juvenile gags, subsequent analyses were restricted to presumed age-0 gags only; age-0 gags were defined primarily as fish of $\leq$300 mm SL (Hood and Schlieder 1992), although smaller individuals that were clearly from prior cohorts based on examination of monthly length-frequency histograms were excluded as well.

Mean values of the environmental conditions sampled, as well as means of the conditions sampled in areas occupied by juvenile gags, were explored using principal-component analysis (PCA). A PCA that included data from all four estuarine systems (Apalachicola Bay, Cedar Key, Tampa Bay, and Charlotte Harbor) was conducted to resolve five correlated environmental covariates (bag depth, bottom slope, salinity, SAV cover, and temperature) into three orthogonal components based on the correlation matrix. The PCA was conducted by using the FACTOR procedure and SAS software (SAS Institute 2006a), and the first three principal components (PCs) were rotated by using the varimax option to facilitate the interpretability of each component. Variable loadings and PC scores were calculated independently for each sample. Mean environmental conditions sampled were calculated by averaging all PC scores for each estuarine system. Mean environmental conditions occupied by juvenile gags were calculated in a similar manner, although each observation was weighted by the relative abundance of juvenile gags (individuals per seine haul). Mean PC scores were then plotted in three-dimensional PC space to explore differences between environmental conditions sampled and environmental conditions occupied by juvenile gags for each estuarine system.

The effects of several environmental and habitat metrics on the variability of the relative abundance of gags (individuals per seine haul) were explored for three of the four estuaries (Apalachicola Bay, Tampa Bay, and Charlotte Harbor) by using generalized linear modeling; data from Cedar Key were excluded from subsequent statistical analyses because juvenile gags were rarely collected there. The relative abundance of gags represents count data, the distribution of which is bounded by zero and therefore often highly nonnormal. Accordingly, generalized linear models based on the Gaussian distribution with a $\log_{10}$ transformation, the Poisson distribution, and the negative binomial distribution were fit to the data, and residual diagnostics and goodness-of-fit statistics were examined to determine the most appropriate model. For all three estuaries, the model based on the negative binomial distribution was deemed the most appropriate. Year and bottom type were included as categorical explanatory variables in the model, while temperature, salinity, distance to shore, bag depth, bottom slope, and SAV cover were included as covariates. Variables identified as nonsignificant ($\alpha = 0.05$) were excluded, and the analysis was repeated in a stepwise fashion until only significant variables remained in the model. Results are reported only for statistically significant variables. For each estuarine system, annual least-squares-mean estimates ± SEs of gag relative abundance were plotted in an assessment of temporal variability in juvenile gag recruitment. All analyses were fit by using the GLIMMIX procedure and SAS software (SAS Institute 2006b).

For each factor that significantly explained a portion of the variability in the relative abundance of gags for at least one estuarine system, habitat suitability curves were constructed to characterize patterns of habitat selection (Baltz 1990). Suitability curves allow for an examination of resource use that accounts for nonuniform sampling across environmental gradients and provide valuable information regarding patterns of habitat selection. For each univariate habitat suitability analysis, environmental data were subdivided into equal intervals. For each interval, habitat suitability values (S) were then calculated as

$$S = P(E|F)/P(E),$$

where $P(E|F)$ represented the proportion of samples within which a species occurred (resource use) that fell within a specific environmental interval, while $P(E)$ represented the proportion of all samples collected, regardless of whether a given species occurred (resource availability), that fell within the same environmental interval (Baltz 1990). Suitability values for each analysis were then standardized by dividing by the greatest observed suitability so that values ranged from 0 (least suitable) to 1 (optimal). Suitability curves were constructed independently for each estuarine system.

TABLE 1. Summary of long-term monthly sampling effort and overall catch and size data for gags in four estuarine systems in the eastern Gulf of Mexico.

Estuarine system	Years sampled	Number of total samples	Number of samples containing gags (%)	Number of gags collected	Standard length (mm)		
					Mean ± SE	Minimum	Maximum
Apalachicola Bay	1999–2009	2,520	123 (4.9%)	447	161 ± 2.2	45	380
Cedar Key	1998–2009	2,232	13 (0.6%)	22	175 ± 13.8	94	334
Tampa Bay	1997–2009	3,115	107 (3.4%)	357	196 ± 3.8	75	645
Charlotte Harbor	1997–2009	2,652	262 (9.9%)	1,295	186 ± 1.6	58	499
Total		10,519	505 (4.8%)	2,121			

RESULTS

From 1997 through 2009, a total of 10,519 seine haul samples were collected within four estuarine systems along the Florida Gulf coast, of which 505 samples (4.8%) contained gags (Table 1). In total, 2,121 gags were collected during haul-seine surveys. Gags were most frequently collected in Charlotte Harbor, where they occurred in nearly 10% of the samples, although gags were routinely collected in the lower portions of all three semi-enclosed estuarine systems (Apalachicola Bay, Tampa Bay, and Charlotte Harbor; Figure 1). Gags were rarely collected in Cedar Key (Table 1; Figure 1). Gags ranged from 45 to 645 mm SL (Table 1), although most individuals were generally smaller than 300 mm SL and presumably were age 0 (Figure 2). Juvenile gags began appearing in May and June, although young juveniles ($\leq$70 mm SL) were rarely collected within haul-seine samples, especially in the southernmost estuaries. Early in the recruitment season (June), clear latitudinal differences in the size structure of gags were evident, and larger

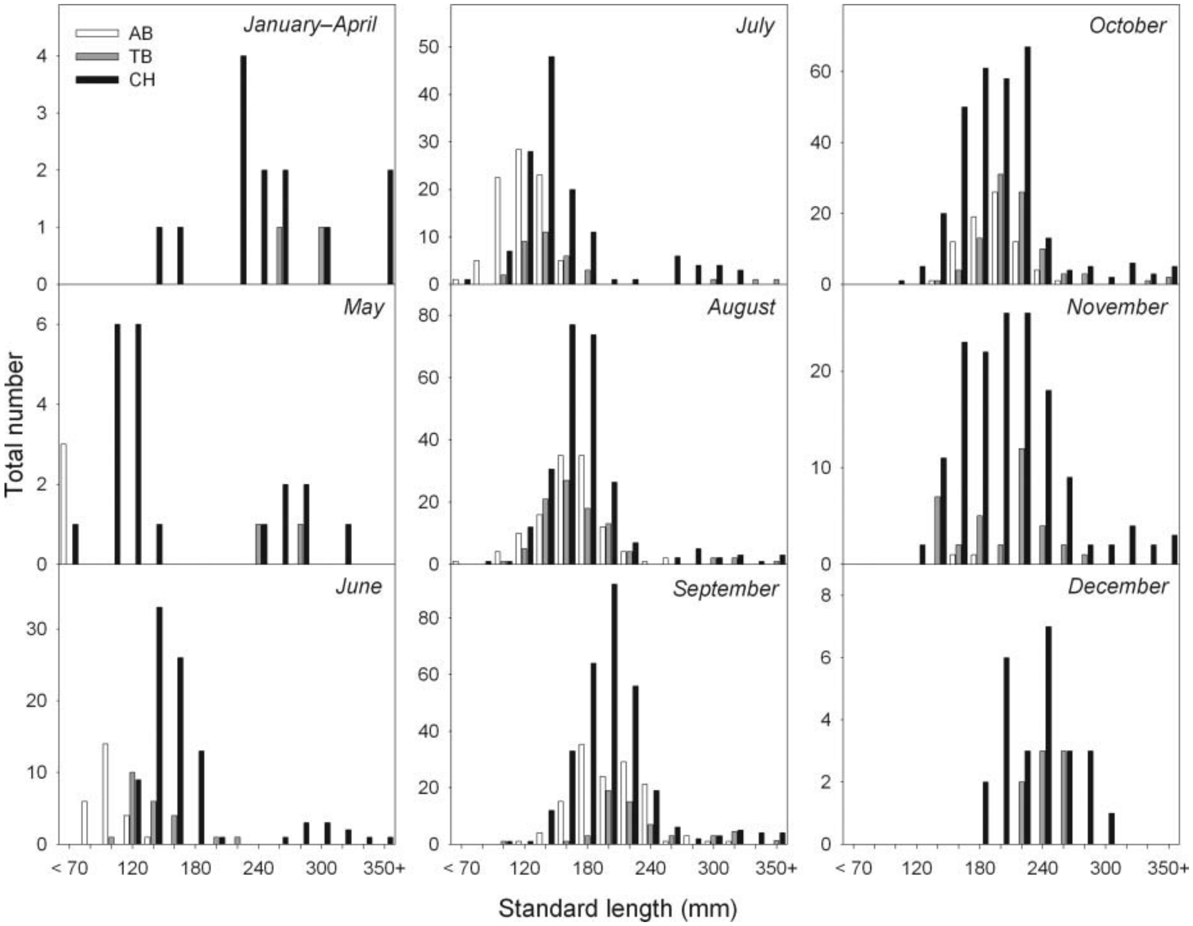

FIGURE 2. Monthly length-frequency distributions for gags collected in three estuarine systems in the eastern Gulf of Mexico. Data for January–April were pooled due to the exceptionally small numbers of gags collected during those months.

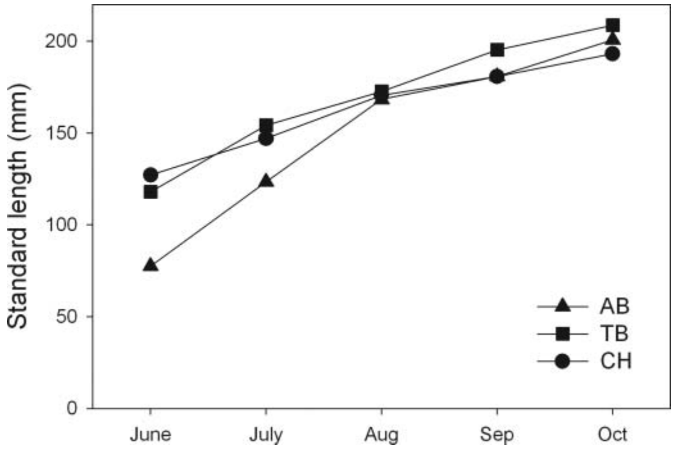

FIGURE 3. Monthly mean standard lengths of juvenile gags collected within three estuarine systems in the eastern Gulf of Mexico.

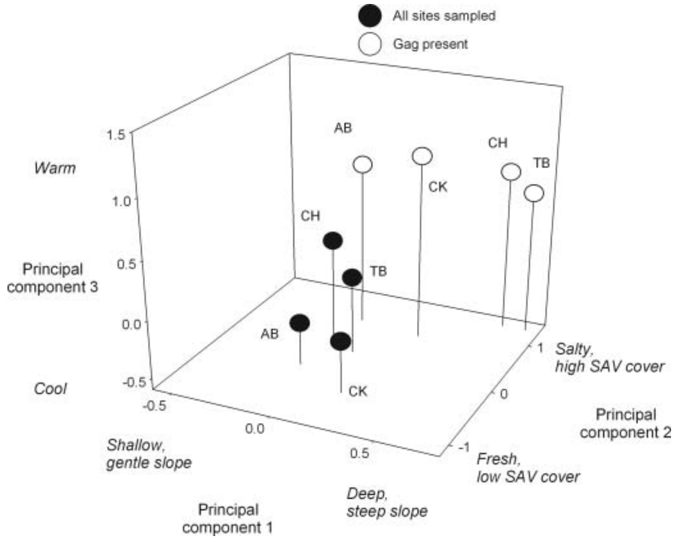

FIGURE 4. Estuary-specific patterns of microhabitat use (open circles) and availability (filled circles) for juvenile gags in three-dimensional principal-component space within four estuarine systems in the eastern Gulf of Mexico. Circles indicate the locations of the mean principal-component centroids.

individuals were collected in the more southerly estuaries (Figures 2 and 3). By August, latitudinal differences in the mean size of gags collected were no longer evident. In Apalachicola Bay, the number of gags collected declined sharply in November, and no gags were collected from December through April (Figure 2). Both juvenile (≤300 mm SL) and subadult–adult (>300 mm SL) gags were collected year-round in Tampa Bay and Charlotte Harbor, although numbers were smallest from January through April (Figure 2).

The PCA of combined environmental data from all four estuaries identified three major axes of environmental variability (eigenvalues > 1) that together accounted for 86% of total variability (Table 2). The first PC was generally a factor of water depth, with large, positive loadings for both bag depth and bottom slope. The second component had large, positive loadings for salinity and SAV cover and was interpreted as a gradient from the inner to the outer estuary. The third component had a large, positive loading for temperature alone. A plot of mean estuarine-specific PC scores for all samples identified moderate differences in environmental conditions sampled within the four estuarine systems (Figure 4). On average, the northern estuaries (Apalachicola Bay and Cedar Key) were cooler than the southern estuaries (Tampa Bay and Charlotte Harbor), reflecting latitudinal differences in solar input. Sites sampled within the two northern estuaries also had lower salinities and less SAV cover than did the two southern estuaries. Sampling sites within Cedar Key were generally deeper and had steeper bottom slopes than those sampled in the other estuaries. For all four estuaries, a plot of mean PC scores indicated that mean environmental conditions of sites occupied by juvenile gags differed markedly from overall mean conditions observed in all sites sampled (Figure 4). In general, sites that contained juvenile gags were warmer and deeper with steeper bottom slopes, higher salinities, and greater SAV coverage than the average conditions sampled; these differences were most pronounced in Tampa Bay and Charlotte Harbor.

TABLE 2. Results of a principal components analysis examining the interrelatedness of five environmental variables quantified during monthly sampling of shoreline habitats in four estuarine systems (Apalachicola Bay, Cedar Key, Tampa Bay, and Charlotte Harbor) along the Florida Gulf coast.

	Principal component		
Environmental variable	1	2	3
Bag depth	0.96	0.02	0.05
Bottom slope	0.96	−0.02	−0.09
Salinity	0.12	0.84	−0.02
SAV cover	−0.13	0.82	0.12
Temperature	−0.02	0.07	0.99
Variance explained	1.89	1.39	1.01
Proportion of variance explained	0.38	0.29	0.19
Cumulative variance explained	0.38	0.67	0.86

Results from generalized linear modeling analyses indicated that for all three estuarine systems the relative abundance of juvenile gags was significantly related to temperature, salinity, bottom slope, and SAV cover (Table 3). The relative abundance of juvenile gags was also significantly related to bottom type in both Apalachicola Bay and Charlotte Harbor; neither distance to shore nor bag depth were significantly related to juvenile gag relative abundance. Significant interannual variability in the relative abundance of juvenile gags was evident for all three estuarine systems (Table 3). Observed temporal patterns of juvenile gag abundance were cyclical, with strong juvenile recruitment occurring every 2 to 4 years (Figure 5). Observed interannual variability in juvenile recruitment was generally concordant among estuaries, with strong year-classes of gags evident in 1999, 2002–2003, and 2007.

TABLE 3. Results of generalized linear modeling analyses of the effect of year and several habitat and physiochemical variables on the catch per unit effort (number of individuals per 183-m haul seine) of juvenile (≤300 mm SL) gags in three estuarine systems in the eastern Gulf of Mexico. The significance level for inclusion in the final model was set at 0.05; model variables that were eliminated from the final model via an iterative stepwise process are identified as nonsignificant (NS). Abbreviations are as follows: Ndf = numerator degrees of freedom, Ddf = denominator degrees of freedom.

		Apalachicola Bay (Ddf = 2,405)		Tampa Bay (Ddf = 2,591)		Charlotte Harbor (Ddf = 2,508)	
Model variable	Ndf	*F*	*P*	*F*	*P*	*F*	*P*
Temperature	1	81.4	<0.0001	41.5	<0.0001	82.9	<0.0001
Salinity	1	8.1	0.0046	6.2	0.0125	7.0	0.0084
Distance to shore			NS		NS		NS
Bag depth	1		NS		NS		NS
Bottom slope	1	5.6	0.0185	41.0	<0.0001	90.6	<0.0001
SAV cover	1	60.9	<0.0001	62.9	<0.0001	143.6	<0.0001
Bottom type	3	3.8	0.0104		NS	5.1	0.0016
Year	12[a]	5.0	<0.0001	2.2	0.0095	6.0	<0.0001

[a]For Apalachicola Bay, df = 10 because sampling did not begin year-round until 1999.

Univariate habitat suitability analyses of factors found to significantly contribute to the relative abundance of juvenile gags (temperature, salinity, bottom slope, SAV cover, and bottom type) identified clear patterns of resource use that were generally consistent across all three estuarine systems (Figures 6–7). Warm temperatures (24–36°C) and high salinities (28–40 psu) were the most suitable physicochemical conditions for juvenile gags (Figure 6); no gags were collected at temperatures <16°C or at salinities <10 psu. Habitat suitability for juvenile gags was

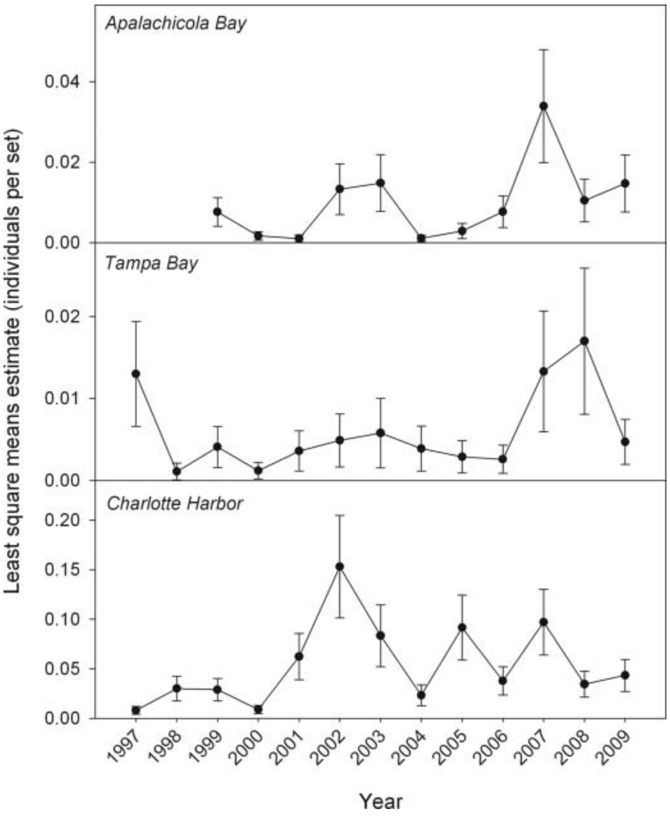

FIGURE 5. Annual least-squares means of the abundance of juvenile gags within three estuarine systems in the eastern Gulf of Mexico, as estimated via generalized linear modeling. The error bars represent SEs; note the differences in the scales of the *y*-axis.

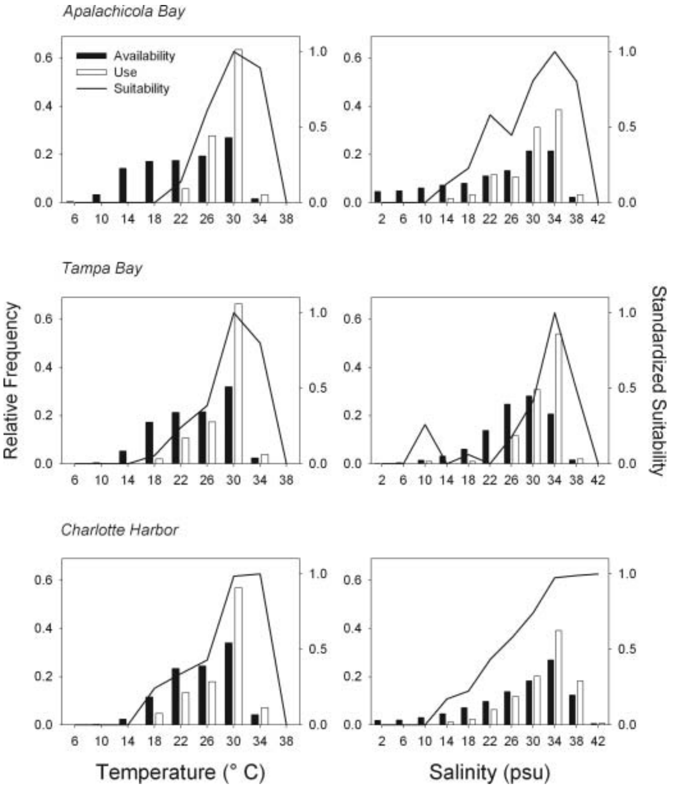

FIGURE 6. Habitat suitability along temperature (left panels) and salinity gradients (right panels) for juvenile gags collected within three estuarine systems in the eastern Gulf of Mexico. Filled bars represent the relative frequencies of the total number of samples collected, open bars represent the relative frequencies of samples that contained juvenile gags, and lines represent the results of habitat suitability analyses.

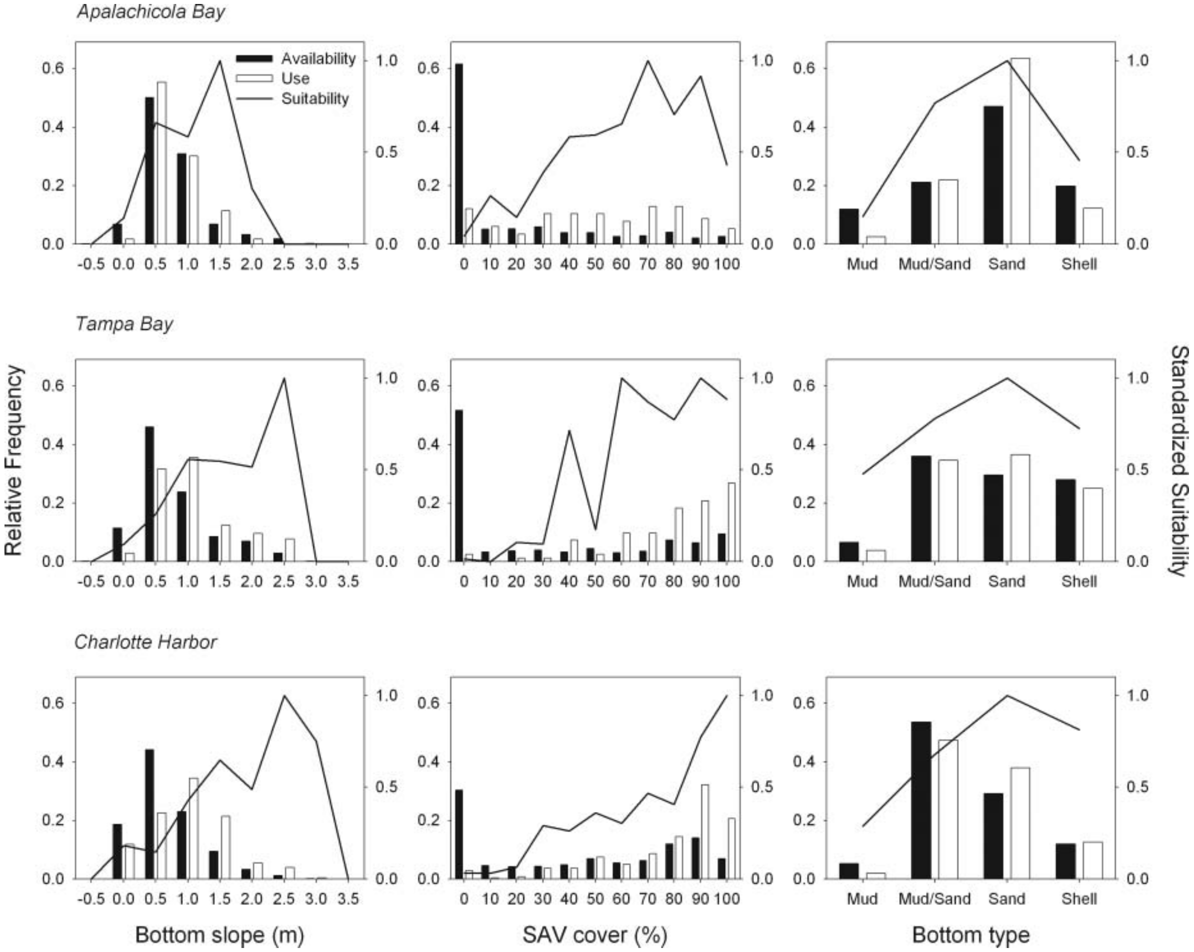

FIGURE 7. Habitat suitability along bottom slope (left panels), estimated percentage cover by submerged aquatic vegetation (SAV; center panels), and bottom type gradients (right panels) for juvenile gags collected within three estuarine systems in the eastern Gulf of Mexico. Filled bars represent the relative frequencies of the total number of samples collected, open bars represent the relative frequencies of samples that contained juvenile gags, and lines represent the results of habitat suitability analyses.

also high at locations with steeply sloping bottoms, >50% SAV coverage, and either sand or oysters and shell hash as a major component of bottom type (Figure 7).

DISCUSSION

Results from this study corroborated the paradigm that high-salinity seagrasses function as nursery habitat for juvenile gags. Various studies have documented the use of polyhaline seagrass habitat by juvenile gags, although several were conducted exclusively within polyhaline seagrass beds (Koenig and Coleman 1998; Fitzhugh et al. 2005; Renán et al. 2006) and did not explicitly examine the relative importance of non-seagrass habitats. Juvenile gags have been documented in nearshore waters off Tampa Bay but in substantially smaller numbers than in estuarine waters (Hood and Schlieder 1992). Ross and Moser (1995), who studied a North Carolina estuary, reported that small juvenile gags (<200 mm SL) were collected predominantly at polyhaline seagrass stations and were generally absent from unvegetated stations, but they did not attempt to quantify the observed distributional patterns. Casey et al. (2007) significantly correlated greater catch per unit effort of juvenile gags with greater seagrass coverage in a subtropical Florida estuary. By examining data collected from multiple estuarine systems at sites with widely ranging salinity levels and SAV coverage, this study builds upon previous work by characterizing patterns of habitat use and selection (Baltz 1990). In this study, juvenile gags generally were collected more frequently at euhaline and, to a lesser extent, polyhaline sites, although the factors contributing to observed patterns of selection along a salinity gradient remain unclear. It is unlikely that juvenile gags exhibit direct mortality as a result of lower salinity in mesohaline waters, since juveniles were collected at salinities as low as 10 psu, although indirect mortality, through physiological stress and concomitant reductions in growth, is possible (Bachman and Rand 2008). Alternately, juvenile gags may settle at the first suitable habitat they encounter, after which their relatively low general mobility may keep them from entering lower-salinity regions (Koenig and Coleman 1998). Juvenile gags were also found to select sites with substantial SAV coverage. Juveniles are thought to select structured habitat such as seagrass because it provides both food and refuge, although reconciling the relative importance of these two factors is difficult. Results of a series of mesocosm experiments indicated that juvenile gags actively select structured seagrass habitats, especially those with greater shoot densities; observed patterns appear to reflect a selection of refugia, since the addition of a small shelter was found to dramatically increase the usage of habitats that were previously not selected (Levin and Hay 2003). With respect to diet, juvenile gags appear to feed opportunistically on prey abundant in seagrass habitat (Ross and Moser 1995; Stallings 2010), although feeding success may decline in high-density seagrass habitats (Levin and Hay 2003). It was beyond the scope of the present study to conduct a detailed assessment of key seagrass metrics such as shoot density; nevertheless, the threshold of SAV coverage that defined highly suitable habitat varied among the estuaries studied. In Apalachicola Bay and Tampa Bay, where more than half of all sites sampled were unvegetated, habitat suitability for juvenile gags was consistently high for sites with greater than 50% SAV coverage. In Charlotte Harbor, where seagrass was absent in only 30% of the sites sampled, only sites with more than 90% SAV coverage were highly suitable. Whether these patterns indicate that juvenile gags occupy sites with suboptimal levels of SAV coverage in estuaries with presumably limited SAV availability (e.g., Apalachicola Bay, Tampa Bay) or reflect differential processes of habitat selection among the various estuaries studied remains unclear. Either way, it appears that juvenile gags face an important trade-off between feeding and refugia when selecting specific attributes within seagrass landscapes.

Although the general patterns of habitat use by juvenile gags were consistent among estuaries, latitudinal differences in the timing and duration of estuarine occupancy were evident. Few postsettlement gags were collected in this study, so observed trends do not necessarily reflect the timing of larval ingress. Juvenile gags did, however, appear earlier in the year and remained later at more southerly latitudes, which is consistent with results from other published studies. Throughout the eastern Gulf of Mexico, mean fertilization and settlement dates for juvenile gags collected in the north (April–May) were several weeks later than dates for juvenile gags collected in more southerly estuaries and off the Yucatan peninsula (March–April; Fitzhugh et al. 2005; Renán et al. 2006). Latitudinal variability in the timing of ingress and settlement of juvenile gags has been well documented (Keener et al. 1988; Ross and Moser 1995; Fitzhugh et al. 2005; Renán et al. 2006), but the causative mechanisms are poorly understood. These differences probably are not attributable to differences in larval duration, since gags throughout the southeastern United States consistently settle after residing for approximately 40 d in the plankton community (Keener et al. 1988; Fitzhugh et al. 2005). Observed differences in timing of settlement could indicate regional differences in the timing of spawning, but given the long-held assertion that gag spawning aggregations on the West Florida Shelf function as the sole source of larvae for coastal estuaries throughout the eastern Gulf of Mexico, this would appear not to be the case. Fitzhugh et al. (2005) did not detect regional differences in the timing of spawning on the West Florida Shelf; peak spawning occurred from February through April, consistent with earlier studies in the northeastern Gulf of Mexico (Hood and Schlieder 1992; Coleman et al. 1996; Collins et al. 1998). Another possibility, initially proposed by Fitzhugh et al. (2005), is that some juveniles collected within southwest Florida estuaries originated from a second spawning location. Brulé et al. (2003) documented peak spawning activity of gags on the Campeche Bank off the Yucatan Peninsula from January through March, a full month earlier than in the northeastern Gulf of Mexico. Under certain conditions, the Loop Current can intrude onto the West Florida Shelf (Hetland et al. 1999; He and Weisberg 2003) and could function as a conduit for larval transport from the Campeche Bank to southwest Florida (Toner et al. 2003; Jue 2010). An examination of regional patterns of genetic variability in gags of the southeastern United States indicated that for some gene loci there were differences between gags collected in north Florida and those collected on Florida's west coast (Chapman et al. 1999). Although the relative importance of gag populations of the Campeche Bank in supplying larvae to southwest Florida estuaries is unknown, that the region may have a second source of larval gags has important implications for our understanding of recruitment processes for juvenile gags in the eastern Gulf of Mexico.

Factors other than regional differences in the timing of peak spawning may also contribute to latitudinal differences in the timing and duration of estuarine occupancy. In the present study, juvenile gags collected in early summer (June–July) were larger in the more southerly estuaries than they were to the north (Figures 2 and 3). We did not explicitly examine the age of juvenile gags in this study, although observed latitudinal variation in mean size is consistent with the notion that juvenile gags are generally younger in more northerly estuaries (Fitzhugh et al. 2005). Throughout most of Florida, estuarine seagrasses experience significant winter leaf dieback, with a concomitant decline in overall productivity; seagrass recovery occurs earlier in the south than it does in more northerly estuaries (Zieman and Zieman 1989; Fitzhugh et al. 2005). Gags that settle earlier in the year may have greater mortality rates in the north, where seagrass habitat has not yet recovered, which could explain the observed latitudinal variability in mean size and, presumably, age. By fall (September–October), juvenile gags reach a similar size in all estuaries, suggesting that gags in the north compensate through increased growth compared with those farther south. The egress of juvenile gags is thought to be triggered by sharp (5–10°C) reductions in water temperature that follow the passage of strong cold fronts (Ross and Moser 1995; Koenig and Coleman 1998), although a shift in energy allocation from growth to storage in preparation for egress occurs well before the temperature decreases significantly (Stallings et al. 2010).

Although most juvenile gags leave the estuary and migrate to nearshore reefs in the fall (Ross and Moser 1995; Koenig and Coleman 1998), this behavior is not universal. Gags that were presumably age 1 or older were routinely collected in both Tampa Bay and Charlotte Harbor; whether age-1 and older gags overwintered in estuarine nurseries or returned to their natal estuary after moving into the nearshore Gulf of Mexico is not clear (Heinisch and Fable 1999; Casey et al. 2007). It is also uncertain whether continued reliance by individual gags on estuarine habitats represents an alternate life history strategy or reflects the response of individuals to external environmental cues. Gags that continue to occupy estuarine habitats beyond the first year of life will undoubtedly exhibit different rates of growth, feeding, and survival than will individuals that egress and remain near shore; these differences may have important population-level implications, especially if continued reliance on estuarine habitat is evident in a substantial proportion of the population.

Although commonly collected within the three semi-enclosed estuaries considered in this study, gags were rarely encountered in Cedar Key, the only open coastal system sampled. There are several possible explanations for the relative paucity of gags in Cedar Key. Cedar Key is not a classical estuarine system (i.e., a semi-enclosed body of water where freshwater and saltwater mix; Day et al. 1989); nevertheless, freshwater discharge from the Suwannee River does result in the formation of an estuarine salinity gradient. It is possible that the highly variable nature of the discharge from the Suwannee River (Tsou and Matheson 2002; Purtlebaugh and Allen 2010), the second-largest river in Florida, reduces overall habitat quality for newly recruiting gags. Another key difference between Cedar Key and the three semi-enclosed estuaries is the nature of available submerged aquatic vegetation. Cedar Key is part of the Big Bend, a broad (3,000-km^2) expanse of generally contiguous seagrass that is second only to Florida Bay in extent of SAV and that covers a greater area than all other west Florida seagrass habitat combined (Zieman and Zieman 1989). Gags that settle in the Big Bend may simply be diluted by the large quantity of available seagrass habitat, or they may settle at the leading edge of available seagrass habitat at depths greater than those at which our sampling gear could be deployed. Alternatively, differing hydrodynamic regimes between semi-enclosed and open coastal systems may contribute to observed differences in the abundance of juvenile gags by concentrating individuals near the mouths of semi-enclosed estuarine systems. Various aspects of larval behavior could strongly influence the dispersal of gags and other demersal teleosts (Leis 2007), especially vertical migration (Weinstein et al. 1980). Some larvae exhibit turbulence-mediated behaviors whereby individuals sink when they encounter strong turbulence, increasing their settlement near high-energy environments such as tidal inlets (Fuchs et al. 2007). Several studies have documented significantly greater abundances of postsettlement nekton in seagrasses near inlets (Bell et al. 1988; Brown et al. 2005; Jelbart et al. 2007). After settlement, individuals generally do not move between seagrass beds but rather to specific sites within the seagrass bed of settlement that favor survival (Bell and Westoby 1986). Future efforts to characterize behavior and settlement of larval gags would undoubtedly improve our understanding of recruitment, although such efforts in the Gulf of Mexico are complicated by the difficulty in identifying larval serranids such as gag (Marancik et al. 2010).

The results from this study yielded valuable insight into the recruitment dynamics of juvenile gags in the eastern Gulf of Mexico, although important questions remain as to the causes of variability in recruitment. Decades of fishing pressure on gags in the Gulf of Mexico contributed to significant changes in adult populations, such as a reduction in mean size and in the proportion of males (Hood and Schlieder 1992; Coleman et al. 1996, 2000). We did not detect any marked decline in the relative abundance of juvenile gags over the course of this study, although documented changes in adult populations (Hood and Schlieder 1992; Coleman et al. 1996) occurred well before we began it. Instead, recruitment of juvenile gags was highly variable, with strong year-classes evident every 2 to 4 years. The periodicity in recruitment strength for juvenile gags is consistent with results from prior studies in the eastern Gulf of Mexico (Fitzhugh et al. 2005; Johnson and Koenig 2005), although factors contributing to recruitment variability are not well understood. Strong year-classes were often evident within multiple estuarine systems (i.e., 1999, 2002–2003, 2007), so the relative strength of juvenile gag recruitment may be at least partly attributable to presettlement processes such as ocean circulation, adult spawning, or larval mortality. An examination of surface circulation in the eastern Gulf of Mexico indicated that wind-driven circulation alone was insufficient for cross-shelf transport and delivery of larval gags to estuarine nurseries (Fitzhugh et al. 2005), although those authors stated that the use of three-dimensional circulation models might provide additional insight. Collins et al. (1998) detected especially high gonadosomatic indices and spawning frequency in gags of the northeastern Gulf of Mexico in 1993; recruitment of juvenile gags later that year was strong (Johnson and Koenig 2005). Despite the fact that strong year-classes are often evident within multiple estuaries, concordance of strong year-classes is not universal. The relative abundance of juvenile gags increased markedly in Charlotte Harbor in 2005; this peak was not evident in either Apalachicola Bay or Tampa Bay (Figure 5). A large, persistent red tide event occurred along the West Florida Shelf over much of 2005, contributing to significant alterations to fish community structure and declines in annual recruitment for several taxa (Gannon et al. 2009; Flaherty and Landsberg 2011). Although no direct evidence links the 2005 red tide event to the relative abundance of juvenile gags, red tides and other factors that affect postsettlement gags clearly can contribute to recruitment strength. Alternatively, concordance of strong year-classes, especially to the south, may be confounded by recruitment from multiple spawning populations. Accordingly, focused efforts to unravel the relative importance of presettlement and postsettlement processes in determining the strength of recruitment of juvenile gags appear warranted.

Continued efforts to better characterize the strength of juvenile gag recruitment are essential for the effective assessment and management of gag stocks in the eastern Gulf of Mexico. The linkage between recruitment strength of early life history stages and the quantity of biomass available to the fishery is generally thought to increase as fishing effort increases (Smith 1993), resulting in increased utility of forecasting models that use an index of juvenile recruitment to predict fisheries productivity (Koenig and Coleman 1998; Coleman et al. 1999). Recent studies documented a close correspondence between the strength of juvenile gag recruitment and subsequent fishery productivity; year-classes exhibiting strong recruitment of juvenile gags are often reflected in the age structure of nearshore populations, representing a substantial proportion of fisheries productivity that persists for a number of years (Fitzhugh et al. 2003; Johnson and Koenig 2005). A recent update to the stock assessment of gags in the Gulf of Mexico documented the persistence of the strong year-classes of 1999 and 2002 into the fishery that, combined with several earlier strong year-classes, has contributed to a slight increase in the abundance of older fish in the past decade (SEDAR 2009). Several aspects of the early life history of gags—including a generally short recruitment window, a defined period of estuarine occupancy, and the fact that they generally recruit to estuarine habitat and egress to nearshore reefs as discrete cohorts—make the gag a model species for estimating the relative strength of juvenile recruitment (Coleman et al. 1999). The utility of forecasting models will be minimal, however, without accurate regional estimates of juvenile recruitment. The availability of long-term data from multiple estuarine systems offers an opportunity to develop a robust regional index of juvenile gag recruitment, although incorporating data from multiple estuarine systems poses its own set of challenges, such as interannual variability in the quantity and quality of available habitat as well as uncertainties as to the relative contribution of various presumed estuarine nurseries to nearshore gag populations. Studies that quantify the relative value of presumed estuarine nurseries (Beck et al. 2001), especially in terms of connectivity to nearshore populations, will undoubtedly improve the accuracy of the models used to construct regional indices of juvenile gag recruitment and enhance our ability to correlate indices of recruitment to subsequent fisheries productivity.

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