Title: Age, growth, and diet of crevalle jack (*Caranx hippos*) in the Gulf of Mexico

Running Title: Crevalle jack age, growth, and diet

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Ethics Approval Statement: This study was conducted in accordance with the laws of the states of Alabama and Florida. All sampling occurred in the state waters of Alabama and Florida through scientific sampling conducted by the Alabama Department of Conservation and Natural Resources, Marine Resources Division and Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute. All efforts were made to reduce animal suffering during capture and handling.

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Title

Age, growth, and diet of crevalle jack (Caranx hippos) in the Gulf of Mexico

Abstract

The goals of this study were to generate baseline population dynamics parameters for Gulf of Mexico crevalle jack Caranx hippos and examine the foraging habits of Mississippi and Alabama crevalle jack. Specimens were collected from Mississippi, Alabama, and Florida, and age was estimated from sagittal otoliths. Stomachs from some specimens were retained for dietary analyses. Age classes spanned 0 - 20 years. Overall growth was best represented by the logistic growth model, whereas sex-specific growth was best represented by a version of the von Bertalanffy growth function that allowed L_∞ to vary by sex while holding k and t_0 constant between sexes. Fishes were more important to crevalle jack diet than invertebrates, and diet varied among locations and years. These findings will address fundamental knowledge gaps to inform age-based stock assessments for crevalle jack and ecosystem approaches to fisheries management in the Gulf of Mexico.

Keywords

Otolith, von Bertalanffy, Gompertz, logistic, stomach contents, Gulf of Mexico

Introduction

The strong-swimming, deep-bodied crevalle jack Caranx hippos is a member of the marine family Carangidae (Carpenter, 2002). The species was historically classified as circumtropical (Briggs, 1960) but is now recognized as one member of a three-species complex comprised of C. hippos, Pacific crevalle jack C. caninus, and longfin crevalle jack C. fischeri (Smith-Vaniz & Carpenter, 2007). The Pacific crevalle jack is

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found in the eastern Pacific Ocean and the longfin crevalle jack is found in the eastern Atlantic Ocean, whereas the crevalle jack is found on both sides of the Atlantic Ocean (Smith-Vaniz & Carpenter, 2007). In the western Atlantic, its distribution extends from Nova Scotia southward to Uruguay including the Caribbean and Gulf of Mexico (Carpenter, 2002). Although this euryhaline species can occupy offshore and inshore waters as well as coastal rivers, these preferences vary by life stage (Berry, 1959; Benson, 1982). Specifically, larvae lead a pelagic existence, juveniles favor estuaries, and adults use a wide variety of habitats (Berry, 1959; Johnson, 1978; McBride & McKown, 2000; Mohan, Sutton, Cook, Boswell, & Wells, 2017).

Relatively few studies have investigated the biology of crevalle jack. The species is thought to spawn offshore from March to September in southeastern U.S. Atlantic and Gulf of Mexico waters (Berry, 1959), with males and females in Florida waters reaching peak gonadosomatic index in April and June (Snelson, 1992) and larval abundance over the Gulf of Mexico outer continental shelf peaking in May and June (Ditty, Shaw, & Cope, 2004). Adult crevalle jack can reach large sizes; the present all-tackle world record for the species is 30 kg, set in Angola in 2010 (International Game Fish Association). The maximum reported ages of crevalle jack from Florida's east and west coasts (Palko, 1984; Snelson, 1992) and Trinidad (Kishore & Solomon, 2005) range from 13 to 19 years. Similarly, cohort analysis of crevalle jack from Colombia (Caiafa, Narváez, & Borrero, 2011) resulted in an estimated age of 14 years for the largest specimen (Table 1). Maximum age was older for females (19 years) than males (15 years) in Florida (Snelson 1992), but older for males (13 years) than females (10 years) in Trinidad (Kishore & Solomon 2005). Females grow larger than males (Kishore & Solomon 2005). Female crevalle jack reach maturity as early as age 5 to 6 (about 66 to 70 cm fork length [FL]) and males at age 4 to 5 (about 55 to 60 cm FL) (Thompson & Munro, 1983; Snelson, 1992; Caiafa, Narváez, & Borrero, 2011).

Crevalle jack are generally diurnal predators, often creating surface-water turbulence by feeding in schools on schooling prey near the surface (Kwei, 1978; Correia et al. 2017), though larger crevalle jack can be solitary (Carpenter, 2002). The diet of crevalle jack has been most thoroughly investigated in the eastern Atlantic off the coast of Africa. There, adults feed predominantly on fishes in the family Clupeidae

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(Correia et al., 2017), juveniles on a mix of small fishes and shrimps (Fagade & Olaniyan, 1972; Kwei, 1978), and post-larval individuals primarily on copepods (Kwei, 1978). However, some of these studies may have included longfin crevalle jack (Smith-Vaniz & Carpenter, 2007). Crevalle jack diet has also been examined in the southeastern U.S. Atlantic and Gulf of Mexico in Florida, Louisiana, and Texas (Saloman & Naughton, 1984). Like in Africa, these crevalle jack specimens were primarily piscivorous; clupeids represented the most prevalent prey, though larger crevalle jack were more opportunistic than smaller crevalle jack and fed on a variety of invertebrate prey, such as penaeids and portunids, as well as fishes (Saloman & Naughton, 1984).

Crevalle jack are fished both commercially and recreationally (Smith-Vaniz & Carpenter, 2007). Most of the commercial harvest in the Gulf of Mexico occurs along Florida's west (Gulf) coast (National Marine Fisheries Service Fisheries Statistics Division [NMFS] personal communication, date of inquiry: 1 October 2020). However, since the implementation of a net ban in Florida waters in 1995, Gulf of Mexico recreational catch of crevalle jack has far exceeded commercial harvest (Adams, Jacob, & Smith, 2001). Over the past three decades, annual recreational catch has fluctuated between 2 and 10 million fish, with approximately 90% released after capture (Figure 1; National Marine Fisheries Service Fisheries Statistics Division [NMFS] personal communication, date of inquiry: 1 October 2020). Crevalle jack have substantial amounts of red muscle, which results in a rather unpleasant taste (Smith-Vaniz & Carpenter, 2007). For this reason, along with the strong fighting ability of crevalle jack, recreational effort for the species is driven by catch-and-release (Shipp, 2012). Crevalle jack are currently unregulated commercially and recreationally in all five Gulf states and in federal waters. As an unregulated species in Florida, crevalle jack defaults to a recreational bag limit of two fish or 100 pounds per person per day, whichever is greater (Florida Statutes, Title XXVIII, Chapter 379, 379.361 Licenses). However, stakeholder concern about the Florida Keys crevalle jack population (Gervasi et al., 2021) has prompted the state to consider proactive management action(s) for the stock (Florida Fish and Wildlife Conservation Commission, 2020).

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Age and growth data represent the foundation of age-based stock assessments (Legault & Restrepo 1998), and diet data are critical for ecosystem approaches to fisheries management (Anstead et al. 2021). Although age, growth, and diet of crevalle jack have previously been described, further work on these topics is needed for several reasons. First, age and growth of crevalle jack has not been estimated in Gulf of Mexico waters west of Florida. Second, only two studies modeled crevalle jack growth based on ages estimated from hard structures; a third used Electronic LEngth Frequency ANalysis or "ELEFAN" (Snelson, 1992; Kishore & Solomon, 2005; Caiafa, Narváez, & Borrero, 2011). The former two studies used samples that were collected 20 to 30 years ago and lacked older fish. Third, only one study has modeled sex-specific growth, and that study was conducted in Trinidad (Kishore & Solomon, 2005). Lastly, while Saloman & Naughton (1984) examined a robust sample size of 3,643 stomachs across a broad sampling region, none of their sampling was in estuaries, no fish were collected from Mississippi or Alabama, and the study was conducted almost 30 years ago. Given the emerging stakeholder concern for crevalle jack and their prominent roles as sportfish and voracious predators in coastal ecosystems, these fundamental knowledge gaps must be addressed to provide a basis for potential future management measures (Gervasi et al., 2021). The objectives of this study were to generate baseline population dynamics parameters for Gulf of Mexico crevalle jack Caranx hippos and examine the foraging habits of Mississippi and Alabama crevalle jack. Therefore, we 1) modeled up-to-date overall and sex-specific growth for Gulf of Mexico crevalle jack and 2) quantified the diet of Mississippi and Alabama crevalle jack.

Methods

Fish Sampling

Large, adult crevalle jack were sampled from recreational harvest on Dauphin Island, Alabama during 2017 to 2019. Only these fish were used for dietary analyses. Specifically, crevalle jack data and samples were collected in July during annual Roy Martin Young Anglers Tournaments and Alabama Deep Sea Fishing Rodeos. These fish were captured by hook-and-line in Mississippi, Alabama, or west Florida waters and landed in Alabama. Exact catch locations were undocumented for most fish, so general

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catch locations were obtained when possible (Figure 2). Also, for the purpose of stomach content analysis, anglers were asked whether they used non-artificial bait or chum, and if so, what species were used. A small number of other crevalle jack were captured near Dauphin Island via recreational harvest.

Small crevalle jack were sampled via two different sources. Some of these fish were collected from fishery-independent surveys in Alabama during 2020. These specimens were captured by gillnet (stretch mesh size ranging from 5.1 cm to 15.2 cm), 15.2-m bag seine, or 14.9-m benthic otter trawl in Mobile Bay and the Alabama waters of Mississippi Sound. The remainder of the small crevalle jack were collected from fishery-independent surveys in Florida during 2002 to 2014. Most of these specimens were captured by 183-m haul seine, but a few were collected by 548.6-m nylon trammel net (11.75-cm inner stretch mesh, 35.60-cm outer stretch mesh), 365.8-m monofilament trammel net (7.0-cm inner stretch mesh, 30.50-cm outer stretch mesh), or hook-and-line. Collection areas ranged across much of the west (Gulf) coast of Florida from Alligator Point (near Apalachicola, Florida in the Florida panhandle) to the Florida Keys.

Fish Processing & Morphometrics

For each fish, FL was measured to the nearest millimeter, weight was measured in kilograms, and both sagittal otoliths were extracted and stored for age estimation (Palko 1984). For fish used in dietary analyses, stomachs were excised and then either stored in 200 proof ethanol or frozen at -29℃ until they could be examined . Sex was assigned macroscopically for all fish measuring at least 500 mm FL. However, fish measuring less than 500 mm FL were designated as unknown sex due to difficulty in distinguishing between female and male gonads prior to maturity (at least 660 mm FL for females and 550 mm FL for males; Snelson, 1992; Thompson & Munro, 1983). Two-sample Kolmogorov-Smirnov tests were conducted in R version 4.1.0 (R Core Team, 2021) to test for differences in length and weight distributions between sexes ($\alpha = 0.05$). Length-weight regressions were generated in R version 4.1.0 (R Core Team, 2021) using the add-on package FSA: Fisheries stock analysis (Ogle, Wheeler, & Dinno, 2021) to model the overall and sex-specific relationship between FL and weight.

Otolith Processing

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Otolith processing followed guidelines described by VanderKooy, Carroll, Elzey, Gilmore, & Kipp (2020). For consistency, the left sagittal otolith from each individual was embedded in epoxy and allowed to cure. If the left otolith was missing or broken through the core, the right otolith was used. Each embedded otolith was mounted on a slide or cardstock using heat-activated adhesive and sectioned using a low-speed saw. Three consecutive 0.5-mm transverse sections were cut simultaneously with four diamond-coated blades, each separated from another by a 0.5-mm spacer. The sections were affixed to a slide using a low-viscosity, quick-drying mounting medium and allowed to air-dry for at least 24 hours.

Otolith Age Estimation

Crevalle jack otolith sections were viewed for age estimation using a stereomicroscope with transmitted light (brightfield illumination). Although age has not been validated in crevalle jack, the number of opaque zones was assumed to represent the age of the fish in years, as in previous studies (Palko 1984, Snelson 1992, Kishore & Solomon 2005). Age was estimated using guidelines described by VanderKooy, Carroll, Elzey, Gilmore, & Kipp (2020). The best section from each otolith, defined as the section that was cut closest to the otolith core and at the most perpendicular angle, was selected for age estimation. Thin opaque zones were enumerated along an axis near the sulcal groove from the core to the edge. Margin codes (1 to 4) were assigned according to criteria described by VanderKooy, Carroll, Elzey, Gilmore, & Kipp (2020). Age class was then determined based on summer annulus deposition (Snelson, 1992). Specifically, age class was equal to the number of opaque zones, except when a fish was collected between January 1 and July 31 and the margin code was 3 or 4, in which case age class was equal to the number of opaque zones plus one.

For the samples from Alabama, age of each fish was estimated by two readers independently and blindly. However, fish measuring less than 100 mm FL were automatically assigned to age 0 due to the small size of the otoliths (Snelson 1992, Kishore & Solomon 2005). Otoliths deemed unreadable (due to poor processing or lack of alternating opaque and translucent zones) were assigned a code of “U,” and all fish assigned a code of “U” by at least one reader were omitted from further analyses. Next, average percent error (APE) was calculated to evaluate between-reader precision

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(Beamish & Fournier, 1981; Campana, 2001). In the event of a disagreement in age class between the first two readers, a third reader estimated the age of the otolith. The final age class assigned to the fish was the agreed-upon age class between two of the three readers. If all three readers disagreed, then the first two readers consulted with each other and either reached an agreement or deemed the otolith unreadable.

For the samples from Florida, age of each fish was estimated either by a single reader or by two different readers independently and blindly. When possible, APE was calculated to evaluate between-reader precision (Beamish & Fournier, 1981; Campana, 2001). In the event of a disagreement in age class between readers, age of the otolith was estimated again blindly by the original readers to resolve the discrepancy.

For all three datasets, fractional age (years) was then calculated from the final age classes using a June 1 birthdate, which was estimated based on gonadosomatic index peaking in April and June (Snelson 1992) and larval collections peaking in May and June (Ditty, Shaw, & Cope 2004). Specifically, the birthdate was subtracted from the date of capture, the resulting number was divided by the number of days in the year of capture, and that number was added to the age class. A two-sample Kolmogorov-Smirnov test was conducted in R version 4.1.0 (R Core Team, 2021) to examine differences in fractional age distributions between sexes (α = 0.05).

Growth Modeling

A multimodel framework was used to investigate overall growth (Katsanevakis & Maravelias, 2008; Smart, Chin, Tobin, & Simpfendorfer, 2016). The von Bertalanffy growth function (VBGF)

$$l_t = L_\infty (1 - e^{-k(t-t_0)}), \tag{1}$$

Gompertz growth model

$$l_t = L_\infty (e^{-e^{(-g(t-\alpha))}}), \tag{2}$$

and logistic growth model

$$l_t = \frac{L_\infty}{1+e^{-g(t-\alpha)}} \tag{3}$$

where l_t = predicted FL in millimeters, L_∞ = mean asymptotic FL in millimeters, k and g = growth coefficients in year^{-1}, t = time (age) in years, t_0 = hypothetical age at which length equals 0 in years, and α = inflection point of the Gompertz and logistic models (von Bertalanffy, 1938; Gompertz, 1825; Ricker, 1975) were each fit to all fractional age data

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combined, including female, male, and unknown sex observations. Akaike's information criterion (AIC) was used to rank the fit of the three resulting models; the model with the smallest AIC value and greatest Akaike weight was chosen as the best-fitting model (Akaike, 1998; Katsanevakis & Maravelias, 2008).

Sex-specific growth was also examined using a multimodel framework. First, unknown sex observations were omitted from the fractional age data. Then, eight candidate versions of each growth model (VBGF, Gompertz, and logistic) were fit to the remaining (female and male) fractional age data: a general version, which allowed all three growth parameters (L_∞, k or g, and t_0 or α) to vary between sexes; three versions that allowed two of the three parameters to vary between sexes; three versions that allowed only one parameter to vary between sexes; and a common version, which held all three parameters constant between sexes (Ogle, 2016; Nelson et al., 2018; Jefferson et al., 2019). Akaike's information criterion was used to rank the fit of all 24 resulting model versions; the version with the smallest AIC value and greatest Akaike weight was chosen as the best-fitting version (Akaike, 1998; Katsanevakis & Maravelias, 2008; Ogle, 2016). All growth parameters were modeled in R version 4.1.0 (R Core Team, 2021) using the add-on packages FSA: Fisheries stock analysis (Ogle, Wheeler, & Dinno, 2021) and nlstools: Tools for nonlinear regression analysis (Baty et al., 2015).

Stomach Processing

All stomach contents were examined using instruments that were sterilized in a 10% bleach solution. Stomach contents that matched the description of the bait or chum used to catch the fish or showed any evidence that they could have been used as bait were excluded from further analyses. Furthermore, any stomachs that appeared purposely "stuffed" (i.e., filled by an angler with bait or ice to increase the weight of the fish) were also excluded from further analyses. All other prey items were identified to the lowest possible taxa, blotted dry, counted, and weighed to the nearest 0.01 g. All free otoliths were also separated, identified to the lowest possible taxa, and counted. Prey items that could not be visually identified to species were stored in 200 proof ethanol until they could be examined genetically.

Genetic analysis of stomach contents was performed as a complement to macroscopic dietary analysis. All DNA extraction from muscle samples, PCR

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amplification, post-PCR processing and pooling, and bioinformatics were conducted at the Genomics Core Laboratory at Texas A&M University-Corpus Christi (TAMU-CC). A metagenetics approach was used for species identification following protocols described in Jargowsky, Cooper, Ajemian, Colvin, & Drymon (2020). Specifically, a 313 bp section of the coI locus was sequenced via a paired end fashion at the New York University School of Medicine's Genome Technology Center on an Illumina MiSeq (www.illumina.com). The primers used in PCR amplification were the universal metazoan primers MlcoIint-F (primer sequence: 5’-GGWACWGGWTGAACWGTWTAYCCYCC-3’, Leray et al., 2013) and Jghc-02198 (5’-TAIACYTCIGGRTGICCRAARAAYCA-3’, Geller, Meyer, Parker, & Hawk, 2013). Additionally, a crevalle jack blocking primer (CVJ_blk_COIF; 5’-TCCCCCATTAGCTGGTAATCTTGCCCATGCC-C3-3’) was used to decrease the amplification of predator DNA; however, this primer was omitted for prey items appearing to be from the family Carangidae to prevent the blocking of any closely related prey DNA. Following bioinformatic processing, each prey item was assigned a single, final operational taxonomic unit (OTU) following protocols from Jargowsky, Cooper, Ajemian, Colvin, & Drymon (2020), with each prey item discriminated at the species level having a > 98% sequence match with a species in the reference libraries (Leray et al., 2013).

Dietary Analyses

Prey groups were quantified using single and compound indices, including average percent number (%N), average percent weight (%W), prey-specific number (%PN), prey-specific weight (%PW), and frequency of occurrence (%FO) (Hyslop, 1980; Chipps & Garvey, 2007; Brown, Bizzarro, Cailliet, & Ebert, 2012). To compare among prey groups, the prey-specific index of relative importance (%PSIRI) was calculated (Brown, Bizzarro, Cailliet, & Ebert, 2012). The equations for %N (4), %W (4), %PN (5), %PW (5), %FO (6), and %PSIRI (7) are as follows:

$$\%A_i = \left(\sum\nolimits_{j=1}^{n} \%A_{ij}\right)(n)^{-1} \tag{4}$$

$$\%PA_i = \left(\sum\nolimits_{j=1}^{n} \%A_{ij}\right)(n_i)^{-1} \tag{5}$$

$$\%FO_i = (n_i)(n)^{-1} \tag{6}$$

$$\%PSIRI = (FO_i(\%PN_i + \%PW_i))(0.5) \tag{7}$$

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where $\%A_{ij}$ is the percent abundance (by number or weight) of prey category i in stomach sample j, n_i is the number of stomachs containing prey i, and n is the total number of stomachs containing prey (Brown, Bizzarro, Cailliet, & Ebert, 2012). An index of vacuity was calculated by dividing the total number of stomachs without prey by the total number of stomachs sampled (Hyslop, 1980).

Using the Mao tau estimate, cumulative prey curves were created for prey richness, starting at the species level, to determine if a sufficient number of stomachs had been sampled to adequately describe the diet of crevalle jack (Colwell et al., 2012; Ferry & Cailliet, 1996). Sample size was considered sufficient once a prey curve approached an asymptote, defined by whether the slope of a linear regression (b), fit to the final five randomly sampled stomachs, was < 0.05 (Bizzarro et al., 2009). If a prey curve failed to approach an asymptote at one taxon level (e.g., species), new prey curves were generated at higher taxa levels until this criterion was met.

The Bray-Curtis index was used to create a dissimilarity matrix for the dependent variables %N and %W, with each individual stomach treated as an individual sampling event and prey taxa treated as the response variables (Clarke, Gorley, Somerfield, & Warwick, 2014). A permutational multivariate analysis of variance (PERMANOVA) was conducted on the dissimilarity matrix to test whether the measured independent variables (sex, FL, location, and year) showed significant explanatory value to the primary dietary variables. The variables sex, location (north Mobile Bay, Alabama; south Mobile Bay, Alabama; north Mississippi Sound, Mississippi/Alabama; south Mississippi Sound, Mississippi/Alabama; east nearshore [i.e., state waters in the Gulf of Mexico east of Mobile Bay, Alabama/west Florida]; west nearshore [i.e., state waters in the Gulf of Mexico west of Mobile Bay, Mississippi/Alabama]; and offshore [i.e., federal waters south of Mississippi, Alabama, and west Florida]), and year (2017 to 2019) were treated as factors and the variable FL was treated as a covariate. These variables were tested independently, and a final model was then created using forward, stepwise model selection to determine which combination of explanatory variables best explained dietary variability (Anderson & Burnham, 2002; Bizzarro; Yoklavich, & Wakefield, 2017). To test for sample dispersion, permutation tests for heterogeneity of multivariate group dispersions were run for all explanatory variables (Anderson & Walsh, 2013). All

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PERMANOVAs were permutated 9999 times and differences were considered significant if P-values were < 0.05.

As a complement to the final model of the PERMANOVA analysis, canonical correspondence analysis (CCA) was conducted and biplots were created to help visualize the association of the prey groups and the explanatory variables (ter Braak & Verdonschot, 1995). Rare species that can strongly influence CCA were defined as having a %FO of less than 2% and excluded to help maximize the explanatory power of the models (Kemper, Bizzarro, & Ebert, 2017). Additional permutational tests were conducted on the CCA to examine the significance of overall models, constraining axes, and explanatory variables. All dietary parameters were modeled in R version 4.1.0 (R Core Team, 2021) using vegan: Community ecology package (Oksanen et al., 2019).

Results

Morphometrics

Overall, 803 crevalle jack were sampled during the study, including 544 from fishery-dependent sampling in Alabama, 22 from fishery-independent sampling in Alabama, and 237 from fishery-independent sampling in Florida. Of all sampled fish, 263 were female, 286 were male, and 254 were of unknown sex. The female-to-male ratio of 0.92:1 did not significantly differ from 1:1 ($X^2 = 0.96$, df = 1, P = 0.33). Fork length of 801 specimens ranged from 27 to 975 mm. Size ranges were 166 to 975 mm for fishery-dependent Alabama specimens, 27 to 340 mm for fishery-independent Alabama specimens, and 158 to 728 mm for fishery-independent Florida specimens (Figure 3). Weight of 790 specimens and ranged from 0.001 to 16.5 kg. Females were significantly longer in FL than males (D = 0.14, P < 0.01). In contrast, weight did not differ significantly between sexes (D = 0.06, P = 0.68). The overall length-weight regression indicated that crevalle jack become progressively slender as they increase in length:

$$log_{10}[weight] = -16.47 + 2.79 * log_{10}[FL] \text{ } (R^2 = 0.99). \quad (8)$$

Sex-specific length-weight relationships did not differ in either their slopes (P = 0.58) or intercepts (P = 0.38).

Age

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Overall, 793 pairs of otoliths were examined for age estimation. However, otoliths from 53 individuals were broken and therefore could not be sectioned, and otoliths from an additional 11 individuals were deemed unreadable. Therefore, ages of 729 fish (514 from fishery-dependent Alabama samples, 22 from fishery-independent Alabama samples, and 193 from fishery-independent Florida samples) were available for further analyses (Table 1). Notably, 7 fish measured less than 100 mm FL and were therefore automatically assigned an age class of 0 years. Fractional ages ranged from 0.02 to 20.14 years with a median age of 10.13 years (Figure 4). Female fractional ages ranged from 3.27 to 19.14 years with a median age of 11.15 years. Male fractional ages ranged from 2.84 to 20.14 years with a median age of 12.15 years. Males were significantly older than females ($D = 0.14$, $P < 0.01$). Between-reader APE was 1.74% for the Alabama samples and 3.60% for the Florida samples.

Growth

Overall growth was best represented by the logistic growth model (Figure 5; AIC = 7270.3; Akaike weight = 1.00):

$$l_t = \frac{884.37}{1+e^{-0.66(t-2.83)}} \text{ (Figure 5).} \qquad (9)$$

The Gompertz model (AIC = 7319.7, Akaike weight < 0.01) and VBGF (AIC = 7647.5, Akaike weight < 0.01) were less well supported by comparison. Although the VBGF model was less well supported than the logistic model, those parameters are also reported here for comparison with previous studies, all of which only used the VBGF:

$$l_t = 925.73(1 - e^{-0.26(t-0.04)}) \text{ (Table 2, Figure 5).} \qquad (10)$$

In contrast, sex-specific growth was best represented by a VBGF model version with a different L_∞ for males and females and a common k and t_0 for both males and females (AIC = 4906.5, Akaike weight = 0.43):

$$l_{t(F)} = 903.04(1 - e^{-0.39(t-0.73)}) \qquad (11)$$

and

$$l_{t(M)} = 887.16(1 - e^{-0.39(t-0.73)}) \text{ (Table 2, Figure 5).} \qquad (12)$$

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This model version was followed closely by three other VBGF versions. A total of 19 of the 24 candidate versions had Akaike weights of < 0.01, indicating poorer fit among those versions (Supplemental Table 1).

Stomach Content Analysis

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Overall, 528 stomachs were sampled for stomach content analysis. Most stomachs (99.2%) were sampled from recreational fishermen in July at Roy Martin Young Anglers Tournaments and Alabama Deep Sea Fishing Rodeos. Only three fish were excluded from further analyses because their stomachs appeared to be purposely “stuffed”. Fork length of fish sampled for stomach content analysis ranged from 670 to 975 mm. General catch locations were obtained for 77.9% of fish and included north Mobile Bay (n = 121), south Mobile Bay (n = 105), north Mississippi Sound (n = 12), south Mississippi Sound (n = 42), east nearshore (n = 26), west nearshore (n = 69), and offshore (n = 36). Notably, 68.1% of fish were collected from inshore locations (i.e., Mobile Bay or Mississippi Sound).

Of the 528 stomachs examined, 57.6% contained prey and 42.4% were empty. Crevalle jack stomachs were often very full of partially digested medium-sized prey. In addition, stomachs were often full of hard parts, particularly free otoliths, with 6,479 free otoliths found in total and multiple stomachs containing greater than 200 free otoliths each. Most free otoliths were from Atlantic croaker (Micropogonias undulatus, 78%), other species of Sciaenidae (9%), and prey from the family Ariidae (i.e., sea catfishes, 10%), all of which have large otoliths relative to their body size. These results indicate that the composition of free otoliths greatly overrepresented prey groups with large otoliths (97% of all free otoliths), so free otoliths were excluded from further analyses.

From the 304 stomachs containing prey, 2,867 prey items (9.4 prey items per non-empty stomach), weighing 40.8 kg, were identified macroscopically. Of these, 178 prey items were analyzed genetically, and 102 (57.3%) were ultimately assigned a final species-level OTU. In total, 29 prey families were identified. From those 29 families, 45 prey species were identified, 34 of which were fishes. Six families (20.7%) and nine species (20.0%) were only identified through genetic analyses. Overall, the use of metabarcoding increased the number of family-level prey identified by 3.2% and species-level prey identified by 3.8%. Fish prey was more important than invertebrate

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prey (Table 3). Atlantic croaker was the most important prey species. The second and third most important prey species were Gulf menhaden (Brevoortia patronus) and brown shrimp (Farfantepenaeus aztecus). Cumulative prey curves indicated that the sample size of this study was insufficient to adequately describe the diet of crevalle jack at the species level (b = 0.072) but was sufficient to describe diet at the family level (b = 0.050) (Supplemental Figure 1). Thus, all multivariate analyses were performed at the family level.

Dietary Variation

Based on the analysis of the standardized diet data, location explained the greatest amount of dietary variability, although all four explanatory variables were significant (Table 4). The interaction between location and year was significant, indicating that prey communities at each location were likely inconsistent across years. The variables in the final models accounted for 18.9% (%N) and 19.0% (%W) of the dietary variability. Dispersion analysis suggested that some of the dietary variability explained by location, year, and FL may be due to within-group variation in diet composition (Table 4).

For the CCA, sex was insignificant and was thus excluded from the models. The resulting CCA, which included location, year, and FL, explained 6.6% (%N) and 6.4% (%W) of the overall dietary variability (Figure 6). Prey in the families Carangidae and Sparidae, along with nondigestible materials (e.g., wood, vegetation), were most common in the diets of crevalle jack from the east and west nearshore locations. Prey in the families Ariidae and Penaeidae were correlated with the locations north Mobile Bay, south Mobile Bay, and north Mississippi Sound, along with the year 2019. Lastly, prey families Squillidae, Loliginidae, Triglidae, and Portunidae were correlated with the locations offshore and south Mississippi Sound, the year 2018, and small FL.

Discussion

Crevalle jack in the Gulf of Mexico have a moderate lifespan of approximately 20 years, with maximum ages of 17 years in northwest Florida and the Keys (Palko, 1984), 19 years on the east and west coasts of Florida (Snelson, 1992), and 13 years in Trinidad (Kishore & Solomon, 2005) (Table 1). Although similar to the maximum age

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from our study, other studies lacked older fish, with only 12 specimens older than age 5 from northwest Florida and the Keys (Palko 1984) and only 10 specimens older than age 5 from the east and west coasts of Florida (Snelson 1992). By comparison, 495 specimens in our study were age 6 years or greater. Thus, our study is the first to adequately describe the upper age range of crevalle jack, which are likely the individuals most often caught in recreational fisheries.

While a variety of factors could be responsible for these differences in crevalle jack age between studies, a possible explanation stems from differences in size of crevalle jack between sampling regions (i.e., Mississippi/Alabama versus Florida). The mean size of fishery-dependent Alabama crevalle jack captured by hook-and-line was 868 mm FL. In contrast, the mean size of fishery-independent Alabama crevalle jack captured by gillnet, seine, or trawl was 126 mm FL. Noting a striking absence of medium-sized crevalle jack from the Alabama datasets (Figure 3A, 3B), we hypothesized that medium-sized fish were lacking from the fishery-independent Alabama dataset due to small sample size (n = 22). Therefore, we examined all catch data from fishery-independent gillnet sampling in Alabama during 2000 to 2019. Surprisingly, many crevalle jack were sampled with gillnets (n = 341), but none were between 230 and 620 mm FL (Figure 7; J. Mareska / Alabama Marine Resources Division, unpublished data). Together, these three datasets indicate that the Mississippi/Alabama region may be lacking discrete age classes that represent medium-sized crevalle jack, though gear selectivity could be a contributing factor.

To further investigate this observation, we examined recent (2011 to 2020) Marine Recreational Information Program length frequency data for noticeable differences between sizes of crevalle jack caught by recreational anglers in Mississippi, Alabama, and Florida’s west (Gulf) coast (National Marine Fisheries Service Fisheries Statistics Division [NMFS] personal communication, date of inquiry: 8 September 2021). Strikingly, 62.6% of crevalle jack caught in Mississippi and Alabama measured greater than 620 mm FL, whereas only 1.5% of fish caught in Florida met this criterion. Moreover, while only 28.4% of Mississippi and Alabama crevalle jack measured between 230 and 620 mm FL, 85.9% of Florida fish fell into this length range. Thus, we conclude that the lack of older (ages 6+) crevalle jack in the Florida-based studies was

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most likely driven by a scarcity of larger crevalle jack in Florida waters, more so than differences in sampling design. Perhaps these differences between Florida and the northern Gulf of Mexico are driven by an ontogenetic shift, wherein subadults reside in Florida before moving northwest as adults. Saloman & Naughton (1984) sampled many large crevalle jack from northwest Florida, so a lack of larger crevalle jack may not apply to that region. Clearly, further research is necessary to understand size and age distribution patterns, particularly in light of stakeholder concerns over crevalle jack populations in south Florida (Gervasi et al., 2021).

Our growth models were generated from the broadest ranges of crevalle jack length and age data ever reported, and therefore are the most comprehensive to date for this species. Our study was also the first to use a multimodel framework to investigate overall and sex-specific growth of crevalle jack. Although growth may vary across our sampling region to some degree, we assumed that these differences would be negligible relative to modeling growth since all samples were collected from the eastern half of the Gulf of Mexico. The logistic growth model best fit the overall age data, presumably because it better fit intermediate-aged fish (age range of approximately 4 to 10 years) than the VBGF (Figure 5). The overall VBGF growth parameters estimated from our study are somewhat different from those reported in previous otolith-based studies (Snelson, 1992; Kishore & Solomon, 2005) (Table 2). The k estimate from the east and west coasts of Florida was very close to ours, yet the L_∞ estimate from the same location was much larger than ours (Snelson 1992). Furthermore, the L_∞ estimate from Trinidad was relatively close to ours, but the k estimate from that location was considerably smaller than ours (Kishore and Solomon 2005). Both situations (larger L_∞ estimate, smaller k estimate) are likely due to a lack of older specimens in the previous studies, as further evidenced by the large standard error value associated with the L_∞ estimate from Trinidad (Kishore and Solomon 2005).

Although overall growth was best represented by the logistic growth model, sex-specific growth was best represented by the VBGF (Figure 5). This can be attributed to the absence of sexed fish measuring less than 500 mm FL, which corresponds to an age of approximately 3 years. The best-fitting version of the VBGF suggests sexual dimorphism, with female crevalle jack reaching greater maximum lengths than males

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(Table 2, Figure 5). The only other study to model sex-specific growth reported a larger L_∞ estimate and smaller k estimate for females than males (Kishore & Solomon, 2005). However, sex-specific growth was only modeled for ages 1 to 9 years. Snelson (1992) did not model sex-specific growth, but the author reported that males were uncommon at lengths greater than 800 mm FL. Length-weight relationships did not differ significantly between sexes in our study area, unlike near Bocas de Ceniza, Colombia, where females weighed significantly more than males at the same length (Caiafa, Narváez, & Borrero, 2011).

While most previous crevalle jack diet studies reported prey in the order Clupeiformes as the most dominant prey (Fagade & Olaniyan, 1972; Kwei, 1978; Saloman & Naughton, 1984; Correia et al., 2017), we found that prey in the order Sciaeniformes (48.8% PSIRI), particularly Atlantic croaker (42.0% PSIRI), was far more important in diets of crevalle jack in Mississippi and Alabama. Since most of our diet data were obtained through fishery-dependent sampling, and fishes were the most common bait (86.9%), it is possible that our results could be biased by our sampling design. However, any bias is likely minimal because the degree of piscivory in our study is consistent with that from other studies. The significance of location and the interaction between location and year demonstrate that crevalle jack in the Gulf of Mexico have a large dietary breadth, allowing them to consume the more available prey in spatially and temporally varying assemblages. Unsurprisingly, crevalle jack caught at inshore locations consumed estuarine prey, including Ariidae, Penaeidae, and Clupeidae, whereas crevalle jack caught at nearshore sites consumed prey more associated with nearshore habitats, such as Carangidae and Sparidae. The common consumption of Ariidae further demonstrates the influence of prey availability on crevalle jack diet, as these species are hazardous to consume due to their large, venomous, serrated spines (Ronje et al., 2017; Jargowsky, Cooper, Ajemian, Colvin, & Drymon, 2020). Collectively, our results indicate that crevalle jack diet should be expected to consist of the most spatially and temporally available prey rather than specific prey deemed important in other studies.

Although previous studies have designated crevalle jack as primarily active feeders, the species has been observed following commercial shrimp trawlers to feed

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out of their nets and on trawl discards (Johnson, Murray, & Griffith, 1985). Interestingly, this behavior has been observed in other active pelagic predators in the Gulf of Mexico, such as yellowfin tuna (Thunnus albacares) (Lovell, 2021). This behavior was strikingly evident among a large portion of crevalle jack stomachs examined during our study. Stomachs were often filled to capacity with various partially digested prey species commonly discarded by commercial shrimp trawlers. Even when stomachs were not filled to capacity, many contained evidence of massive past feeding events in the form of loose otoliths. While the length of time these otoliths would remain in a crevalle jack stomach before passing is unknown, the process is not likely to take much more than 24 hours (Jobling & Breiby, 1986). These results, combined with on-the-water observations by commercial and recreational fishermen, indicate that the commercial shrimp fishery subsidizes a large portion of the diet of adult crevalle jack in Mississippi and Alabama.

While the majority of the crevalle jack stomachs examined in our study were collected during the month of July, our results are likely an adequate representation of adult crevalle jack diet throughout the year in Mississippi and Alabama for several reasons. First, adult crevalle jack only occur seasonally in this area. From 2011 to 2020, 91.7% of recreational landings for the species in Mississippi and Alabama occurred during July through October. The fishery-independent gillnet data from Alabama also suggest seasonal occurrence of crevalle jack, as 56 of the 62 adult crevalle jack collected from this survey, or 90.3%, were captured during July through October. Additionally, this summer to early fall time frame overlaps with the commercial shrimp seasons in Mississippi and Alabama. Therefore, shrimp trawl discards should be expected to remain important to the diet of adult crevalle jack throughout their seasonal presence in these waters. Although the diet of adult crevalle jack in Mississippi and Alabama may change from July to October as prey assemblages shift, the impacts of crevalle jack on coastal food webs likely remain the same.

Our study provides the most comprehensive crevalle jack ages and growth parameters to date, and our extensive sampling of adult crevalle jack enabled us to confidently estimate the maximum age of the species in the Gulf of Mexico. Although our study area was limited to the Gulf of Mexico, our findings can be used in future age-based stock assessments for crevalle jack in the Gulf and in other portions of its range,

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particularly where region-specific management plans are lacking. It also contributes novel insight into the dietary preferences of adult crevalle jack in estuaries and in Mississippi and Alabama and illustrates differences in diet across spatial and temporal scales. This information is useful for ecosystem approaches to fisheries management, particularly for species like Gulf menhaden (Brevoortia patronus), which comprises the largest commercial fishery in the U.S. Gulf of Mexico by weight (Brown-Peterson, Leaf, Schueller, & Andres, 2017; Anstead et al. 2021). Despite these findings, our study highlights critical research needs for the species. Until crevalle jack movement and migration patterns are fully understood, especially as they relate to ontogeny, it will be challenging to explain stark differences in size distributions across regions, including the one we observed between Mississippi/Alabama and Florida. Additionally, although most crevalle jack caught by recreational anglers are released after capture, post-release mortality of the species is presently unknown. Given the importance of crevalle jack as coastal sportfish (Gervasi et al., 2021) and predators, additional research is essential to address these and other knowledge gaps before future management measures are initiated for the species.

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Tables

Table 1. Study period, study location, sample size (N), sex ratio, size range, weight range, structure(s) aged, and age ranges for each published crevalle jack age and growth study to date from the southeastern U.S., Gulf of Mexico, and Caribbean. Studies are listed in chronological order.

	Palko (1984)	Snelson (1992)	Kishore & Solomon (2005)	Caiafa, Narváez, & Borrero (2011)	This Study
Study Period	1982	1991 - 1992	1996 - 1997; 1999 - 2003	2005 - 2006	2002 - 2020
Study Location	Northwest Florida and Florida Keys	East and west coasts of Florida	Trinidad	Colombia	Mississippi, Alabama, and west coast of Florida
N	102; 59 successfully aged	369; 279 successfully aged	327; 268 successfully aged	1,151; 264 used for biological analysis	803; 729 successfully aged
Sex Ratio (F:M)	NA	166:190 or 0.87:1	115:120 or 0.96:1	84:180 or 0.47:1	263:286 or 0.92:1
Size Range (mm FL)	84 - 934	135 - 959	58 - 848	105 - 965	27 - 975
Weight Range (kg)	NA	0.07 - 15.2	NA	0.28 - 10.5	0.001 - 16.5
Structure(s) Aged	Scales, otoliths (sectioned), vertebrae, dorsal fin rays, anal fin rays	Otoliths (sectioned)	Otoliths (whole and sectioned)	None; cohort/length frequency analysis (ELEFAN) was used	Otoliths (sectioned)
Overall Age Range (yr)	0 - 17	0 - 19	0 - 13	NA	0.02 - 20.14

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Female Age Range (yr)	NA	0 - 19	0 - 10	NA	3.27 - 19.14
Male Age Range (yr)	NA	0 - 15	0 - 13	NA	2.84 - 20.14

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Table 2. von Bertalanffy growth function (VBGF) parameters published to date for overall (female, male, and unknown sex) and sex-specific crevalle jack data. Studies are listed in chronological order, and parameters include predicted fork length in millimeters (L_∞), growth coefficient in year^{-1} (k), and the hypothetical age at which length equals 0 in years (t_0). Standard error values are shown in parentheses.

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	VBGF Parameters	Snelson (1992)	Kishore & Solomon (2005)	Caiafa, Narváez, & Borrero (2011)	This Study
Overall	L_∞ (SE)	980	908.47 (299.50)	910	925.73 (3.69)
	k (SE)	0.22	0.12 (0.08)	0.38	0.26 (0.01)
	t_0 (SE)	-1.2	-1.63 (1.00)	0.32	0.04 (0.03)
Female	L_∞ (SE)	NA	1044.00 (303.28)	NA	903.04 (2.51)
	k (SE)	NA	0.10 (0.06)	NA	0.39 (0.01)
	t_0 (SE)	NA	-1.67 (0.86)	NA	0.73 (0.13)
Male	L_∞ (SE)	NA	709.42 (174.15)	NA	887.16 (2.23)
	k (SE)	NA	0.19 (1.09)	NA	0.39 (0.01)
	t_0 (SE)	NA	-1.09 (1.05)	NA	0.73 (0.13)

Table 3. Diet composition of crevalle jack stomach contents sampled from 2017 to 2019 in Mississippi, Alabama, and west Florida. Metrics include frequency of occurrence (%FO), average percent number (%N), prey-specific number (%PN), average percent weight (%W), prey-specific weight (%PW), and prey-specific index of relative importance (%PSIRI). Prey are reported at the class, order, family, and species levels and are ordered by hierarchical classification. Class-level results are indicated by bold text.

Class	Order	Family	Species	%FO	%N	%PN	%W	%PW	%PSIRI

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Miscellaneous vegetation			**Unidentified**	**3.3%**	**0.5%**	**15.1%**	**0.5%**	**15.2%**	**0.5%**
Malacostraca				**43.6%**	**16.8%**	**38.6%**	**15.1%**	**34.8%**	**16.0%**
	Unidentified Malacostraca		Unidentified	0.7%	0.1%	12.9%	0.2%	26.2%	0.1%
	Decapoda			42.6%	16.0%	37.6%	14.3%	33.6%	15.1%
		Unidentified Dendrobranchiata	Unidentified	0.3%	0.0%	3.2%	0.0%	0.8%	0.0%
		Sicyoniidae	Unidentified	0.7%	0.4%	53.1%	0.4%	53.3%	0.4%
		Penaeidae		34.3%	10.9%	31.9%	9.1%	26.5%	10.0%
			Farfantepenaeus aztecus	23.8%	6.4%	27.1%	4.8%	20.0%	5.6%
			Litopenaeus setiferus	12.5%	4.5%	35.9%	4.3%	34.6%	4.4%
		Unidentified Pleocyemata	Unidentified	3.0%	1.3%	42.3%	1.4%	47.5%	1.3%
		Palaemonidae	Macrobrachium ohione	0.3%	0.2%	50.0%	0.3%	87.1%	0.2%
		Panopeidae	Unidentified	0.3%	0.1%	16.7%	0.0%	0.2%	0.0%
		Portunidae		6.3%	3.2%	51.5%	3.1%	50.1%	3.2%
			Callinectes sapidus	2.6%	1.3%	50.3%	1.3%	50.4%	1.3%

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			Callinectes similis	3.0%	1.7%	57.7%	1.7%	56.8%	1.7%
			Portunus gibbesii	0.7%	0.2%	28.1%	0.1%	18.9%	0.2%
	Stomatopoda	Squillidae	Squilla sp.	2.3%	0.7%	32.3%	0.7%	29.8%	0.7%
Bivalvia				**0.7%**	**0.2%**	**33.3%**	**0.4%**	**55.4%**	**0.3%**
	Unidentified Bivalvia		Unidentified	0.3%	0.1%	16.7%	0.1%	19.4%	0.1%
	Ostreida	Ostreidae	Crassostrea virginica	0.3%	0.2%	50.0%	0.3%	91.5%	0.2%
Cephalopoda	**Myopsina**	**Loliginidae**	**Lolliguncula brevis**	**4.6%**	**1.0%**	**22.7%**	**1.0%**	**21.5%**	**1.0%**
Gastropoda	Littorinimorpha			1.0%	0.7%	66.7%	0.4%	39.2%	0.5%
		Littorinidae	Littoraria irrorata	0.3%	0.3%	100.0%	0.3%	100.0%	0.3%
		Naticidae	Sinum perspectivum	0.3%	0.1%	25.0%	0.0%	1.1%	0.0%
	Neogastropoda	Olividae	Oliva sayana	0.3%	0.2%	75.0%	0.1%	16.5%	0.2%
Elasmobranchii	**Carcharhiniformes**	**Carcharhinidae**	**Rhizoprionodon terraenovae**	**0.3%**	**0.0%**	**8.3%**	**0.2%**	**52.4%**	**0.1%**
Teleostei				**91.7%**	**80.7%**	**88.0%**	**82.4%**	**89.8%**	**81.6%**
	Unidentified Actinopterygii		Unidentified	14.2%	5.3%	37.1%	4.3%	30.4%	4.8%

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Clupeiformes			21.5%	9.1%	42.3%	9.2%	42.7%	9.1%
	Clupeidae		19.8%	8.3%	41.8%	8.8%	44.3%	8.5%
		Brevoortia patronus	18.2%	7.4%	40.7%	8.0%	43.8%	7.7%
		Dorosoma petenense	0.3%	0.2%	50.0%	0.0%	12.9%	0.1%
		Harengula jaguana	1.3%	0.4%	28.8%	0.4%	33.0%	0.4%
		Opisthonema oglinum	0.3%	0.3%	100.0%	0.3%	100.0%	0.3%
	Engraulidae		4.0%	0.8%	20.6%	0.4%	9.7%	0.6%
		Anchoa hepsetus	3.0%	0.7%	23.4%	0.4%	11.8%	0.5%
			1.0%	0.1%	12.2%	0.0%	3.6%	0.1%
Siluriformes	Ariidae		19.1%	7.3%	38.2%	6.8%	35.5%	7.1%
		Ariopsis felis	6.6%	2.9%	44.6%	2.9%	44.0%	2.9%
		Bagre marinus	10.6%	3.2%	30.1%	2.8%	26.5%	3.0%
		Unidentified	2.3%	1.2%	51.5%	1.1%	47.4%	1.1%
Aulopiformes	Synodontidae	Synodus foetens	1.0%	0.3%	25.3%	0.2%	16.7%	0.2%
Ophidiiformes	Ophidiidae	Ophidion josephi	0.3%	0.1%	16.7%	0.0%	5.6%	0.0%
Scombriformes			18.8%	5.4%	28.6%	5.6%	29.7%	5.5%

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	Scombridae		0.7%	0.0%	7.5%	0.1%	18.6%	0.1%
		Scomberomorus cavalla	0.3%	0.0%	2.5%	0.0%	5.8%	0.0%
		Scomberomorus maculatus	0.3%	0.0%	12.5%	0.1%	31.4%	0.1%
	Stromateidae	Peprilus paru	0.3%	0.3%	100.0%	0.3%	100.0%	0.3%
	Trichiuridae	Trichiurus lepturus	18.2%	5.0%	27.5%	5.1%	28.2%	5.1%
Carangiformes	Carangidae		5.0%	1.7%	35.1%	1.9%	37.4%	1.8%
		Caranx crysos	0.3%	0.5%	50.0%	0.6%	93.3%	0.2%
		Chloroscombrus chrysurus	3.0%	1.0%	32.2%	1.0%	34.7%	1.0%
		Selene setapinnis	1.3%	0.3%	20.0%	0.2%	13.3%	0.2%
		Selene vomer	0.3%	0.0%	6.5%	0.0%	2.9%	0.0%
Pleuronectiformes			1.3%	0.5%	39.4%	0.5%	35.9%	0.5%
	Achiridae	Trinectes maculatus	1.0%	0.5%	51.5%	0.5%	47.1%	0.5%
	Paralichthyidae	Etropus crossotus	0.3%	0.0%	3.2%	0.0%	2.4%	0.0%
Eupercaria incertae sedis	Sciaenidae		68.0%	47.7%	70.1%	50.6%	74.4%	49.1%
		Bairdiella chrysoura	0.3%	0.0%	2.8%	0.0%	6.9%	0.0%

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		Cynoscion arenarius	7.3%	1.3%	17.6%	1.4%	19.2%	1.3%
		Larimus fasciatus	4.6%	0.5%	10.8%	0.3%	5.5%	0.4%
		Leiostomus xanthurus	12.9%	3.7%	28.8%	4.9%	38.1%	4.3%
		Menticirrhus americanus	1.3%	0.5%	35.5%	0.6%	43.6%	0.5%
		Micropogonias undulatus	63.7%	41.4%	64.9%	43.3%	67.9%	42.3%
		Stellifer lanceolatus	3.0%	0.3%	11.3%	0.2%	6.5%	0.3%
Lutjaniformes	Lutjanidae	Lutjanus campechanus	0.3%	0.2%	55.6%	0.2%	66.4%	0.2%
Spariformes	Sparidae		4.0%	2.2%	54.6%	1.9%	46.9%	2.0%
		Lagodon rhomboides	1.3%	0.6%	42.4%	0.7%	51.0%	0.6%
		Stenotomus caprinus	3.0%	1.6%	53.9%	1.2%	39.8%	1.4%
Tetraodontiformes	Tetraodontidae	Lagocephalus laevigatus	0.3%	0.1%	16.7%	0.0%	6.8%	0.0%
Perciformes	Serranidae	Centropristis philadelphica	0.3%	0.0%	3.6%	0.0%	0.6%	0.0%
Scorpaeniformes	Triglidae	Prionotus longispinosus	2.6%	1.0%	39.7%	1.4%	51.4%	1.2%

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Table 4. Outputs of the permutational multivariate analysis of variance models for the diet composition of crevalle jack stomach contents sampled from 2017 to 2019 in Mississippi, Alabama, and west Florida. Metrics include degrees of freedom (df), F-statistic (F), amount of variability explained (R^2), P-value (P), and results of dispersion analysis (*P < 0.05, **P < 0.01). Metrics are reported for average percent number (%N) and average percent weight (%W).

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			%N				%W			
Model(s)	Variables(s)	df	F	R^2	P		F	R^2	P	
Independent variables	Sex	2	2.413	0.016	0.010		2.470	0.016	0.009	
	Fork length	1	6.070	0.020	< 0.001	**	6.037	0.020	< 0.001	*
	Location	7	2.615	0.058	< 0.001	**	2.427	0.054	< 0.001	**
	Year	2	4.259	0.028	< 0.001	**	3.912	0.025	< 0.001	*
Interactions	Sex x fork length	2	1.634	0.010	0.080		1.563	0.010	0.109	
	Sex x location	9	1.205	0.034	0.160		1.321	0.037	0.080	
	Sex x year	3	1.023	0.010	0.410		1.050	0.010	0.379	
	Fork length x location	7	1.387	0.030	0.059		1.558	0.034	0.020	
	Fork length x year	2	1.162	0.007	0.278		1.073	0.007	0.353	
	Location x year	14	1.904	0.080	< 0.001		2.018	0.085	0.001	
Final model	Location	7	2.842	0.058	< 0.001	**	2.650	0.054	< 0.001	**
	Year	2	4.223	0.025	< 0.001	**	3.843	0.023	< 0.001	*
	Fork length	1	4.470	0.013	0.001	*	4.964	0.015	< 0.001	*
	Sex	2	2.993	0.018	0.003		3.003	0.018	0.003	
	Location x year	14	1.837	0.076	< 0.001		1.952	0.080	< 0.001	
	Residuals	276		0.811				0.810		

Figures

Figure 1. Gulf of Mexico crevalle jack recreational catch by type (released alive, reported harvest, and observed harvest) from 1981 to 2020 according to NOAA Fisheries' Marine Recreational Information Program data. Catch is reported in millions of fish.

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Figure 2. Map showing the locations where crevalle jack were sampled during the present study (2002 to 2020) via hook-and-line, gillnet, seine, trawl, haul seine, or trammel net. Circle size corresponds to the number of samples, with larger circles indicating greater numbers of samples. While fishery-independent points (yellow) represent exact catch locations, fishery-dependent points (maroon) represent general catch locations. The map was generated using Quantum GIS (Quantum GIS Development Team 2021).

Figure 3. Length frequency distributions, with females in red, males in blue, and unknown sex in gray, of crevalle jack sampled from (A) fishery-dependent sampling in Alabama from 2017 to 2019, (B) fishery-independent sampling from gillnet, seine, and trawl surveys in Alabama during 2020, and (C) fishery-independent sampling from haul seine, trammel net, and hook-and-line surveys along Florida's west coast from 2002 to 2014.

Figure 4. Cross-sections, with ventral annotations, of crevalle jack otoliths from individual fish with assigned age classes of (A) 0 years, (B) 4 years, (C) 9 years, and (D) 20 years sampled from 2017 to 2020 in Alabama. Opaque zones counted for age estimation are marked with a white dot.

Figure 5. Overall logistic (black solid line), overall von Bertalanffy growth function (black dashed line), and sex-specific von Bertalanffy growth function (red and blue dashed lines) growth curves based on crevalle jack fractional ages estimated from otoliths collected in Mississippi, in Alabama, and along Florida's west coast from 2002 to 2020.

Figure 6. Canonical correspondence analysis biplots for (A) percent number of prey (%N) and (B) percent weight of prey (%W) from the present study, showing the relationships between the explanatory variables (blue) from the final model in the permutational multivariate analysis of variance analysis and prey families (red). Crevalle jack stomach contents used for this analysis were collected from fishery-dependent sampling in Alabama from 2017 to 2019.

Figure 7. Length frequency distribution of all crevalle jack sampled during Alabama's fishery-independent gillnet survey from 2000 to 2019.

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Supplemental Figure 1. Cumulative prey curves (± standard deviation) showing prey richness (number of prey taxa) at the (A) family level and (B) species level for crevalle jack sampled from 2017 to 2019 in Mississippi, Alabama, and west Florida.

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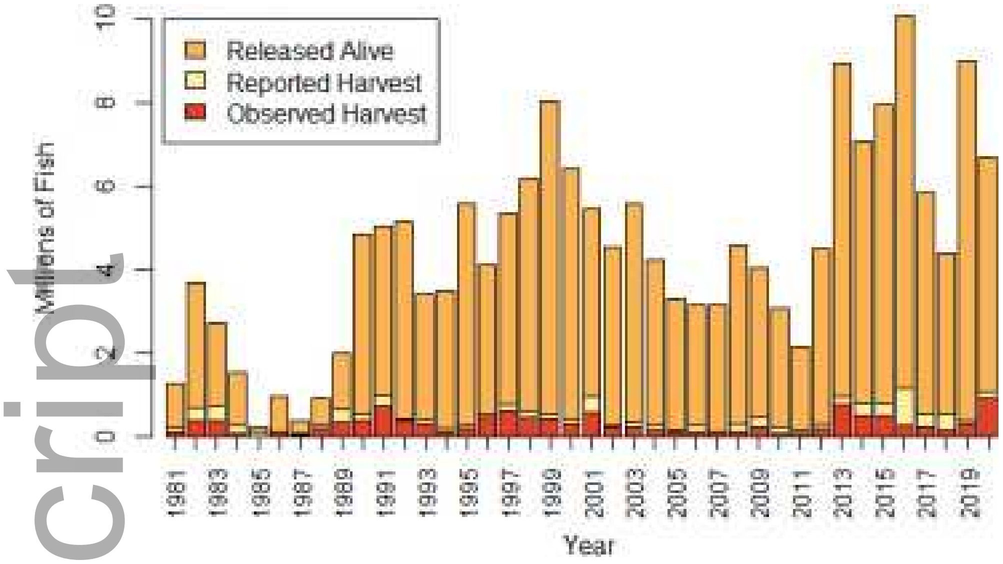

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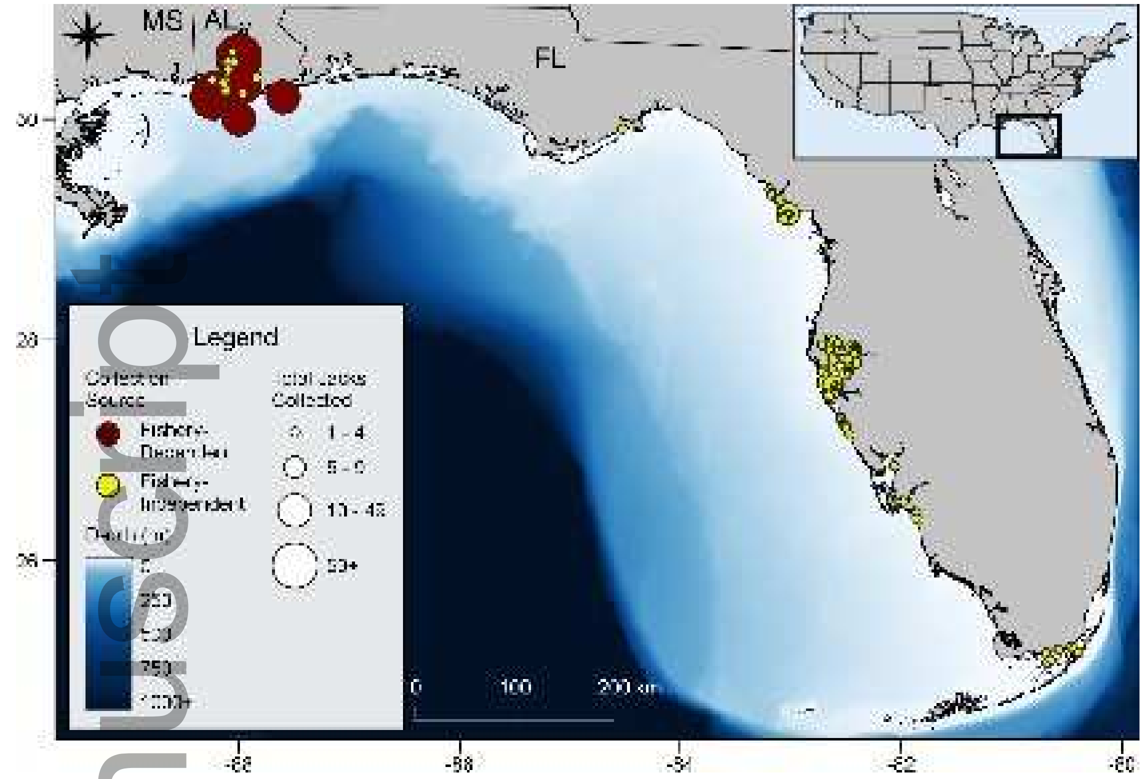

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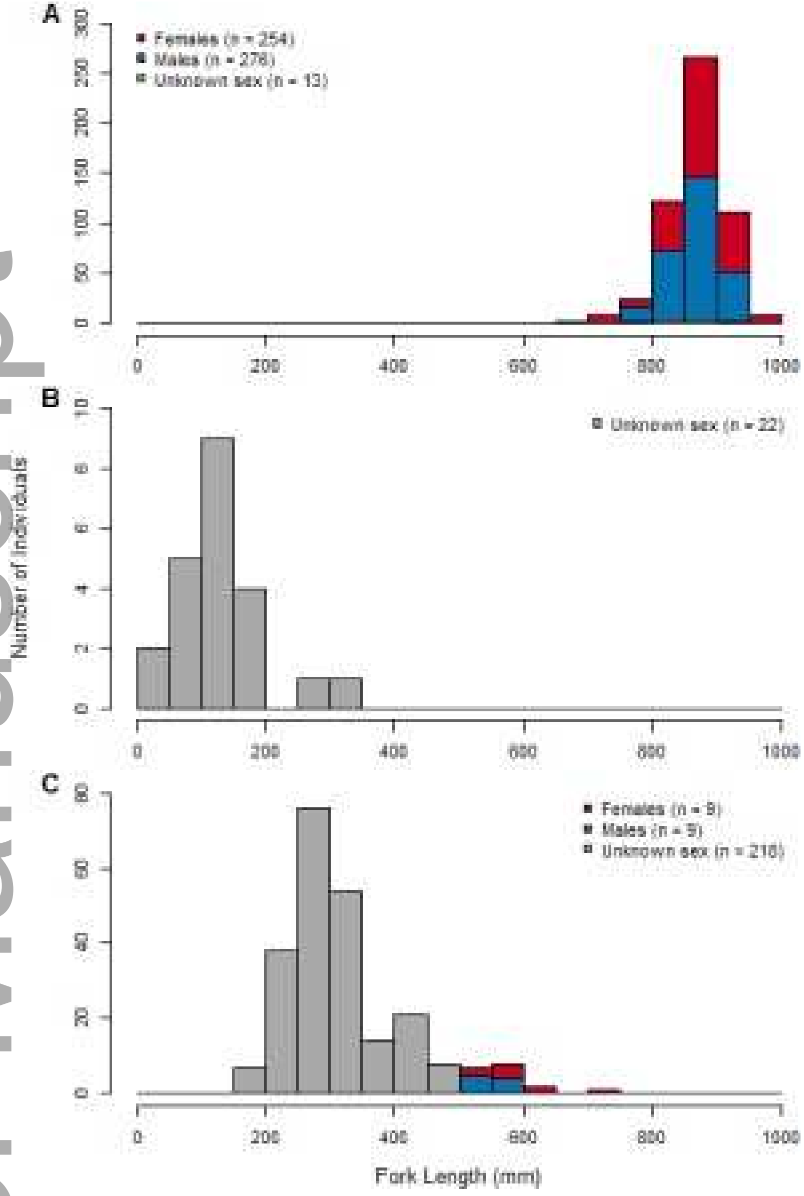

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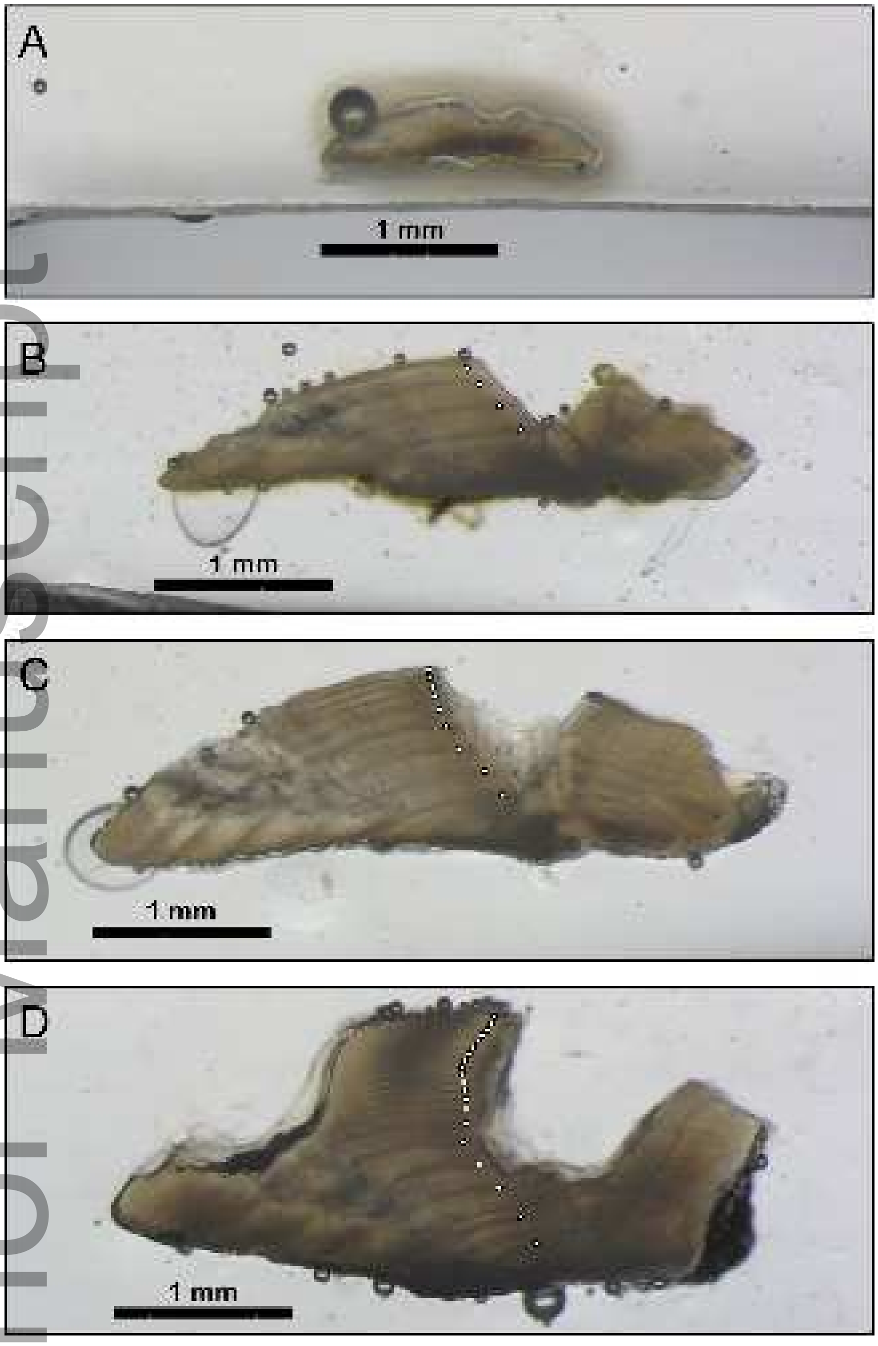

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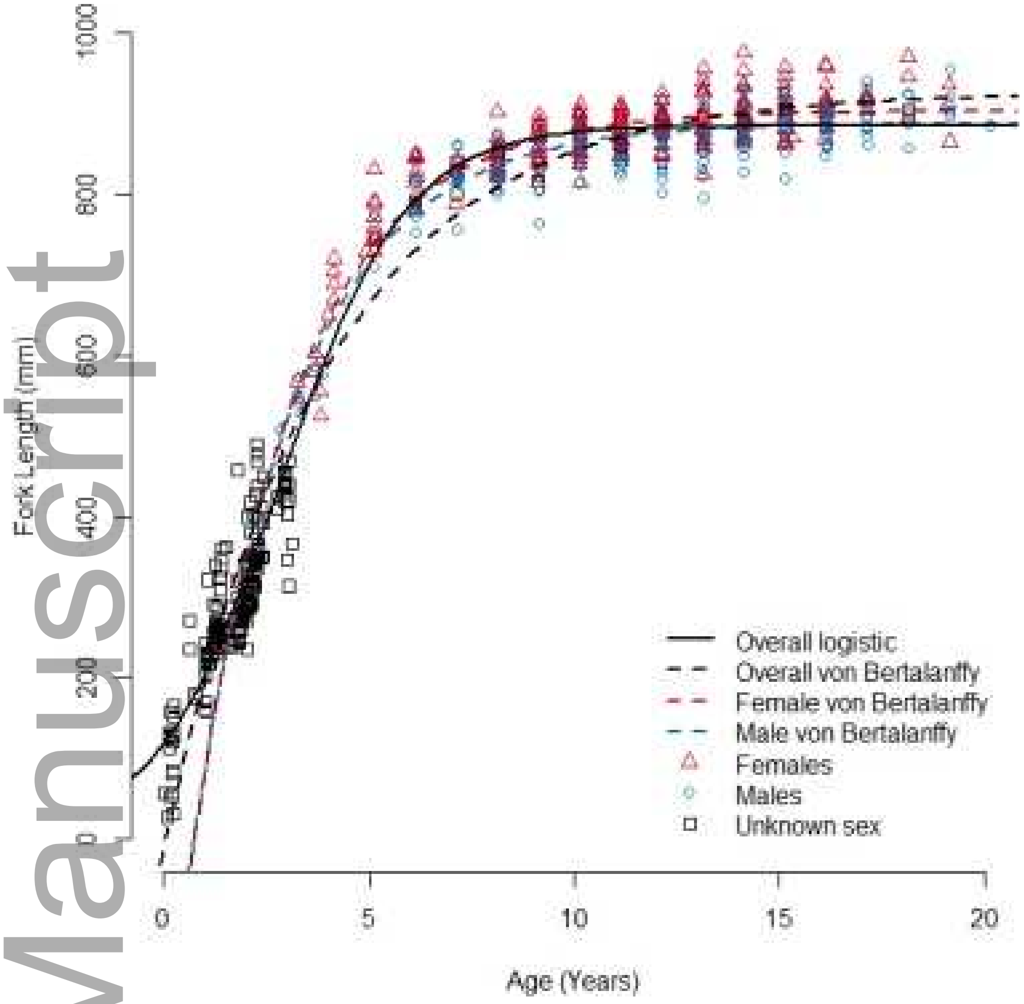

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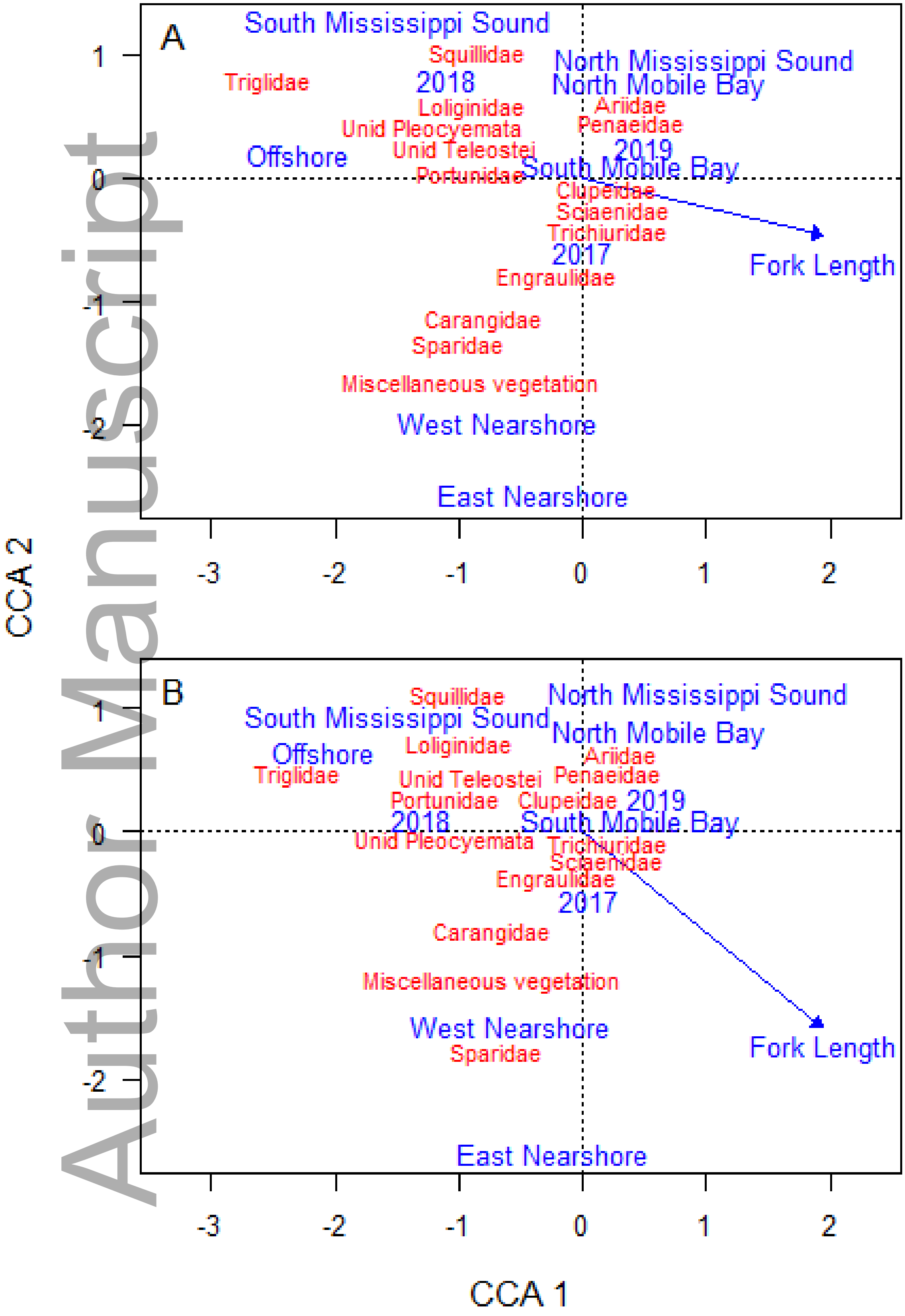

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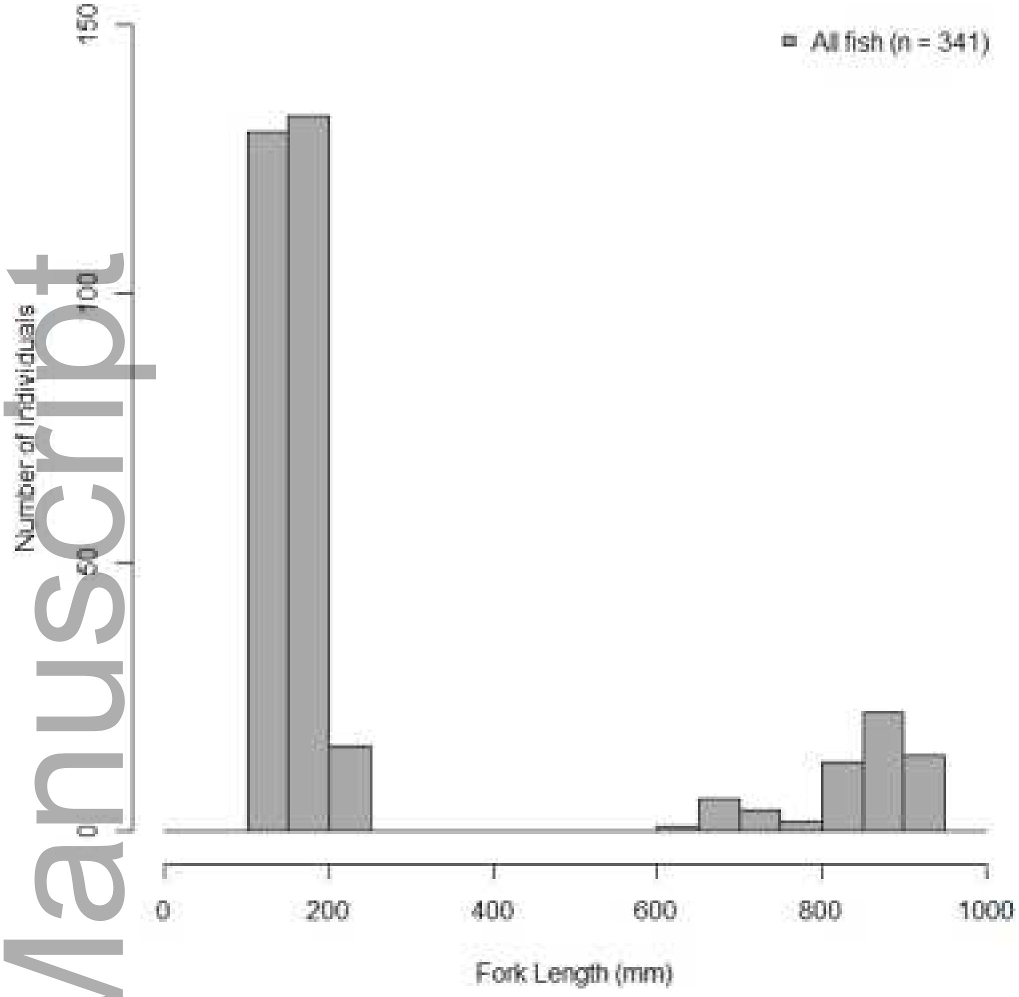

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