Dietary composition of black drum *Pogonias cromis* in a hypersaline estuary reflects water quality and prey availability

K.S. RUBIO[1], M. AJEMIAN[2], G.W. STUNZ[3], T.A. PALMER[1], B.LEBRETON[4] AND J. BESERES POLLACK[1]

[1] Department of Life Sciences, Texas A&M University – Corpus Christi, 6300 Ocean Drive, Corpus Christi, TX 78412-5800, U.S.A.

[2] Florida Atlantic University, Harbor Branch Oceanographic Institute, Fort Pierce, FL, 34946, U.S.A.

[3] Harte Research Institute for Gulf of Mexico Studies, Texas A&M University—Corpus Christi, 6300 Ocean Drive, SL2 101 Corpus Christi, TX 78412-5869, U.S.A.

[4] UMR Littoral, Environment et Societies, CNRS – University of La Rochelle, Institut du littoral et de l'environnement, 2 rue Olympe de Gouges, 17000 La Rochelle, France

Correspondence

J. Beseres Pollack

Department of Life Sciences, Texas A&M University – Corpus Christi, 6300 Ocean Drive, Corpus Christi, TX 78412-5800, U.S.A.

Email: jennifer.pollack@tamucc.edu

Funding information

This article has been accepted for publication in the *Journal of Fish Biology* and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jfb.13654

The authors thank the organizations and agencies that helped fund this research, including the Texas Coastal Bend Bays & Estuaries Program (CBBEP), Harvey Weil Sportsman Conservation Award, Texas Sea Grant, and Texas A&M University-Corpus Christi.

Running headline: *POGONIAS CROMIS* DIET IN A HYPERSALINE ESTUARY

The Baffin Bay estuary is a hypersaline system in the Gulf of Mexico that supports an important recreational and commercial fishery for black drum *Pogonias cromis*, a benthic predator. Seasonal measurements of water quality variables, benthic macrofauna densities and biomass, and determination of *P. cromis* food sources using stomach-content and stable-isotope analyses were carried out to determine how *P. cromis* food sources change with water quality and how this may affect *P. cromis* diet. Gut-content analysis indicated *P. cromis* selectively consumed bivalves *Mulinia lateralis* and *Anomalocardia auberiana*. Isotope compositions demonstrated that *P. cromis* relied on these benthic food resources produced in the Baffin Bay estuary year-round. Biomass and densities of these bivalves were influenced by changes in water quality variables, particularly salinity and dissolved oxygen. Thus, this paper demonstrates the relationship between water quality variables, benthic macrofauna, and their use as food resources by a carnivorous fish species, and emphasizes the need for integrated assessments when studying the effects of water quality on ecosystem function. Holistic approaches such as these can provide important information for management and conservation of fishery resources and can improve predictions of ecosystem response to climate variability.

KEYWORDS

Baffin Bay (U.S.A.), black drum; food resources; macrofauna; salinity; stable isotopes.

1 | INTRODUCTION

Estuaries are important habitats for fishes due to high levels of primary production (Nixon, 1982) supporting high density and diversity of prey, and providing nursery and feeding grounds for ecologically and economically important species (Blaber & Blaber, 1980; Whitfield, 1999; Beck *et al.*, 2001; Levin *et al.*, 2001). Because estuaries are located at the land–ocean interface, anthropogenic and environmental changes affect the structure and dynamics of biotic communities (Kennish *et al.*, 2002; Nixon & Buckley, 2002). In particular, the availability of individual food resources fluctuates over time and space in response to environmental changes (Montagna & Kalke, 1992; Beseres Pollack *et al.*, 2009), altering energy flow pathways (Whitfield, 1986; Elliott *et al*., 2007). This may be especially the case for systems already experiencing environmental stressors such as hypersalinity.

In coastal ecosystems, salinity is an important factor influencing fish abundance and distribution (Alber, 2002; Harrison & Whitfield, 2006). The often abrupt salinity changes common to estuaries can cause considerable physiological demands on fishes (Whitfield, 1999). Although fishes living in estuaries are adapted to salinity fluctuations, individual response to salinity stress varies by species and scale (Williams *et al.,* 1990; Blaber, 1997). Low diversity and richness of fishes in hypersaline systems has been attributed to osmoregulatory stress and associated biotic interactions such as disappearance of particular food resources (Boltt, 1975; Whitfield, 1999). Freshwater inflow is typically delivered in pulses governed by stochastic and complex long-term cycles (Montagna *et al*., 2013). Reduced freshwater inflows increase salinity stress and can lead to negative effects on estuarine biodiversity and productivity (Fourqurean *et al.,* 1993; Scavia *et al.,* 2002; Nicholson *et al.,* 2008). Increases in upstream water withdrawals (Montagna *et al*., 2002) coupled with predicted increases in aridity (Seager *et al.,* 2007) and increased storminess will lead to stronger and longer periods of hypersaline conditions and more frequent salinity disturbances (Pachauri & Meyer, 2014). Improved scientific understanding of the response of fish to acute salinity fluctuations in hypersaline systems is critical for supporting effective management and conservation of fishery resources (Ludwig *et al.,* 1993).

The Baffin Bay estuary is a shallow, subtropical estuarine system on the Gulf of Mexico coastline experiencing hypersaline conditions as a function of a semi-arid climate and high evaporation rates (Wetz *et al.*, 2017). Within this system, the large-bodied sciaenid black drum, *Pogonias cromis* (L. 1766), supports an important recreational and commercial fishery (Ross *et al.*, 1983; Osburn & Matlock, 1984; Olsen, 2016). *Pogonias cromis* movement between Gulf of Mexico estuaries is minimal, indicating populations are largely isolated from one another (Osburn & Matlock, 1984; Ajemian *et al.*, 2018) and probably rely on locally produced food resources. Juvenile and adult *P. cromis* exploit a variety of benthic food resources and can use their strong pharyngeal teeth to crush the shells of molluscs and crustaceans (Simmons & Breuer, 1962; Dugas, 1986). Gut content analyses have identified the dwarf surf clam *Mulinia lateralis*, a species whose densities are highly variable over time (Breuer, 1962; Simmons & Breuer, 1962; Montagna *et al.*, 1993), as a primary food resource of *P. cromis* (Sutter *et al.* 1986). Changes in water quality variables, especially salinity, can affect benthic macrofauna density, diversity and community composition (Montagna *et al.*, 1995), which may affect food resource availability to this fish species.

Gut-content analysis reveals information about fish food resources at a relatively precise taxonomic level, but provides only a snapshot of prey items recently ingested (Pinnegar & Polunin, 1999). Differential digestion of prey may cause errors in determination of diet, as some food resources composed primarily of soft tissues (*e.g.* annelids) are more rapidly digested

(Kennedy, 1969) and may be underrepresented compared with food resources with calcium carbonate shells or chitinous pieces (Hyslop, 1980). It is also not always clear from gut-content analysis how much a particular ingested food resource will contribute to consumer production in relation to its assimilation rate. A complementary approach, stable-isotope analysis, can be used to elucidate what food resources are actually ingested and assimilated (Pinnegar & Polunin, 2000; Fry *et al.*, 2008). Isotope composition of gut contents reflects what has been ingested but not yet assimilated. This provides information about material that cannot be identified through standard gut-content analysis (*e.g.* soft tissue animals) but, like gut-content analysis, it only provides a snapshot of what has been recently ingested. Muscle isotope composition reflects food resources assimilated over a relatively long period due to slow tissue turn over (Vander Zanden *et al.*, 2015) and is thus less biased by short-term (*i.e.* day to day) variability (Pinnegar & Polunin, 2000). Carbon isotope composition in particular can be useful for identifying the origin of food resources (Fry & Sherr, 1984; Peterson & Fry, 1987) while nitrogen isotope composition is commonly used to determine trophic levels (Post, 2002). Therefore, thse different techniques, applied on different materials (*i.e.* gut content, muscle), are useful to get a more complete picture of food resources used by consumers.

Determining relationships between water quality variables, composition of benthic macrofauna community (*i.e.* fish prey) and food resources used by fish is needed to better understand how changes in environmental conditions may affect fish populations through cascading effects, particularly in ecosystems already under stress. Flooding caused by heavy rains provided an opportunity to assess the response of *P. cromis* and benthic macrofauna to acute salinity fluctuation in the hypersaline Baffin Bay estuary. To this end, the aims of this paper are: to determine the food resources (*i.e.* benthic macrofauna) of *P. cromis* based on a combination of gut-content and stable-isotope analyses, to define how densities and biomass of *P. cromis* food resources change on a temporal and spatial basis when water quality variables are modified and to assess if these changes affect use of food resources by fish.

2 | MATERIALS AND METHODS

2.1 | Study site

The Baffin Bay estuary is adjacent to the western edge of the upper Laguna Madre on the Texas Gulf of Mexico, U.S.A. (Figure1). This 248 km^2 subtropical estuary comprises a secondary bay: Baffin Bay and three tertiary bays: Alazan Bay, Cayo del Grullo and Laguna Salada (Figure 1). Freshwater inflow occurs sporadically *via* several ephemeral streams. Long residence times (> 1 year), minimal freshwater inflow and high evaporation rates create a system that is prone to hypersaline conditions (Armstrong, 1987; Buskey *et al.*, 1998; Tunnell and Judd, 2002; Wetz *et al.*, 2017).

2.2 | Water quality, benthic macrofauna and sediment organic matter

Ten stations throughout the Baffin Bay estuary were sampled seasonally for water quality, benthic macrofauna and surface sediment organic matter (SSOM) from March 2014 to March 2015 (Figure 1). Four additional stations (CG3, AL6, AL7, AL9) were sampled from September 2014 to March 2015 to increase spatial coverage. Stations were characterized by muddy sediments and absence of macrophytes. Water quality measurements [temperature, dissolved oxygen (DO), pH, turbidity, salinity, Secchi depth] were collected during the day at each station, each season, at the surface and bottom of the water column using a multi-variable monitoring instrument (Hydrolab Surveyor II; OTT-Hydromet; www.ott.com or YSI 6 series; YSI-Xylem; www.ysi.com) and a Secchi disc.

Benthic macrofauna were sampled using 35.4 cm^2 cylindrical cores to a depth of 10 cm. Five replicate cores were collected from each station, each season: three for community composition and two for stable-isotope measurements. Community composition samples were immediately preserved with 10% buffered formalin for 48 hours and then preserved in 70% ethanol. Macrofauna were extracted on a 500 µm sieve in the laboratory, sorted using a dissecting microscope, identified to the lowest possible taxonomic level (usually species) and enumerated. Species names were verified using Tunnell *et al.,* (2010) and WoRMS Editorial Board, (2017). Biomass measurements were obtained after grouping species into higher taxonomic levels (Cnidaria, Polychaeta, Gastropoda, Bivalvia, Crustacea) and drying at 55° C for 24–48 h until reaching a constant mass. Mollusc shells were removed with 10% HCl prior to drying and weighing.

Cores for stable-isotope analyses were sieved on a 500 µm-mesh screen in the field and macrofauna were transported live to the laboratory in coolers. Macrofauna for stable-isotope analyses were kept separately in artificial seawater for 24–48 h to evacuate gut contents before being stored at –20° C.

SSOM was collected using 35.4 cm^2 cylindrical cores. The top 3 cm of sediment were collected and immediately placed on ice. In the laboratory, samples were sieved on a 500 µm-mesh screen to remove macrofauna, shell hash and large detrital particles and then freeze-dried and ground using a mortar and pestle.

2.3 | *Pogonias cromis* muscle and gut contents

Pogonias cromis were collected throughout the Baffin Bay estuary over five seasons (winter, spring, summer, autumn 2014, winter 2015) as part of the Texas Parks and Wildlife Department fisheries-independent sampling programme (Martinez-Andrade *et al.*, 2005) (Figure 1). Fish were collected using gill nets [183 m long x 1.2 m deep with 46 m sections of 7.6, 10.2, 12.7 and 15.2 cm stretch mesh (Matlock & Weaver, 1979)] set perpendicular to the shoreline and immediately placed on ice in the field. In the laboratory, epaxial muscle tissue (*n* = 5–14 individuals per season) was removed from the anterior portion of all *P. cromis* specimens for stable-isotope analysis and frozen at –20° C. No muscle sample was collected for stable-isotope measurements in autumn 2014.

Whole digestive tracts (guts) of *P. cromis* were removed beginning with the oesophagus and ending with the anal vent. Five non-empty digestive tracts per sampling month (*P. cromis* 200–400 mm total length) were selected for stable-isotope analyses and frozen at –20° C before further processing. Digestive tracts for stable-isotope analyses were thawed and gut-content items larger than 500 µm were identified to the lowest possible taxonomic level, enumerated and weighed. Highly digested organic material (< 500 µm) was weighed and then centrifuged. The remaining digestive tracts (if more than five fish were collected) were fixed in 10% buffered formalin for 48 h and then preserved in 70% ethanol for quantifying the abundance and biomass of macrofauna in the gut. Macrofauna were extracted on a 500 µm sieve, sorted using a dissecting microscope, identified to the lowest possible taxonomic level and enumerated. Biomass measurements were obtained after grouping species into higher taxa levels (Polychaeta, Gastropoda, Bivalvia, Crustacea), drying at 55° C for 24–48 h and then weighing. Fish handling methods followed a university-approved animal use protocol (AUP #09-14, Texas A&M

University-Corpus Christi).

2.4 | Stable-isotope composition measurements

Macrofauna from sediment samples and gut contents collected for stable-isotope analyses were freeze-dried and ground to a homogenous powder using a ball mill (MM 400, Retsch; www.retsch.com). SSOM samples and soft tissues from shelled organisms occurring in sediments and guts were decarbonated with 1 mol l^{-1} HCl before $\delta^{13}C$ measurements. Samples were then dried at 60° C using a dry block heater under air flow. Dried samples were re-homogenized into ultrapure water using an ultrasonic bath, freeze-dried and ground again. $\delta^{15}N$ measurements on all samples were carried out on non-acidified samples.

Isotope composition was determined for benthic macrofauna, SSOM, *P. cromis* muscle and gut content samples using an elemental analyzer (ECS 4010 with a Zero Blank autosampler, Costech; www.costechanalytical.com) connected to a continuous-flow isotope-ratio mass spectrometer (Delta V Plus, Thermo Scientific; www.thermofisher.com) *via* a Conflo IV interface. Analyses were conducted at the stable-isotope facility at Texas A&M University-Corpus Christi. Carbon and nitrogen isotope compositions are expressed in δ-notation in parts per thousand (‰) as deviation from international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) and following the formula: $\delta x‰ = [(R_{\text{sample}}R^{-1}{}_{\text{standard}}) - 1]10^3$, where x is ^{13}C or ^{15}N and R is $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$, respectively. Two-point calibration was done using international reference materials (USGS-40: $\delta^{15}N = -4.52‰$; $\delta^{13}C = -26.39‰$ and USGS-41: $\delta^{15}N = 47.57‰$; $\delta^{13}C = 37.63‰$) (Paul *et al.*, 2007). Laboratory standards [Acetanilide (gold nanoparticles, GNPs) and rice (SIGF standards)] were analyzed after every 12 samples to monitor instrument performance and check data normalization. The precision of the laboratory standards was ± 0.2‰ for carbon and nitrogen.

2.5 | Data analysis

Principal component analysis (PCA) was used to determine spatio-temporal patterns in water quality. Variables were first log-transformed and then standardized. Another multivariate approach, non-metric multidimensional scaling (nMDS) was used to determine patterns in both macrofauna community composition and gut content composition (Clarke & Warwick, 1994). nMDS analyses were carried out using a Bray-Curtis similarity matrix on square-root transformed data. Differences in macrofauna composition of the gut content compositions among seasons and bays were tested with two-way crossed analyses of similarities (ANOSIM) with bay and season as factors (Supporting Information Tables S1, S2). ANOSIM tests were run using two separate times, each using different data because of the uneven sampling pattern (Table 1): fish from Alazan and Baffin Bays over the four sampling seasons in 2014 (winter, spring, summer, autumn) and fish collected throughout the entire Baffin Bay estuary in spring and fall 2014. Spring and fall 2014 were the only seasons where all bays within the Baffin Bay estuary were sampled contiguously for fish. Neither ANOSIM included fish collected in winter 2015 because fish were only collected in Baffin Bay during this season. A 3-way ANOSIM (*P. cromis* Size class x Bay x Season) showed no significant difference in gut composition among size classes ($P > 0.05$; total length, L_T size classes < 300, 300–450, > 450 mm). Prey are usually < 5 mm in length, whereas the range of fish sizes analyzed had L_T 166–622 mm; there is no reasonable assumption that the prey ingested in this system are limited by gape size.

Relationships among water quality variables and macrofauna community composition were determined using BIO-ENV (Clarke & Ainsworth, 1993; Supporting Information Table S3). Spearman rank correlations were calculated to characterize the relationships between individual water quality variables and benthic macrofauna abundance, biomass and Hill's $N1$ diversity (Hill, 1973; Sanders, 1968). Partial correlations were used to take into account simultaneous changes in other water quality variables when running correlations (*e.g.* salinity was correlated with macrofauna metrics using partial correlations with temperature and DO). All univariate metrics and correlations were calculated using SAS 9.3 software (SAS Institute Inc.; www.sas.com). All multivariate statistics were calculated using PRIMER 6 software (Clarke & Gorley, 2006).

Comparisons between isotope compositions were conducted using parametric procedures (Student's *t*-test) when conditions of normality (Shapiro-Wilk test) and equality of variances (*F*-test) were respected. Non-parametric procedures (Wilcoxon and Kruskal–Wallis tests) were used when one of these conditions was not respected (Zar, 2010).

Gut contents were described using four metrics. The percent frequency of occurrence ($\%F$) was calculated as: $\%F = 100S_aS^{-1}$, where S_a is the number of guts containing prey item a and S is the total number of non-empty guts examined (Hyslop, 1980). Prey selection was assessed using the Strauss Index (L_{SI}) (L; Strauss, 1979): $L = r_a + p_a$, where r_a is the relative abundance of prey type a in the diet (as a proportion of the total number of prey in the diet) and p_a is the relative abundance of prey type a in the environment (from benthic core data). Values range from –1 to +1, with positive values representing preference and negative values representing avoidance or inaccessibility. Percent mass of total identifiable contents ($\%M$) and percentage of empty guts (vacuity index) were also calculated.

3 | RESULTS

3.1 | Water quality

Comparisons of all water quality variables over space and time were achieved simultaneously using the first two components of the PCA (Figure 2). Principal components 1 and 2 accounted for 57.6% and 18.5% of the variation in the data. Water quality separated into two main groups along PC 1. Water quality among all samples varied more by sampling date than by location. This resulted in two periods of distinct water quality conditions in the Baffin Bay estuary: first, March, June and September 2014 had higher salinity, temperature and turbidity and lower DO; second, December 2014 and March 2015 had lower salinity, temperature and turbidity and higher DO.

Mean salinity of the Baffin Bay estuary ranged from 49.2 in March to 53.6 in September 2014 and decreased to 44.8 in December 2014 and 40.9 in March 2015 [Figure 3(a)]. A reverse salinity gradient, where salinity increases upstream, occurred in all months sampled except in March 2014 and March 2015. The mean salinity in Baffin Bay was 2.2–4.1 lower than in the tertiary bays in March, June and September 2014 and 0.4–2.1 lower in December 2014 and March 2015.

Mean temperature of the Baffin Bay estuary varied seasonally from 15.9° C in December 2014 to 30.0° C in June and September 2014 [Figure 3(b)]. Mean DO concentrations were lowest in September 2014 (5.2 mg l^{-1}) and highest in March 2015 [8.8 mg l^{-1}, Figure 3(c)].

3.2 | Benthic macrofauna

Polychaete worms dominated macrofauna densities, in particular *Streblospio benedicti,* ranging from 2219 n m^{-2} in Baffin Bay to 6486 n m^{-2} in Alazan Bay (Figure 4 and Table 2). Other abundant species included the bivalves *Anomalocardia auberiana* and *Mulinia lateralis* and unidentified gastropods. Macrofauna biomass was dominated by the bivalves *Mulinia lateralis* (from 0.25 g m^{-2} in Baffin Bay to 1.82 g m^{-2} in Cayo del Grullo), *Anomalocardia auberiana* (from <0.01 g m^{-2} in Baffin Bay to 1.83 g m^{-2} in Alazan Bay) and unidentified gastropods (from 0.15 g m^{-2} in Laguna Salada to 0.63 g m^{-2} in Alazan Bay). *Streblospio benedicti* dominated polychaete biomass, ranging from 0.12 g m^{-2} in Baffin Bay to 0.24 g m^{-2} in Laguna Salada (Figure 4 and Table 2).

Mean macrofauna density was highest in March 2014 (8046 n m^{-2}) and lowest in March 2015 (2583 n m^{-2}). Mean biomass was lowest in March 2014 (0.9 g m^{-2}) and highest in June 2014 (3.0 g m^{-2}). Increasing salinity led to increasing Hill's N1 diversity ($r_s = 0.28$, $P < 0.05$) and increasing DO concentrations led to increasing macrofauna biomass, Hill's *N*1 diversity and species richness ($r_s = 0.34$, $P < 0.05$; $r_s = 0.38$, $P < 0.01$; $r_s = 0.39$, $P < 0.01$, respectively). Salinity was the main water quality variable influencing macrofauna community composition ($r_s = 0.193$, $P < 0.05$), above any other single or combination of water quality variables (as calculated using the BIO-ENV procedure). At higher salinities, the macrofauna community had greater contributions of *Streblospio benedicti* and *Acteocina canaliculata*. The combination of salinity and DO concentration was the next strongest contributor to changes in macrofauna community composition ($r_s = 0.185$, $P < 0.01$). Macrofauna community composition in a number of samples from March 2015 differed from the rest of the dates, due to high relative densities of the bivalves *Mulinia lateralis* and *Anomalocardia auberiana* (Figure 5).

3.3 | Gut content analysis

Of the 262 *P. cromis* collected within the Baffin Bay estuary between December 2013 and February 2015, 84% of fish (mean ± S.D. L_T = 335 ± 92 mm) contained stomach contents (Table 1). There was an overall decrease in vacuity indices throughout the Baffin Bay estuary over time, from 54.9% in winter 2014 to 2.3% in autumn 2014 and 0.0% in winter 2015. Seven different major taxa groups were identified in the guts (Table 3). Bivalves were the most frequently occurring prey group in the gut contents (in 70% of guts). Bivalves also dominated the gut biomass (64%). Unidentified bivalves were present in 68% of guts and contributed to 61% of gut mass. The most conspicuous and common bivalve from the gut contents was *Anomalocardia auberiana* (in 32% of guts, 2.2% of gut mass), followed by *Mulinia lateralis* (in 11% of guts, 0.5% of gut mass). Polychaetes were the next most frequently encountered and heaviest gut content taxa (in 51% of guts, 17% of gut mass), followed by seagrass (in 26% of guts, 8% of gut mass). Crustaceans and gastropods were each observed in 6% of guts and made up 2.4% and 0% of gut biomass, respectively.

Bivalves were the only positively selected prey group throughout the Baffin Bay estuary, with mean L_{SI} ranging from 0.35 in Baffin Bay to 0.54 in Laguna Salada. Crustaceans were neither positively selected nor negatively selected ($-0.02 < L_{SI} < 0.05$). Polychaetes were the least selected taxa ($-0.49 < L_{SI} < -0.22$) in all bays except Cayo del Grullo, where gastropods were least selected ($L_{SI} = -0.41$). Seagrass did not occur in any benthic samples so could not be included in the analysis of prey selectivity. Some molluscs inside gut tracts could not be easily differentiated between gastropod and bivalve groups so were also not used in prey selectivity analyses. Fish, seagrass and unidentified molluscs composed up to 2.8%, 26% and 7% of total gut contents for each season-bay combination (5.5%, 35% and 38% of identifiable contents; minimum of 0%).

Multivariate analyses (ANOSIM, nMDS) indicate that the gut taxa composition was significantly different among bays ($0.1 \leq$ ANOSIM $R \leq 0.8$, $P < 0.05$) except for spring 2014 and fall 2014 (ANOSIM $R = 0.04$, $P > 0.05$). Gut contents in Baffin Bay were significantly different to those in Laguna Salada (ANOSIM $R = 0.43$, $P < 0.001$) and Alazan Bay (ANOSIM $R = 0.09$, $P < 0.05$). Gut contents in all other bays were not significantly different from each other ($–0.1 \leq$ ANOSIM $R \leq 0.2$, $P > 0.05$). Differences in proportional biomass of unidentified bivalves caused the highest dissimilarity among seasons, with biomass highest in summer 2014 and lowest in winter 2014. The proportions of higher taxa in the guts were dissimilar from those in the sediment cores, with the guts containing relatively more bivalves and fewer polychaetes and gastropods.

3.4 | Stable-isotope composition

Isotope δ^{13}C and δ^{15}N values of SSOM ranged from –22.1 to –19.1‰ and from 4.1 to 10.2‰, respectively (Figure 6). Isotope compositions of SSOM did not show any temporal (Kruskal Wallis tests: δ^{13}C: $P > 0.05$, δ^{15}N: $P > 0.05$) or spatial (Kruskal Wallis tests: δ^{13}C: $P > 0.05$, δ^{15}N: $P > 0.05$) pattern. Seagrass was more enriched in ^{13}C than SSOM (δ^{13}C –14.6‰) and had low δ^{15}N values (4.0‰).

Macrofauna δ^{13}C values ranged from –24.0 (Tanaidacea) to –14.8‰ (Amphipod), which was similar to ranges of δ^{13}C values of seagrass and SSOM. δ^{15}N values of macrofauna ranged from 4.4 (Tanaidacea) to 11.4 (*Leptochelia rapax*).

Isotope $\delta^{13}C$ and $\delta^{15}N$ values of *P. cromis* gut liquid ranged from –26.7 to –12.8‰ (mean ± S.D., –21.2 ± 3.1‰) and from 4.7 to 11.4‰ (mean ± S.D., 7.8 ± 1.1‰), respectively. It was not possible to determine spatial or temporal variations due to unbalanced sampling between bays and dates. $\delta^{13}C$ and $\delta^{15}N$ values of *P. cromis* muscle (mean ± S.D. L_T = 343 ± 65 mm) ranged from –21.1 to –17.7‰ (mean ± S.D., –19.9 ± 0.9‰) and from 9.2 to 12.4‰ (mean ± S.D., 10.4 ± 0.8‰), respectively. Isotope composition of muscle did not show any temporal (Kruskal Wallis tests: $\delta^{13}C$: $P > 0.05$, $\delta^{15}N$: $P > 0.05$) or spatial (Kruskal Wallis tests: $\delta^{13}C$: $P > 0.05$, $\delta^{15}N$: $P > 0.05$) pattern.

Gut-liquid samples had a much larger range of $\delta^{13}C$ values than muscles (13.9‰ *v.* 7.4‰) whereas ranges of $\delta^{15}N$ values were similar (Fisher test, $\delta^{13}C$: $P < 0.001$, $\delta^{15}N$: $P > 0.05$). Gut liquid was significantly more depleted in ^{13}C and ^{15}N than muscle (Wilcoxon test, $\delta^{13}C$: $P <$ < 0.001; Student's *t*-test: $\delta^{15}N$: $P < 0.001$). Average differences between gut liquid and muscle were 1.8 and 2.6‰ for $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

4 | DISCUSSION

4.1 | Effect of a major rain event on Baffin Bay estuary water conditions

The large salinity drop observed from September 2014 to March 2015 is related to a major rain event in September 2014, with monthly precipitation totalling 345 mm (compared with the monthly average of 62 mm throughout the remaining study period). Variations of DO and temperature reflect seasonal patterns. The rain event led to a decrease in salinity from 53.6 to 40.9, compared with the hypersaline conditions that typically exist (40 to 60) due to evaporation exceeding precipitation (Buskey *et al.*, 1998). This provides an interesting case study, period of strongly hypersaline conditions (typical in this estuary) followed by an acute freshwater pulse and lower salinities, that can be used to determine how benthic macrofauna (*i.e*. fish food resources) and fish diet change in relation to salinity drop.

4.2 | Food resources of *P. cromis*

Gut content analyses demonstrate that *P. cromis* ingest a relatively large diversity of prey items originating from the benthic macrofauna. Observed macrofaunal densities were similar to those reported in other studies from this estuary (Montagna & Kalke, 1995; Buskey *et al.*, 1997). Some food resources are actively preyed upon (*i.e*. bivalves, particularly *M. lateralis* and *A. auberiana*; Sutter *et al.,* 1986) whereas some are less selected (*i.e*. polychaetes, gastropods). The lower densities of polychaetes measured in *P. cromis* gut contents may nevertheless be related to the fact that they are made of soft tissues only, leading to a quicker digestion than animals with an exoskeleton (*i.e*. bivalves, gastropods, crustaceans) (Hyslop, 1980).

Isotope δ^{13}C values of SSOM, ranging from –22.1 to –19.1‰, are typical of what has been observed in similar systems, indicating that SSOM in Baffin Bay estuary is a mixture of several primary producers: very likely trapped phytoplankton (Fry & Sherr, 1984; Lebreton *et al.,* 2016) and benthic microalgae (Lebreton *et al.,* 2016), with possible influence of detritus from C_3 and C_4 plants (Fry & Sherr, 1984). The ranges of δ^{13}C values among the benthic macrofauna highlight that they rely on a wide diversity of food resources with coastal origin, from trapped phytoplankton for the most ^{13}C-depleted consumers (–24.0‰) to benthic microalgae for the most ^{13}C-enriched consumers (–14.8‰). The similar isotope compositions of *P. cromis* gut liquids and benthic macrofauna confirm that the food resources ingested by *P.*

cromis predominantly originate from the Baffin Bay estuary, in accordance with previous observations of limited mobility of *P. cromis* outside of the estuary (Osburn & Matlock, 1984; Ajemian *et al.,* 2018). The large range of gut-liquid δ^{13}C values, overlapping the range of benthic macrofauna δ^{13}C values, highlights that this fish species can ingest a large range of prey items. Isotope composition of the *P. cromis* muscle tissue indicates that this species assimilates food resources produced in the Baffin Bay estuary. *Mulinia lateralis* can represent a large contribution to *P. cromis* diet as the range of muscle δ^{13}C values are relatively close to those of *M. lateralis*, taking into account the trophic fractionation between food sources and consumers. Indeed, muscle tissue isotope composition is enriched in ^{13}C and ^{15}N compared with gut contents following trophic fractionation factors (1.8 for δ^{13}C, 2.6 for δ^{15}N) typically observed between a consumer and its food sources (Post, 2002; Vander Zanden & Rasmussen, 2001).

The combination of gut-content analyses and isotope compositions of gut contents and muscle tissues demonstrate that *P. cromis* rely on benthic food resources produced in the Baffin Bay estuary yera-round. Such combination of approaches is highly beneficial to understand trophodynamics, particularly for durophagous predators like *P. cromis*, which use strong pharyngeal teeth to crush their prey (Simmons & Breuer, 1962; Grubich, 2003). Small and soft-bodied benthic prey are indeed quickly digested beyond visible recognition (Kennedy, 1969; Hofsten *et al.,* 1983) compared with those containing digestion-resistant hard parts (Miller, 1974; Sogard, 1984). In addition to providing information about what is ingested (*i.e*. gut content isotope composition) and is actually assimilated by fish (*i.e*. muscle-isotope composition), applying a stable-isotope approach as a complement to traditional gut-content analysis can also provide information about the spatial origin of the food resources at the base of the food web (*i.e*. water column *v*. sediment). Combining trophic data with information related to fish movement and habitat use (Ajemian *et al*., 2018) could also provide complementary information on the mechanisms by which natural and anthropogenic changes affect estuarine species.

4.3 | Changes of water quality conditions affect availability of *P. cromis* food sources

The highest relative densities of the most selected food items *M. lateralis* and *A. auberiana* occurred in March 2015, when salinity was the lowest. Indeed, increases in freshwater inflows can enhance productivity of suspension feeders due to nutrient stimulation of primary production in the water column (Grange & Allanson, 1995; Kim & Montagna, 2012). Due to rapid colonization after freshwater-related salinity variability, previous studies have identified *M. lateralis* as a good indicator species for freshwater inflow effects (Montagna & Kalke, 1995; Beseres Pollack *et al*., 2009). *Anomalocardia auberiana* has been identified as an indicator species as well, with increased densities in areas experiencing regular flooding and reduced salinities (Turney & Perkins, 1972). *Mulinia lateralis* densities are similar to those previously documented in the Baffin Bay estuary (<100–2500 m^{-2}; Montagna & Kalke, 1995; Buskey *et al.,* 1997). In the current study, bivalve biomass increased with increasing DO. Because low DO conditions can significantly reduce macrofauna biomass and diversity (Dauer *et al.,* 1992; Diaz & Rosenberg, 1995), higher DO concentrations may serve to increase benthic secondary production available for higher trophic levels. Variations in water quality therefore have implications for *P. cromis* food resource dynamics. This indicates bivalve communities are important to survey when trying to assess potential food limitation for these fish (Olsen *et al.,* 2014; Olsen, 2016). Because bivalve communities integrate water quality conditions, including

DO variation over diel cycles, they are useful for assessing ecosystem status above that which can be determined with punctuated daily measurements.

4.4 | Effects of water quality changes on *P. cromis* diet

Vacuity index values decreased from winter 2014 (54.9%) to winter 2015 (0.0%), following the trend of decreasing salinity (from 49.2 to 40.9), suggesting that *P. cromis* feeding activity was higher at low salinities. This is probably related to the higher availability of bivalves when salinities were lower. Higher feeding activity of *P. cromis* at low salinity is in accordance with the hypothesis from Ajemian *et al.* (2018), who suggest that high salinities decrease fish capacity to move, due to higher energy costs. Lower fish abundance has been reported in estuaries during hypersaline periods, which has been attributed to the disappearance of certain food resources as well as osmoregulatory stress (Boltt, 1975; Wallace, 1975). The sparid *Acanthopagrus butcheri* (Munro 1949), a commercially and recreationally important fishery species in estuaries in south-western Australia, was shown to be particularly susceptible to elevated salinities when unable to access to areas of lower salinity (Hoeksema *et al.*, 2006). High salinity may therefore lead to cumulative negative effects, reducing the ability of fish to feed in hypersaline ecosystems, on top of decreasing the quantities of their food resources. Nevertheless, such hypotheses need to be confirmed, in particular with the help of physiological measurements.

Within hypersaline systems, acute salinity variability is another key stressor to estuarine organisms (Bachman & Rand, 2008) that may affect food resources for higher trophic levels. Indeed, in the Baffin Bay estuary, the macrofaunal community demonstrated substantial shifts in dominant species before (*Streblospio benedicti, Acteocina canaliculata)* and after (*Mulinia* *lateralis, Anomalocardia auberiana*) the acute salinity disturbance. Similarly, food resource availability in three hypersaline estuaries in Western Australia has been attributed to the degree of salinity variability for *Acanthopagrus butcheri* (Chuwen *et al.,* 2007). The degree of salinity variability in Florida Bay is related to the quality of food resources ingested by tidewater mojarra *Eucinostomus harengulus* Goode & Bean 1879 and goldspotted killifish *Floridichthys carpio* (Günther 1866) (Ley *et al.,* 1994). Similarly, in a hypersaline lagoon in South America, increased food-web complexity has been related to the stability of hypersaline conditions (Almeida-Silva *et al.,* 2015). Longer-term research is warranted to better understand the response and recovery of food-web functioning in hypersaline systems as a result of acute salinity fluctuation.

Better determination of the dependence between the two major species of bivalves (*M. lateralis* and *A. auberiana*) in the Baffin Bay estuary and *P. cromis* is also warranted. Even if the combination of gut content and isotope analyses provided very meaningful information about the role of these two food sources, the broad ranges of δ^{13}C values for *P. cromis* muscle as well as for benthic macrofauna species limit the ability to determine to what degree *P. cromis* relies on these two species of bivalves. If selective feeding continues to occur even when bivalve biomass is reduced, altered macrofauna community composition would have stronger implications for availability of *P. cromis* food resources (Charnov *et al.*, 1976). On the other hand, the standing stock of these bivalves is maybe large enough to support *P. cromis* and other fish populations, even when biomasses are decreasing. Determining the daily ration of bivalves needed by *P. cromis* would help determine the carrying capacity of the estuary to support *P. cromis* populations during changing environmental conditions. Declines in food resources were described as a probable contributor for striped bass *Morone saxatilis* (Walbaum 1792) exceeding carrying capacity (Uphoff, 2003). In the Baffin Bay estuary, such an assessment should take into account other fish species [*e.g.* sheepshead *Archosargus probatocephalus* (Walbaum 1792) (Macreadie *et al.*, 2011); cownose rays *Rhinoptera bonasus* (Mitchill 1815) (Myers *et al.,* 2007)] that rely on bivalve prey.

The reliance of fish on prey items such as bivalves may have higher implications than for other benthic macrofauna species. Bivalves are generally suspension feeders; they rely on primary production occurring in the water column, which demonstrates much larger temporal and spatial variation than primary production in the sediment (Guarini *et al.*, 2006), even at the scale of an embayment such as the Baffin Bay estuary. The dynamics of primary production in the sediment can be characterized by a constant adjustment to steady state conditions (Guarini *et al.,* 2000) because there is low within year variability. In contrast, water column primary production depends more on meteorological conditions including light, temperature and nutrient availability (Cloern 1996), the latter being related to freshwater inflow. Therefore, variations in water column production may disproportionately affect suspension feeder density and biomass compared with macrofauna relying on benthic production (*i.e.* deposit feeders). This suggests that fish relying on food sources of pelagic origin will be more sensitive to salinity variations in hypersaline ecosystems like the Baffin Bay estuary.

This paper highlights the relationship between water quality variables, benthic macrofauna and their use as food resources by a carnivorous fish species. Although many studies have revealed connections between water quality variables and benthic macrofauna (Montagna *et al.*, 2013), this study emphasizes the need for more integrated assessments of food-web functioning when studying effects of changes in water quality. Holistic approaches such as these can serve as an important component toward conservation and sustainable fisheries management

(Ludwig *et al.*, 1993) and improved prediction of estuarine response to increasing climatic variability (Bailey & van de Pol, 2015; Wetz & Yoskowitz, 2013). This may be of particular interest in systems experiencing additional stressors such as hypersalinity.

ACKNOWLEDGEMENTS

We are grateful to Texas Parks and Wildlife Coastal Fisheries for providing *P. cromis* specimens and to M. Wetz and S. Murray for their efforts in developing this collaborative project. We acknowledge P. Rose (Isotope Core Laboratory - Texas A&M University-Corpus Christi) and G. Guillou (University of La Rochelle stable isotope facility) for their advice and support in the analyses. Many thanks are due to members of the Center for Sportfish Science and Conservation and to the Coastal Conservation and Restoration Ecology Lab at TAMUCC for all their assistance in the field and laboratory, especially P. Hajovsky, M. Martinez and N. Breaux. The authors also thank two anonymous reviewers for providing insights and suggestions that greatly improved the quality of this study. The Institutional Animal Care and Use Committee at Texas A&M University-Corpus Christi approved all procedures involving animals in this project.

SUPPORTING INFORMATION

Supporting information can be found in the online version of this paper.

TABLE S1 Analysis of Similarities (ANOSIM) test for temporal differences in gut contents.

TABLE S2 Analysis of Similarities (ANOSIM) **t**est for spatial differences in gut contents.

TABLE S3 Bio-Env (BEST) biota and, or environment matching.

REFERENCES

Ajemian, M.J., Mendenhall, K.S., Beseres Pollack, J., Wetz, M.S., & Stunz, G.W. (2018). Moving forward in a reverse estuary: movement and habitat use of black drum (*Pogonias cromi*s) under distinct hydrological regimes. *Estuaries & Coasts* (online). doi:10.1007/s12237-017-0363-6.

Alber, M. (2002). A conceptual model of estuarine inflow policy. *Estuaries* **25,** 1246–1261. doi:10.1007/BF02692222.

Almeida-Silva, R.H., Tubino, R.A., Zambrano, L.C., Hunder, D.A., Garritano, S.R., Monteiro-Neto, C. (2015). Trophic ecology and food consumption of fishes in a hypersaline tropical lagoon. *Journal of Fish Biology* **86,** 1781-1795.

Armstrong, N. E. (1987). The ecology of open-bay bottoms of Texas: a community profile. *U.S. Fish and Wildlife Service Biological Report* **85** (7.12). 119 pp.

Bachman, P.M., & Rand, G.M. (2008). Effects of salinity on native estuarine fish species in south Florida. *Ecotoxicology* **17,** 591-597.

Bailey, L.D., & van de Pol, M. (2015). Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology* **85,** 85-96.

Beck, M.W., Heck Jr., K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F. & Weinstein, M.P. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* **51,** 833-641.

Beseres Pollack, J. Kinsey, J.W., & Montagna, P.A. (2009). Freshwater inflow biotic index (FIBI) for the Lavaca-Colorado Estuary, Texas, USA. *Environmental Bioindicators* **4,** 153-169.

Blaber, S.J.M. (1997). *Fish and Fisheries of Tropical Estuaries*. *Fish and Fisheries Series* **22.** London: Chapman & Hall.

Blaber, S.J.M., & Blaber, T.J.G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology* **17,** 143-162.

Boltt, R.E. (1975). The benthos of some southern African lakes. Part 5. The recovery of the benthic fauna of St. Lucia following a period of excessively high salinity. *Transactions of the Royal Society of South Africa* **41,** 295–323.

Breuer, J.P. (1962). An ecological survey of the lower Laguna Madre of Texas, 1953-1959. *Publications of the Institute of Marine Science, University of Texas* **8,** 153-183.

Buskey, E.J., Montagna, P.A., Amos, A.F., Whitledge, T.E. (1997). Disruption of grazer populations as a contributing factor to the initiation of the Texas brown tide algal bloom. *Limnology and Oceanography* **45,** 1215-1222.

Buskey, E.J., Wysor, B., Hyatt, C. (1998). The role of hypersalinity in the persistence of the Texas ‘brown tide’ in the Laguna Madre. *Journal of Plankton Research* **20,** 1553-1565.

Charnov, E.L., Orians, G.H, & Hyatt, K. (1976). Ecological implications of resource depression. *The American Naturalist* **110,** 247-259.

Chuwen, B.M., Platell, M.E., & Potter, I.C. (2007). Dietary compositions of the sparid *Acanthopagrus butcheri* in three normally closed and variably hypersaline estuaries differ markedly. *Environmental Biology of Fishes* **80,** 363-376.

Clarke, K.R., & Ainsworth, M. (1993). A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**, 205-219.

Clarke K.R., & Gorley, R.N. (2006). PRIMER v6: User manual/tutorial. Plymouth: PRIMER-E.

Clarke, K.R., & Warwick, R. (1994). Similarity-based testing for community patterns: the two-way layout with no replication. *Marine Biology* **118,**167-176.

Cloern, J.E. (1996). Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics* **34,** 127-168.

Dauer, D.M., Rodi, A.J., & Ranasinghe, J.A. (1992). Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. *Estuaries* **15,** 384-391.

Diaz, R.J., & Rosenberg, R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review* **33,** 245–303.

Dugas, C.N. (1986). Food habits of black drum, *Pogonias cromis*, in southeast Louisiana with emphasis on their predation of the American oyster, *Crassostrea virginica*. *Louisiana Department of Wildlife and Fisheries Technical Bulletin* **40**, 32-38.

Elliott, M., Hemingway, K. L., Costello, M. J., Duhamel, S., Hostens, S., Labropoulou, M., Marshall, S., & Winkler, H. (2007). Links between fish and other trophic levels. In *Fishes in Estuaries* (Elliott, M., Hemingway, K., eds.), pp. 124-216. Oxford: Blackwell Science.

Fourqurean, J.W., Jones, R.D., Zieman, J.C. (1993). Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA: Inferences from spatial distributions. *Estuarine, Coastal, and Shelf Science* **36,** 295-314.

Fry, B., & Sherr, E.B. (1984). δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science* **27**, 13-47.

Fry, B., Cieri, M., Hughes, J., Tobias, C., Deegan, L., & Peterson, B. (2008). Stable isotope monitoring of benthic-planktonic coupling using salt marsh fish. *Marine Ecology Progress Series* **369,** 193-204.

Grange, N., & Allanson, B.R. (1995). The influence of freshwater inflow on the nature, amount, and distribution of seston in estuaries of the eastern cape, South Africa. *Estuarine, Coastal, and Shelf Science* **40,** 403-420.

Grubich, J.R. (2003). Morphological convergence of pharyngeal jaw structure in durophagous perciform fish. *Biological Journal of the Linnean Society* **80,** 147-165.

Guarini J.M., Blanchard G.F., & Gros P., (2000). Quantification of the microphytobenthic primary production in European intertidal mudflats – a modelling approach. *Continental Shelf Research* **20,** 1771-1788.

Guarini J.M., Blanchard G.F., & Richard P. (2006). Modelling the dynamics of the microphytobenthic biomass and primary production in European intertidal mudflats. In *Functioning of Microphytobenthos in Estuaries* (Kromkamp, J.C., de Brouwer, J.F.C., & Blanchard, G.F., eds.), pp. 187-226. Amsterdam:Royal Netherlands Academy of Arts and Sciences.

Harrison, T.D., & Whitfield, A.K. (2006). Temperature and salinity as primary determinants influencing the biogeography of fishes in South African estuaries. *Estuarine, Coastal and Shelf Science* **66,** 335-345.

Hill, M. (1973). Diversity and Evenness: a unifying notation and its consequences. *Ecology* **54,** 427-432.

Hoeksema, S.D., Chuwen, B.M., Potter, I.C. (2006). Massive mortalities of the black bream *Acanthopagrus butcheri* (Sparidae) in two normally-closed estuaries, following extreme increases in salinity. *Journal of the Marine Biological Association of the United Kingdom* **86**, 893–897.

Hofsten, A.V., Kahan, D., Katznelson, R., Bar-El, T. (1983). Digestion of free-living nematodes fed to fish. *Journal of Fish Biology* **21,** 419-428.

Hyslop, E.J. (1980). Gut contents analysis – a review of methods and their application. *Journal of Fish Biology* **17,** 411-429.

Kennedy, C.R. (1969). Tubificid oligochaetes as food of dace *Leuciscus leuciscus* (L.). *Journal of Fish Biology* **1,** 11-15.

Kennish, M.J. (2002). Environmental threats and environmental future of estuaries. *Environmental Conservation* **29,** 78-107.

Kim, H.C., & Montagna, P.A. (2012). Effects of climate-driven freshwater inflow variability on macrobenthic secondary production in Texas lagoonal estuaries: A modeling study. *Ecological Modelling* **235-236,** 67-80.

Lebreton, B., Beseres Pollack, J., Blomberg, B.N., Palmer, T.A., Adams, L., Guillou, G., & Montagna, P.A. (2016). Origin, composition and quality of suspended particulate organic matter in relation to freshwater inflow in a South Texas estuary. *Estuarine, Coastal and Shelf Science* **170**, 70-82.

Levin, L., Boesch, D.F., Covich, A., Dahm, C., Erséus, C., Ewel, K.C., Kneib, R.T., Moldenke, A., Palmer, M.A., Snelgrove, P., Strayer, D., & Weslawski, J.M. (2001). The Function of Marine Critical Transition Zones and the Importance of Sediment Biodiversity. Ecosystems 4, 430-451.

Ley, J.A., Montague, C.L., & McIvor, C.C. (1994). Food habits of mangrove fishes: a comparison along estuarine gradients in northeastern Florida Bay. *Bulletin of Marine Science* **54,** 881-899.

Ludwig, D., Hilborn, R., Walters, C. (1993) Uncertainty, resource exploitation, and conservation: Lessons from history. *Ecological Applications* **3,** 547-549.

Macreadie, P., Geraldi, N., & Peterson, C. (2011). How small-scale variation in oyster reef patchiness influences predation on bivalves. *Marine Ecology Progress Series* **429**, 87-91.

Martinez-Andrade, F., Campbell, P., & Fuls, B. (2005). Trends in relative abundance and size of selected finfishes and shellfishes along the Texas coast: November 1975–December 2003. Management Data Series Number 232. Austin, TX: Texas Parks and Wildlife Department, Coastal Fisheries Division. Available at www.tpwd.texas.gov/publications/pwdpubs/media/mds_coastal/Series%202_MDS232.pdf

Matlock, G.C., & Weaver, J.E. (1979). *Assessment and Monitoring of Texas Coastal Finfish Resources*. Austin, TX: Texas Parks and Wildlife Department Coastal Fisheries Branch.

Miller, J. M. (1974). The food of brook trout *Salvelinus fontinalis* (Mitchill) fry from different subsections of Lawrence Creek, Wisconsin. *Transactions of the American Fisheries Society* **103,** 130-134.

Montagna, P.A., Alber, M., Doering, P., & Connor, M.S. (2002). Freshwater inflow: science, policy, management. *Estuaries* **25,** 1243-1245.

Montagna, P.A., & Kalke, R.D. (1992). The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces Estuaries, Texas. *Estuaries* **15**, 307-326.

Montagna, P. A. & Kalke, R.D. (1995). Ecology of infaunal Mollusca in south Texas estuaries. *American Malacological Bulletin* **11,** 163-175.

Montagna, P.A., Palmer, T.A., & Beseres Pollack, J. (2013). Hydrological Changes and Estuarine Dynamics. *Springer Briefs in Environmental Science* **8,** 94 pp. doi: 10.1007/978-1-4614-5833-3.

Montagna, P.A., Stockwell, D.A., & Kalke, R.D. (1993). Dwarf surfclam *Mulinia lateralis* (Say, 1822) populations and feeding during the Texas brown tide event. *Journal of Shellfish Research* **12,** 433-442.

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315,** 1846-1850. doi: 10.1126/science.1138657.

Nicholson, G., Jenkins, G. P., Sherwood, J., and Longmore, A. (2008). Physical environmental conditions, spawning and early-life stages of an estuarine fish: climate change implications for recruitment in intermittently open estuaries. *Marine and Freshwater Research* **59,** 735–749. doi:10.1071/MF07197.

Nixon, S.W. (1982). Nutrient dynamics, primary production, and fisheries yields of lagoons. Proceedings International Symposium on coastal lagoons SCOR/IABO/UNESCO, Bordeaux, France. *Oceanologica Acta***,** 357-371.

Nixon, S.W., & Buckley, B.A. (2002). "A strikingly rich zone": nutrient enrichment and secondary production in coastal marine ecosystems. *Estuaries* **25,** 782-796.

Olsen, Z.T. (2016). Emaciated black drum (*Pogonias cromis*) in the upper Laguna Madre, Texas: tracking the recovery of the population over two years. *Texas Journal of Science* **68,** 79-90.

Olsen, Z.T., Grubbs, F.P., Morris, A.D., & Tolan, J.M. (2014). Reports of Emaciated black drum (*Pogonias cromis*) in the upper Laguna Madre, Texas. *Texas Journal of Science* **66,** 75-81.

Osburn, H.R., & Matlock, G.C. (1984). Black drum movement in Texas Bays. *North American Journal of Fisheries Management* **4,** 523-530.

Paul, D., Skrzypek, G., & Forizs, I. (2007). Normalization of measured stable isotopic compositions to isotope reference scales –a review. *Rapid Communications in Mass Spectrometry* **21,** 3006-3014.

Pachauri, R. & Meyer, L. (Eds) (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva: IPCC. Available able at www.ipcc.ch/report/ar5/syr/

Peterson, B., & Fry, B. (1987). Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics* **18,** 293-320.

Pinnegar, J.K., & Polunin, N.V.C. (1999). Differential fractionation of δ^{13}C and $\delta\ ^{15}$N among fish tissues: implications for the study of trophic interactions. *Functional Ecology* **13,** 225-231.

Pinnegar, J.K., & Polunin, N.V.C. (2000). Contributions of stable isotope data to elucidating food webs of Mediterranean rocky littoral fishes. *Oecologia* **122,** 399-409.

Post, D.M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83,** 703-718.

Ross, J.F., Pavela, J.S., & Chittenden, M.E. (1983). Seasonal occurrence of black drum, *Pogonias cromis*, and red drum, *Sciaenops ocellatus*, off Texas. *Northeast Gulf Science* **6,** 67-70.

Sanders, H. (1968). Marine benthic diversity: a comparative study. *The American Naturalist* **102,** 243-282.

Scavia, D., Field, J.C., Boesch, D.F., Buddemeier, R.W., Burkett, V., Cayan, D.R., Fogarty, M. Harwell, M.A., Howarth, R.W., Mason, C., Reed, D.J., Royer, T.C., Sallenger, A.H., Tituset, J.G. (2002). Climate change impacts on U.S. Coastal and Marine Ecosystems. *Estuaries* **25,** 149-164. https://doi.org/10.1007/BF02691304.

Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A., Lau, N.-C., Li, C., Velez, J., & Naik, N. (2007). Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* **316,** 1181-1184.

Simmons, E.G., & Breuer, J.P. (1962). A study of redfish, *Sciaenops ocellatus* Linnaeus and black drum, *Pogonias cromis* Linnaeus. *Publications of the Institute of Marine Science, University of Texas* **8,** 184-211.

Sogard, S.M. (1984). Utilization of meiofauna as a food source by a grassbed fish, the spotted dragonet *Callionymus pauciradiatus*. *Marine Ecology Progress Series* **17,** 183-191.

Strauss, R.E. (1979). Reliability estimates for Ivlev's electivity index, the forage ration, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* **108,** 344-352.

Sutter, F.C., Wailer, R.S., & McIlwain, T.D. (1986). Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico) – Black drum. *U.S. Fish and Wildlife Service Biological Report* **82,** 10 pp.

Tunnell, Jr., J.W., & Judd, F.W. (2002). The Laguna Madre of Texas and Tamaulipas. Texas A&M University Press, College Station.

Tunnell, Jr., J.W., Andrews, J., Barrera, N.C., & Moretzsohn, F. (2010). *Encyclopedia of Texas Seashells: Identification, Ecology, Distribution and History*. College Station, TX: Texas A & M University Press.

Turney, W.J., & Perkins, B.F. (1972). *Molluscan Distribution in Florida Bay. Sedimenta* III. Miami, FL: University of Miami.

Uphoff, J. H. (2003). Predator-prey analysis of striped bass and Atlantic menhaden in upper Chesapeake Bay. *Fisheries Management and Ecology* **10,** 313-322.

Vander Zanden, M.J., implications for aquatic food web studies. *Limnology and Oceanography* **46,** 2061-2066.

Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., Weidel, B.C. (2015). Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLoS ONE* **10**, e0116182.

Wallace, J.H. (1975). The estuarine fishes of the east coast of South Africa. Part I. Species composition and length distribution in the estuarine and marine environments. Part II. Seasonal abundance and migrations. *Investigational Report Oceanographic Research Institute (Durban)* **40,** 72 pp.

Wetz, M.S., Cira, E.K., Sterba-Boatwright, B., Montagna, P.A., Palmer, T.A., & Hayes, K.C. (2017). Exceptionally high organic nitrogen concentrations in a semi-arid South Texas estuary susceptible to brown tide blooms. *Estuarine, Coastal & Shelf Science* **188,** 27-37.

Wetz, M.S. & Yoskowitz, D.W. (2013). An ‘extreme’ future for estuaries? Effects of extreme climatic events on estuarine water quality and ecology. *Marine Pollution Bulletin* **69,** 7-18.

Whitfield, A.K. (1986). Fish community structure response to major habitat changes within the littoral zone of an estuarine coastal lake. *Environmental Biology of Fishes* **17,** 41–51.

Whitfield, A.K. (1999). Ichthyofaunal assemblages in estuaries: a South African case study. *Reviews in Fish Biology and Fisheries* **9,** 151-186.

Williams, W.D., Boulton, A.J., Taaffe, R.G. (1990). Salinity as a determinant of Salt Lake fauna: a question of scale. *Hydrobiologia* **197,** 257-266.

WoRMS Editorial Board. (2017). World Register of Marine Species. Available at www.marinespecies.org at VLIZ. Accessed 2017-02-27. doi:10.14284/170

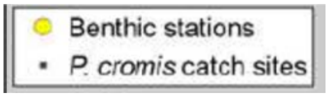
Zar, J.H. (2010). *Biostatistical Analysis*, 5th edn. Upper Saddle River, NJ: Pearson Education.

FIGURE captions

FIGURE 1 Baffin Bay estuary, Texas U.S.A., indicating benthic (●) and *Pogonias cromis* (■) sampling stations.

Typesetter

1 Delete A, B and C from panels.

2 Delete 

and 

.

FIGURE 2 Principal component (PC) analysis (a) loading plot (Sal, salinity; Temp, temperature; DO, dissolved oxygen; Turb, turbidity) and (b) station date scores of water quality data (O, March 2014; +, June 2014; X, September 2014; △, December 2014; □, March 2015) within the Baffin Bay estuary.

Typesetter

1 Replace A, B with (a), (b).

2 No colour necessary on (b).

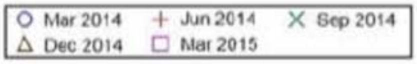
3 Delete 

FIGURE 3 Times series plots of mean (± S.E.) of (a) salinity, (b) temperature and (c) dissolved oxygen concentrations (DO) within the Baffin Bay estuary.

Typesetter

1 Replace A, B etc with (a), (b) etc.

2 Replace y-axis label of (c) with DO (mg l^{-1}).

FIGURE 4 Proportionally sized mean benthic core (a) abundance and (b) biomass for comparison with (c) *Pogonias cromis* gut content biomass from individual bays within the Baffin Bay estuary.

Typesetter

1 Replace A, B etc with (a), (b) etc.

FIGURE 5 Non-metric multidimensional scaling (nMDS) ordination plot of mean macrofaunal community structure for each survey sampling date overlaid with 40% similarity contour. AL, Alazan Bay; BB, Baffin Bay; CG, Cayo del Grullo; LS, Laguna Salada.

Typesetter

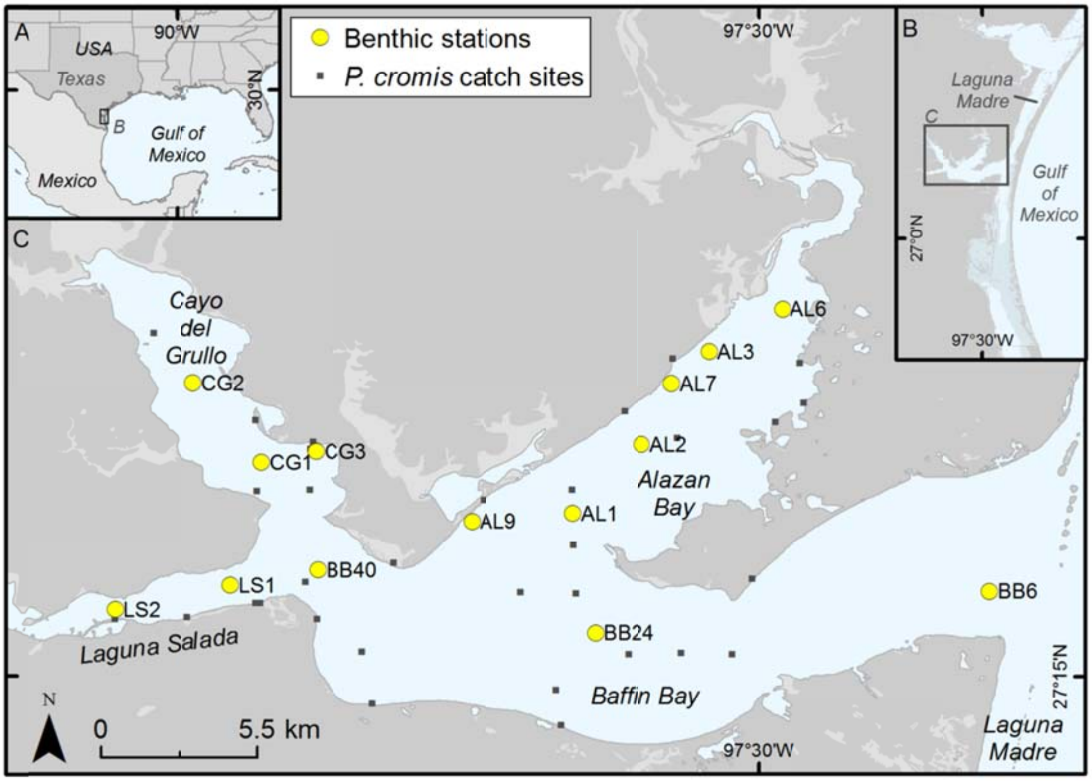
1 Replace A, B etc with (a), (b) etc.

FIGURE 6 Mean (± S.D.) Isotope compositions ($\delta^{13}C$ and $\delta^{15}N$), of potential food sources and of *Pogonias cromis* gut liquid (O, △, □, ◇) and muscle tissue (●,▲, ■,◆) at different seasons in the Baffin Bay estuary. Primary producers and composite food sources are in green, macrofauna in red. A.aub, *Anomalocardia auberiana*; Amphi, Amphipod; Capi, Capitellidae; Goni, Goniadidae; L.rap, *Leptochelia rapax*; M.lat, *Mulinia lateralis*; Nema, Nematodes; Orbi, Orbiniidae; S.ben, *Streblospio benedicti*; SSOM, Surface sediment organic matter; Tana, Tanaidacea.

Typesetter

1 Replace Fall with Autumn.

Fig 1



A
USA
Texas
90°W
30°N
B
Gulf of Mexico
Mexico
● Benthic stations
▪ *P. cromis* catch sites
97°30'W
B
Laguna Madre
C
Gulf of Mexico
27°0'N
97°30'W
C
Cayo del Grullo
CG2
CG1
CG3
AL6
AL3
AL7
AL2
Alazan Bay
AL1
AL9
BB40
LS1
LS2
BB6
BB24
Laguna Salada
Baffin Bay
27°15'N
Laguna Madre
97°30'W
N
0
5.5 km

Fig 2

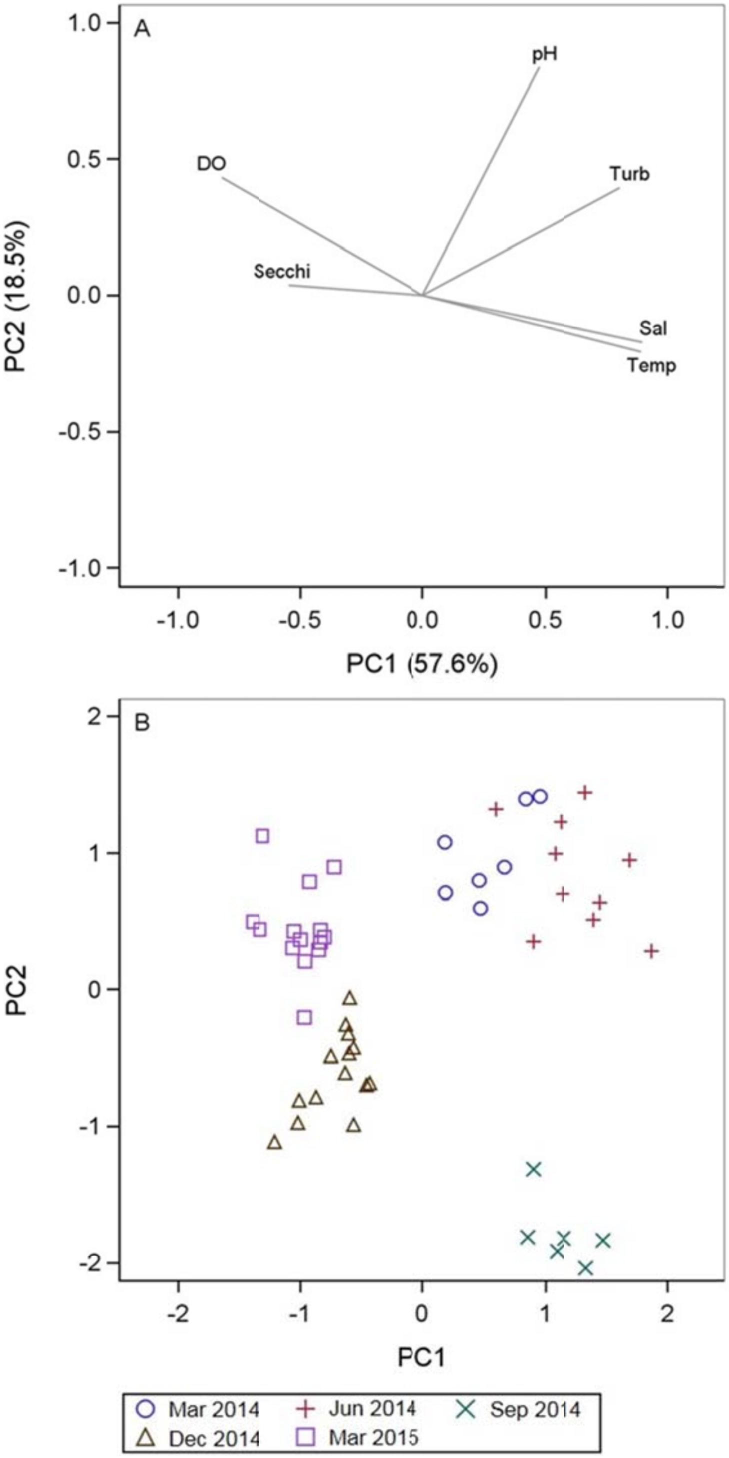

A
pH
DO
Turb
Secchi
Sal
Temp
1.0
0.5
0.0
-0.5
-1.0
PC2 (18.5%)
-1.0
-0.5
0.0
0.5
1.0
PC1 (57.6%)
B
2
1
0
-1
-2
PC2
-2
-1
0
1
2
PC1
○ Mar 2014
+ Jun 2014
× Sep 2014
△ Dec 2014
□ Mar 2015

Fig 3

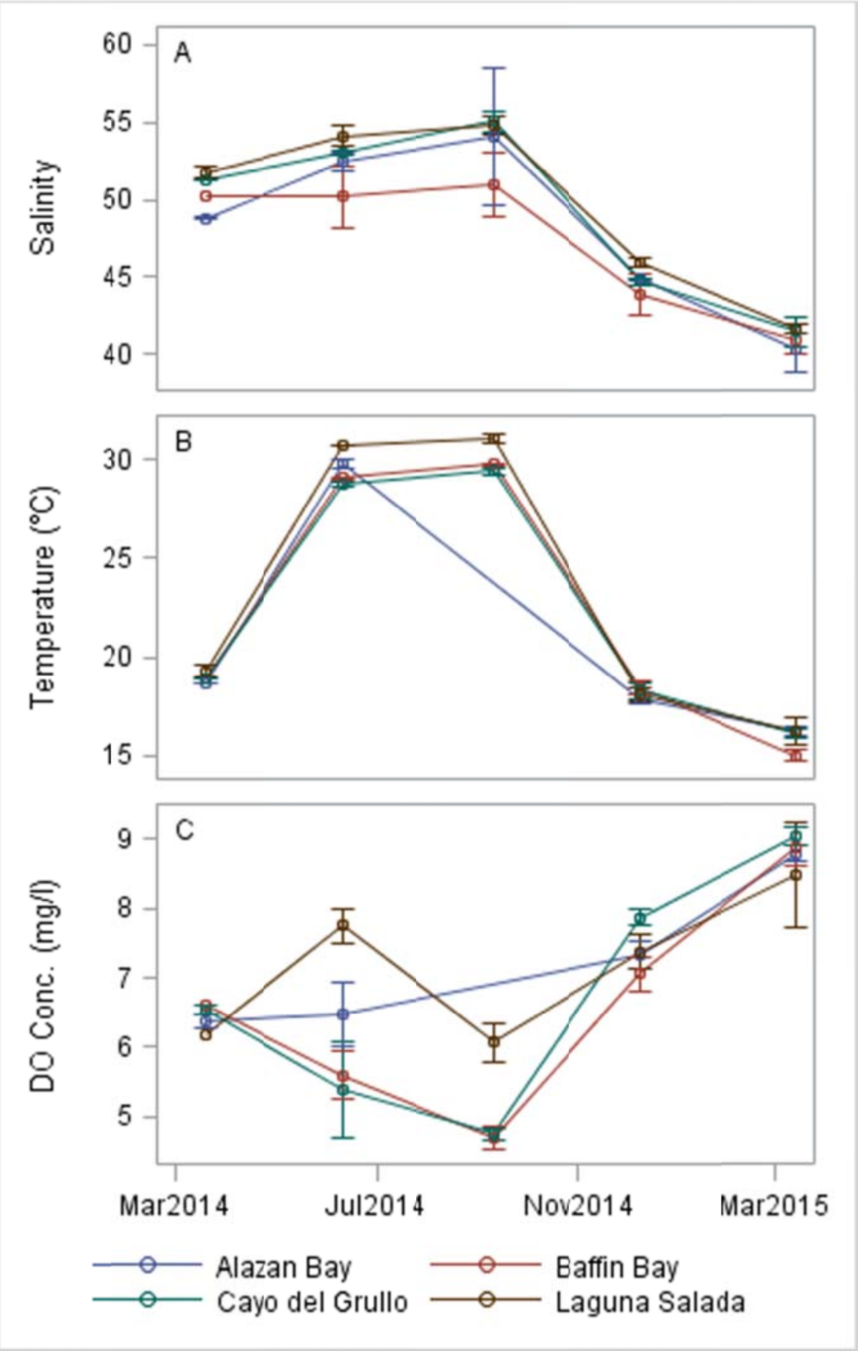

A
Salinity
60
55
50
45
40
B
Temperature (°C)
30
25
20
15
C
DO Conc. (mg/l)
9
8
7
6
5
Mar2014
Jul2014
Nov2014
Mar2015
Alazan Bay
Baffin Bay
Cayo del Grullo
Laguna Salada

Fig 4

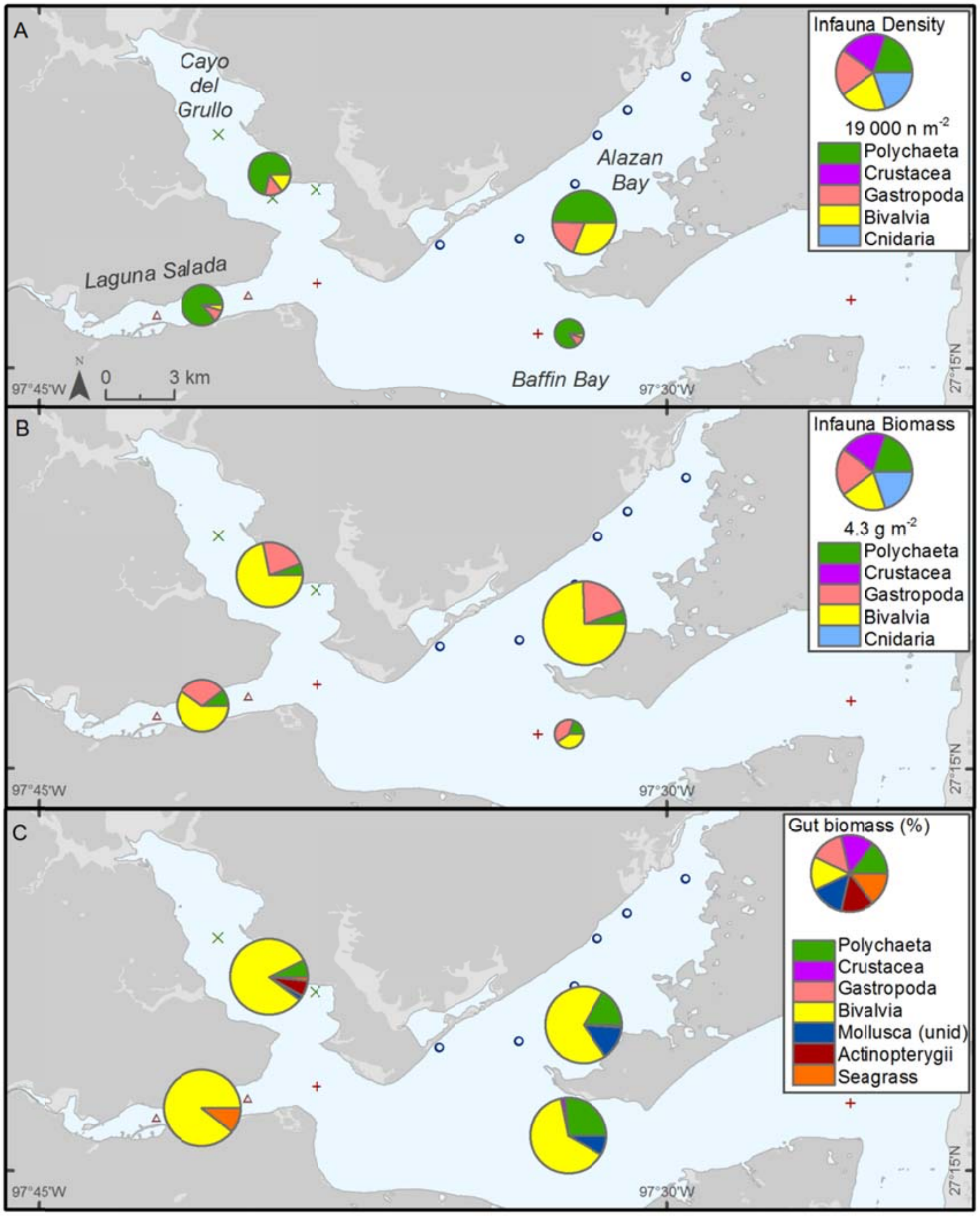

A
Cayo del Grullo
Alazan Bay
Laguna Salada
Baffin Bay
97°45'W
97°30'W
27°15'N
0
3 km
N
Infauna Density
19 000 n m^{-2}
Polychaeta
Crustacea
Gastropoda
Bivalvia
Cnidaria
B
Infauna Biomass
4.3 g m^{-2}
Polychaeta
Crustacea
Gastropoda
Bivalvia
Cnidaria
97°45'W
97°30'W
27°15'N
C
Gut biomass (%)
Polychaeta
Crustacea
Gastropoda
Bivalvia
Mollusca (unid)
Actinopterygii
Seagrass
97°45'W
97°30'W
27°15'N

Fig 5

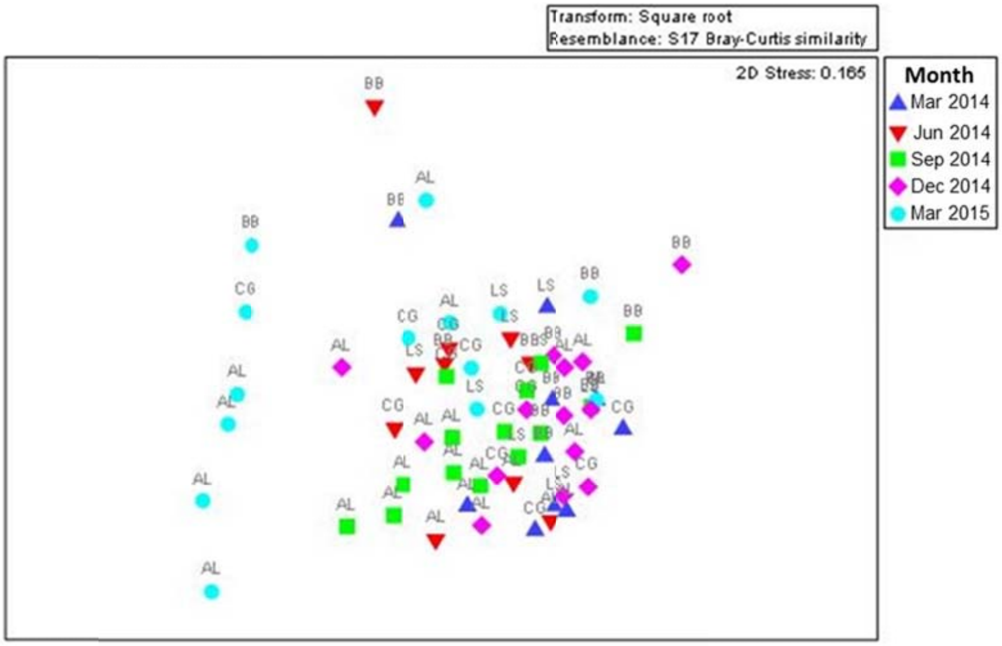

Transform: Square root
Resemblance: S17 Bray-Curtis similarity
2D Stress: 0.165
Month
Mar 2014
Jun 2014
Sep 2014
Dec 2014
Mar 2015
BB
AL
CG
LS

Fig 6

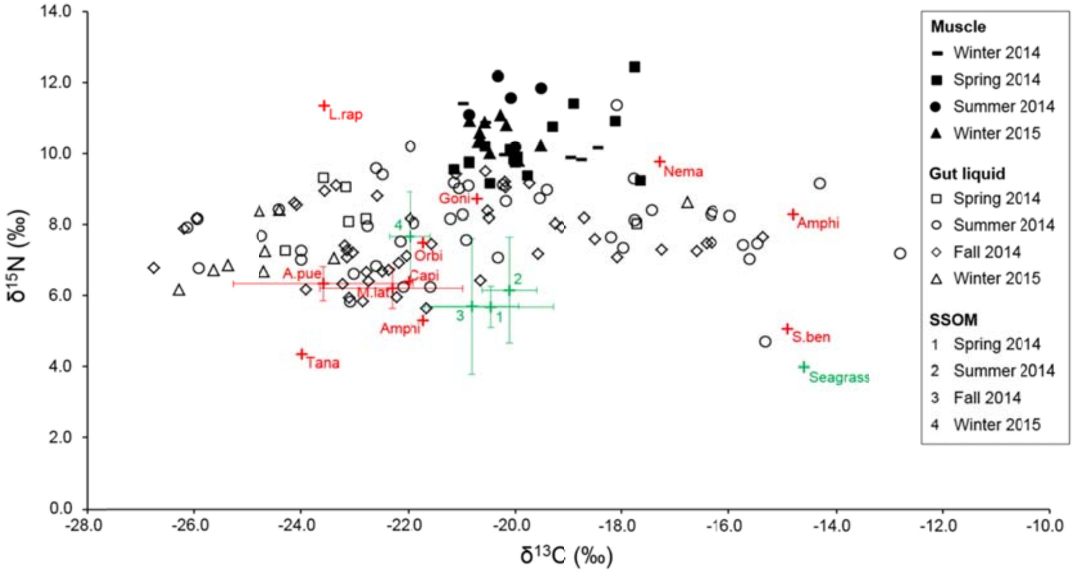

14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
$\delta^{15}N$ (‰)
-28.0
-26.0
-24.0
-22.0
-20.0
-18.0
-16.0
-14.0
-12.0
-10.0
$\delta^{13}C$ (‰)
L.rap
Nema
Goni
Amphi
Orbi
A.pue
Capi
M.lat
Amphi
Tana
S.ben
Seagrass
1
2
3
4
Muscle
Winter 2014
Spring 2014
Summer 2014
Winter 2015
Gut liquid
Spring 2014
Summer 2014
Fall 2014
Winter 2015
SSOM
1 Spring 2014
2 Summer 2014
3 Fall 2014
4 Winter 2015

TABLE 1. Number of *Pogonias cromis* guts examined and vacuity index in each season and bay.

Season	AL	BB	CG	LS	BBE
Number of non-empty fish stomachs processed					
2014-Winter	5	7			12
2014-Spring	18	23	4	5	50
2014-Summer	6	18			24
2014-Fall	10	2	41	41	93
2015-Winter		10			10
Vacuity index (% empty guts)					
2014-Winter	28.6	81.1			54.9
2014-Spring	14.3	8	0	0	5.8
2014-Summer	14.3	0			7.2
2014-Fall	0	0	2.4	6.8	2.3
2015-Winter		0			0
Mean	14.3	17.8	1.2	3.4	

AL, Alazan Bay; BB, Baffin Bay; CG, Cayo del Grullo; LS, Laguna Salada.

TABLE 2. Taxa collected in benthic cores across all *Pogonias cromis* survey sites and sampling seasons

	Density (*n* m^{-2})						Biomass (g m^{-2})					
Taxa	AL	BB	CG	LS	Mean	S.D.	AL	BB	CG	LS	Mean	S.D.
Bivalvia												
Anomalocardia auberiana	3251	6	168	123	887	1541	1.827	0.001	0.112	0.107	0.512	0.878
Mactrotoma fragilis	6	0	95	9	28	45	0.001	0	0.186	0.003	0.048	0.092
Mulinia lateralis	611	123	483	142	340	245	1.793	0.250	1.824	1.209	1.269	0.736
Unidentified Bivalvia	288	0	88	0	94	136	0.183	0	0.127	0	0.078	0.092
Crustacea												
Hargeria rapax	9	9	0	0	5	5	0.001	0.001	0	0	0.001	0.001
Sphaeroma terebrans	3	0	6	0	2	3	0.004	0	0.003	0	0.002	0.002
Unidentified Amphipoda	19	6	32	28	21	12	0.002	0.001	0.005	0.003	0.003	0.002
Gastropoda												
Acteocina canaliculata	43	32	181	307	141	130	0.038	0.026	0.099	0.459	0.156	0.205
Acteon candens	26	0	0	0	7	13	0.007	0	0	0	0.002	0.004
Astyris lunata	6	0	0	0	2	3	0.011	0	0	0	0.003	0.006
Bittiolum varium	0	0	0	9	2	5	0	0	0	0.002	0.001	0.001
Costoanachis semiplicata	0	0	11	0	3	6	0	0	0.027	0	0.007	0.014
Eulimastoma harbisonae	473	47	151	9	170	211	0.251	0.005	0.074	0.019	0.087	0.113
Fargoa gibbosa	221	0	34	28	71	101	0.098	0	0.005	0.021	0.031	0.046
Nassarius vibex	0	0	6	0	2	3	0	0	0.159	0	0.040	0.080
Rissoella galba	9	0	0	0	2	5	0.012	0	0	0	0.003	0.006
Unidentified Gastropoda	1872	221	391	170	663	811	0.634	0.205	0.340	0.154	0.333	0.215
Polychaeta												
Leitoscoloplos foliosus	0	6	0	0	2	3	0	0.001	0	0	<0.001	0.001
Nereididae spp.	0	6	6	0	3	3	0	0.004	0.001	0	0.001	0.002
Orbiniidae spp.	6	0	0	0	2	3	0	0	0	0	0	0
Streblospio benedicti	6486	2219	4028	4671	4351	1762	0.228	0.118	0.169	0.235	0.188	0.055
Unidentified Polychaeta	216	28	6	0	63	103	0.034	0	0.003	0	0.009	0.017
Cnidaria												
Actiniaria	0	19	0	0	5	10	0	0	0	0	0	0
Total	13551	2723	5685	5498	6864	4659	5.127	0.612	3.133	2.210	2.770	1.885

AL, Alazan Bay; BB, Baffin Bay; CG, Cayo del Grullo; LS, Laguna Salada.

TABLE 3. Frequency of occurrence and percentage mass of taxa in *Pogonias cromis* guts.

	Sampling site					
Taxa	**AL**	**BB**	**CG**	**LS**	**Mean**	**S.D.**
Frequency of occurrence (%)						
Actinopterygii	0.0	0.0	2.4	0.0	0.6	1.2
Bivalvia	70.6	61.7	71.6	75.4	69.8	5.8
Anomalocardia auberiana	27.5	17.5	29.9	52.2	31.8	14.6
Mulinia lateralis	6.9	17.3	0	21.2	11.4	9.7
Nuculana acuta	0	0.9	0	0	0.2	0.5
Unidentified Bivalvia	65.6	60.8	71.6	75.4	68.3	6.5
Oligochaeta	0	0.9	0	10	2.7	4.9
Crustacea	1.4	23.2	0	1.2	6.5	11.2
Amphipoda	1.4	15.7	0	0	4.3	7.6
Pericarida	0	7.5	0	0	1.9	3.8
Portunidae	0	0	0	1.2	0.3	0.6
Mollusca Unidentified	14.2	9.7	12.5	0	9.1	6.3
Gastropoda	6.7	5.1	0	11.2	5.7	4.6
Acteocina canaliculata	0	0	0	1.2	0.3	0.6
Rissoina punctostriata	1.4	0.9	0	0	0.6	0.7
Unidentified Gastropoda	5.3	4.2	0	10	4.9	4.1
Polychaeta	50.0	54.6	53.4	44.9	50.7	4.3
Seagrass	12.8	18.8	27.1	43.2	25.5	13.2
Unidentified	93.3	97.8	96.3	95.1	95.6	1.9
Biomass (% of identifiable gut)						
Actinopterygii	0.0	0.0	2.7	0.0	0.7	1.4
Bivalvia	63.9	44.5	67.5	79.2	63.7	14.4
Anomalocardia auberiana	2.7	0.7	2.5	2.8	2.2	1.0
Mulinia lateralis	0.2	0.4	0	1.6	0.5	0.7
Nuculana acuta	0	0.0	0	0	0.0	0.0
Unidentified Bivalvia	61.1	43.4	65.0	74.8	61.1	13.1
Oligochaeta	0	0	0	0.0	0.0	0.0
Crustacea	0.6	8.3	0.0	0.9	2.4	3.9
Amphipoda	0.6	3.6	0	0	1.0	1.7
Pericarida	0	4.7	0	0	1.2	2.4
Portunidae	0	0	0	0.9	0.2	0.5
Gastropoda	0.1	0.0	0.0	0.5	0.0	0.2
Acteocina canaliculata	0	0	0	<0.1	<0.1	0.0
Rissoina punctostriata	<0.1	<0.1	0	0	<0.1	0.0
Unidentified Gastropoda	0.1	<0.1	0	0.5	0.1	0.2
Unidentified Mollusca	12.4	9.0	12.5	0	8.5	5.9

Polychaeta	16.2	37.4	13.8	1.0	17.1	15.1
Seagrass	6.9	0.8	4.4	18.5	7.6	7.7
Biomass (% of total gut)						
Unidentified	71.3	69.7	79.5	64.1	71.2	6.4
Identified	28.7	30.3	20.7	36.8	29.1	6.6

AL, Alazan Bay; BB, Baffin Bay; CG, Cayo del Grullo; LS, Laguna Salada.