An Ecosystem-based Approach to Assess Baffin Bay's Black Drum in Different Hydrological Conditions

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Final Report

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Final Report to:

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EXECUTIVE SUMMARY

Baffin Bay is a predominantly hypersaline estuary adjacent to the more hydrologically stable Laguna Madre in the semi-arid region of South Texas, USA. Baffin Bay and the Laguna Madre collectively support large populations of Black Drum, *Pogonias cromis*, a commercially important benthic predator. In 2012, Black Drum in Baffin Bay experienced a widespread emaciation event, but a lack of hydrological and benthic community data preceding this event made determination of potential causes difficult.

Salinity variability can act as a disturbance to benthic macrofauna communities in estuarine systems, which has indirect effects on higher trophic level organisms like the Black Drum. Climate models predict changes in precipitation patterns will increase future hydrological variability, particularly in the southwestern United States where precipitation events will become less frequent but more intense. This study used infaunal community characterization, stomach content, and stable isotope analyses to evaluate the functioning of the Baffin Bay food web over a range of wet and dry conditions. The objectives of this study were to 1) describe the effects of extreme salinity change on the Baffin Bay benthic community and 2) determine how salinity change affects the trophic structure in the bay, using Black Drum as an indicator species.

Salinity was the best predictor of changes in macrofauna biomass, abundance, and diversity in Baffin Bay. Community biomass was primarily driven by the opportunistic bivalve species, *Mulinia lateralis*, while abundance was largely determined by the polychaetes *Streblospio benedicti* and *Capitellidae sp.*; species characteristic of disturbed communities. Greater biomass of potential Black Drum prey resources were available under normal estuarine salinity ($\leq$ 35) conditions in Baffin Bay, but these resources became limited under hypersaline (> 35) conditions.

The difference in primary producers in the phytoplankton-dominant Baffin Bay and adjacent but seagrass-dominated Laguna Madre causes isotopically distinct organic matter and benthic food resources in the two systems, allowing for determination of food source. Isotopic analyses of muscle tissues indicate that Black Drum use resources from both Baffin Bay and the Laguna Madre under normal estuarine salinity conditions, but are more constrained to Baffin Bay under hypersaline conditions, when prey resources there are limited. This spatial restriction is possibly due to the energetic cost of osmotic regulation in hypersaline conditions, which may limit movement of euryhaline fish. Understanding the impacts of salinity change on benthic prey availability and trophic interaction dynamics is critical to determining the ecosystem-scale effects of salinity variability.

INTRODUCTION

Baffin Bay is a predominantly hypersaline estuary adjacent to the more hydrologically stable Laguna Madre in the semi-arid region of South Texas, USA (Simmons 1957, Figure 1). Baffin Bay supports a large Black Drum (*Pogonias cromis*) fishery, supplying the majority of all commercial Black Drum in the state (Grubbs et al. 2013; Olsen 2016). Climatic cycles such as El Niño Southern Oscillation (ENSO) and tropical systems can generate large changes in inflow and salinity within Baffin Bay, with salinity ranging from near 0 to well over 60 (Breuer 1957; Grubbs et al. 2013). Most recently, a period of drought from 2010 to 2014 followed by exceptionally large rainfall events in 2015 caused substantial salinity changes in the system (Figure 2). Reports of emaciated Black Drum in Baffin Bay during severe drought in 2012 raised major concern amongst industry, state officials, and the public (Olsen 2015), but little was known about Black Drum food resources or movement patterns, challenging the identification of potential drivers (Grubbs et al. 2013).

Figure 2. Map of study area: Baffin Bay and the Laguna Madre, TX

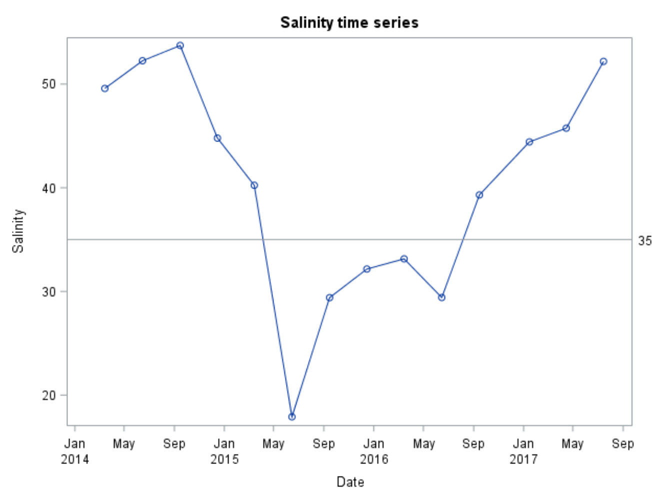

Figure 2. Mean bay-wide salinity in Baffin Bay from March 2014 to July 2017. A horizontal line (at 35) indicates the threshold for hypersalinity.

Estuarine systems like Baffin Bay are transitional zones where fresh and salt water mix. Freshwater inflow delivers influxes of terrestrial nutrients, making estuaries highly productive and critical to coastal fisheries (Schelske and Odum 1962; Houde and Rutherford 1993; Potter and Hyndes 1999; Beck et al. 2001; Hyndes et el. 2014), but subjecting them to frequent hydrological variation (Gaston et al. 1998; Sparks and Spink 1998). Climate models predict increased variability in precipitation patterns in the next century (Chiu and Kuo 2012; Stocker et al. 2013). The southwestern U.S. in particular is expected to become increasingly arid (Seager et al. 2007) and precipitation events, though less frequent, will become more intense (Pachauri et al. 2015).

Changes in environmental conditions can act as a disturbance, altering the structure of ecological communities via physical, biological, and physiological stresses (Sousa 1984; Warwick 1986; Menge and Sutherland 1987; Clarke and Warwick 2001). Benthic macrofauna communities can serve as indicators of these environmental changes—their small size, relatively long-lifespans, and sessile nature make them vulnerable to small-scale disturbances and indicative of long-term trends in water quality (Warwick 1986; Montagna et al. 2002; Salas et al. 2006). Abundance, biomass, and diversity of macrofauna can be strongly influenced by salinity and freshwater inflow (Calabrese 1969; Montagna and Kalke 1995; Van Diggelen and Montagna 2016).

Higher trophic-level organisms such as Black Drum use estuaries as feeding, spawning and nursery grounds, and can be indirectly affected by disturbances to benthic communities via trophic linkages (Day et al. 1989; Houde and Rutherford 1993; Diaz and Rosenberg 1995; Schlacher and Wooldridge 1996; Potter and Hyndes 1999; Beck et al. 2001; Sheaves et al. 2015). Unlike the benthic community, these motile fauna are better able to avoid adverse conditions by moving to seek refuge or resources (Renaud 1986; Menge and Sutherland 1987; Knott et al. 2009). In connected estuarine systems, fish and motile invertebrates can make both small intra-bay and larger inter-bay movements depending on the scale of disturbance and food resource availability (Breuer 1957; Childs et al. 2008; Payne 2011; Dance and Rooker 2015; Moulton et al. 2017).

Analysis of stable isotope (SI) composition, particularly those of carbon and nitrogen, can be used to examine the different food resources used by consumers (Fry and Sherr 1989; Peterson 1999; Fry 2006). Stable isotopes of carbon provide information about the origin of organic matter in consumers and the isotopic composition of nitrogen is indicative of trophic level (Fry and Peterson 1987). Isotopic analyses can serve as a complimentary approach to traditional stomach content analysis by elucidating long-term dietary trends, giving information about trophic position, and inferring movement (Bowen et al. 2005; Cunjak et al. 2005). Traditional methods provide only a ‘snapshot’ view of the diet, but allow for species-level identification of prey (at times) and determination of quantities consumed. The incorporation of both isotopic and traditional analyses simultaneously provides a more robust description of diet and behavior than either method alone.

This study employed traditional and SI methods to link benthic macrofauna community composition and trophic interactions to water quality parameters, in particular salinity change, to better understand ecosystem-scale effects of water quality variability in Baffin Bay. The objectives of this study are to: 1) describe the effects of extreme salinity change on the benthic community of Baffin Bay and 2) determine how salinity change affects the trophic structure in the system, using Black Drum as an indicator species.

MATERIALS AND METHODS

Study area

Baffin Bay (248 km^2) is comprised of a secondary bay (Baffin Bay proper) and three tertiary arms: Laguna Salada, Cayo del Grullo and Alazan Bay, which will collectively be called the Baffin Bay complex (BBC) for the purposes of this study (Figure 3). This shallow (≤ 2-3 m depth) system is characterized by evaporation rates that exceed freshwater delivery, long hydrologic residence times (300 days to several years; Buskey et al. 1998), and largely unvegetated soft-bottom habitat. The primary sources of freshwater inflow to the bay are intermittent streams (Petronila, San Fernando, and Los Olmos creeks, 3), which feed into the BBC's tertiary arms.

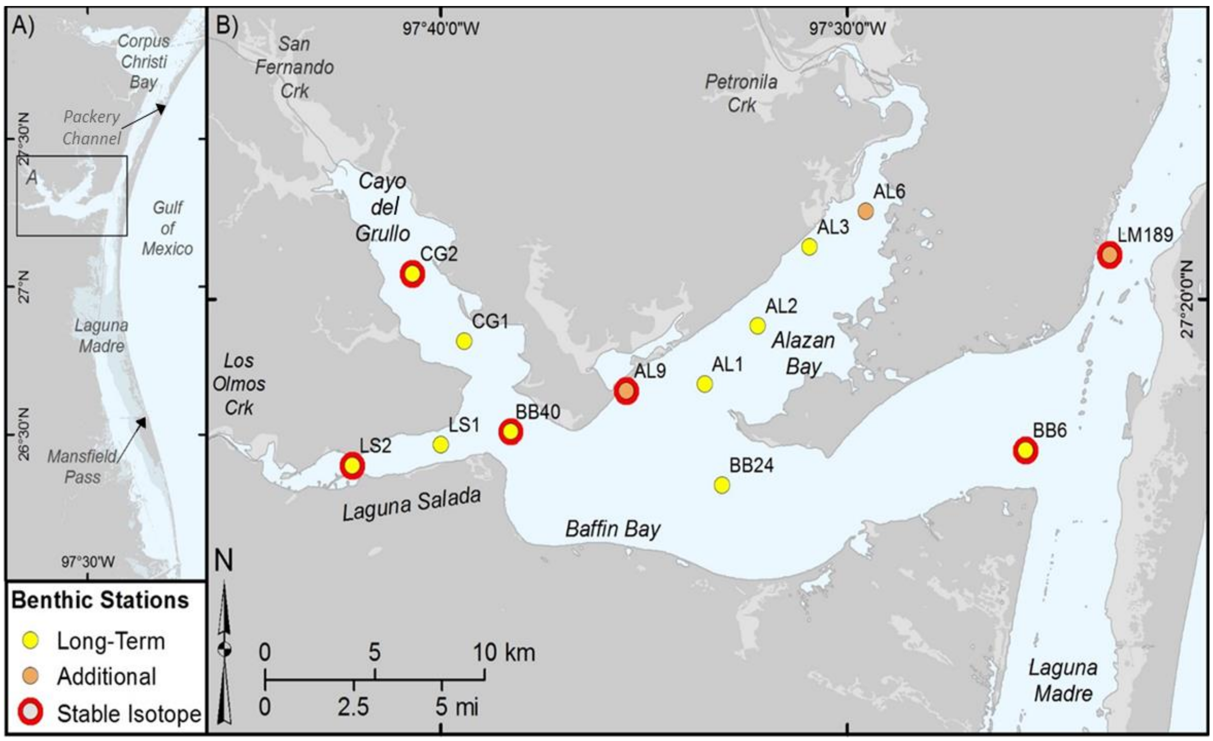

Figure 3. Map of the Baffin Bay Complex and the Laguna Madre, Texas, including 10 long-term (Mar 2014 to Jan 2017), 4 additional (Jun 2015 to Jan 2017), and 6 stable isotope benthic sampling locations. LM189S and LM189G are within 10 m so are depicted as one point (LM189) on the map.

The Laguna Madre is a shallow (≤ 1-2 m depth) lagoon adjacent to the BBC that is characterized by the presence of vast seagrass beds (63% cover; Onuf 2007), and hypersalinity (although to lesser extremes than recorded in the BBC). The Laguna Madre lacks a significant source of freshwater inflow and is influenced by minimal connections with the Gulf of Mexico indirectly at Packery Channel in Corpus Christi Bay (to the North) and directly via Port Mansfield Channel (at the South).

Benthic community characterization

Water quality and benthic macrofauna communities were sampled quarterly at ten locations in the BBC from March 2014 to July 2017 (Long-term sites, Figure 3). An additional four stations were added in the LM and BBC (two each, Additional sites, Figure 3) in June 2015. The substrate in the BBC was bare of macroflora, whereas LM189G was dominated by seagrass (primarily *Halodule wrightii*) and LM189S was dominated by bare sediment but with some seagrass rhizomes present. Samples collected from March 2014 to March 2015 were incorporated from a past study (Mendenhall 2015).

Water quality measurements

Water quality (including water temperature, salinity, dissolved oxygen (DO), and pH) was measured using a Hydrolab Surveyor II or YSI Pro DSS. Measurements were taken approximately 10 cm below the water surface and 20 cm above the sediment bottom. Salinity regimes were defined using mean BBC-wide salinity: salinities greater than that of seawater (> 35) constituted hypersalinity, ≤ 35 was considered normal estuarine salinity for the purposes of this study (Gonzalez 2012; Brauner et al. 2013).

Sampling and preparation of macrofauna

Benthic cores were collected quarterly using a 35.4 cm^2 core tube to a sediment depth of 10 cm. Three replicate cores from each station were preserved in 5% buffered formalin. In the laboratory, these cores were sieved using a 500 µm mesh and sorted with a stereo microscope. Organisms were identified to the lowest practical taxa (usually species), and counted. After enumeration, organisms were dried in an oven at 50 ºC for 24 hours, and then weighed to the nearest 0.01 mg to determine total biomass. Mollusks were placed into a solution of 1 M HCl to remove shells prior to being dried.

Benthic community statistical analysis

Temporal analyses within the BBC were carried out using the 10 long-term sampling sites (AL1, AL2, AL3, CG1, CG2, LS1, LS2, BB6, BB24 and BB40), and the BBC and Laguna Madre were compared using only sampling dates where both were studied (June 2015 to July 2017). Multivariate community analyses were completed using PRIMER v6 (Clarke and Gorley 2006). Principal component analysis (PCA) was used to assess water quality changes in the BBC through the sampling period. Nonmetric multidimensional scaling (nMDS; Warwick and Clarke 1994) using a Bray-Curtis similarity matrix was used to investigate spatial and temporal community trends and similar sites were grouped using similarity percentage (SIMPER) analysis (Clarke 1993; Anderson 2008). BIO-ENV was then used to relate environmental parameters to community assemblage data with weighted Spearman rank correlations (Clarke and Ainsworth 1993; Clarke et al. 2008). The BIO-ENV procedure calculates correlations between dissimilarity matrices for physical and biotic data, and then determines a subset of environmental parameters that maximize this correlation. Macrobenthic community response to disturbance was examined using W-statistics calculated from Abundance-Biomass Comparison (ABC) curves for each bay and sampling date (Warwick 1986; Clarke 1990). The ABC curves operate on the principle that disturbed communities are dominated by large numbers of small opportunistic species (abundance > biomass), while established communities are dominated by larger, more long-lived species (biomass > abundance). W-statistics are calculated from dominance curves using the equation:

$$W = \sum_{i=1}^{S} (B_i - A_i)/[50(S-1)]$$

where S= number of species, B=sample biomass (g m^{-2}), and A= sample abundance (m^{-2}). Values range between -1 (indicating a grossly disturbed system) and +1 (indicating a pristine system). W-statistics from BBC sites were correlated with water quality parameters to determine drivers of benthic disturbance.

Macrofaunal abundance data from replicate benthic cores were used to calculate Hill's N1 diversity and species richness in PRIMER. Spearman rank correlations were fit for overall macrofaunal abundance, biomass, diversity and richness, and abundance of individual groups of macrofaunal taxa (bivalves, gastropods, crustaceans, and polychaetes) to evaluate the effects of salinity change and other water quality variables. One-way Analysis of Variance (ANOVA) was used to test for significant differences in species abundance, biomass, and diversity across salinity regimes, and to compare resources in the BBC and adjacent Laguna Madre. Log transformations were used when necessary to meet assumptions of normality.

Assessment of trophic interactions

Stable isotope analyses of macrofauna

Two additional benthic cores were collected quarterly at six sites interspersed in the system ('Stable isotope sites'= CG2, LS2, AL9, BB40, LM189G and LM189S, Figure 3) for carbon and nitrogen isotope analyses of macrofauna. Cores were sieved over a 500 µm mesh and sorted, with live organisms identified to the lowest possible taxa. For each species identified, 3 individuals of differing size classes were reserved when possible. Live specimens were placed in artificial seawater for 24 hours to evacuate gut contents. Shells were manually removed from mollusks. All samples were freeze dried (Labconco Freezone freeze-drier) and ground to a homogenous powder using a ball mill (Retsch MM 400).

Analyses of Black Drum tissues and stomach contents

Black Drum were collected with the assistance of local commercial trotline fishermen within 6 weeks after quarterly benthic sampling. Five fish of market size (> 355 mm total length) were obtained from each the Laguna Madre and the BBC for each sampling period. These samples were supplemented with Black Drum collected by Texas Parks and Wildlife Department during fall and spring gillnet surveys. Fish were frozen in a -20 ºC freezer until processing, which consisted of measuring total length and the removal of a dorsal muscle plug and stomach contents. Samples of muscle tissues were frozen at -20°C and stomach contents were stored in 70% ethanol.

Stomach contents were sieved over a 500µm sieve and sorted using a stereo microscope. Any identifiable organisms (seagrasses, whole or half bivalves, whole gastropod shells, whole or partial polychaete worms) were identified to the lowest practical taxon, counted and weighed. Polychaetes, seagrasses, and mollusks were frozen, freeze dried, and ground using a ball mill.

Muscle samples were freeze dried and ground using a ball mill. Lipids were removed from muscle tissues with two successive extractions using cyclohexane when C:N ratios of a raw sample were > 4 as lipids are ^{13}C-depleted, leading to a bias in the measurement of the $\delta^{13}C$ values for dietary studies (Sardenne et al. 2015).

Determination of isotopic compositions

All samples were encapsulated in tin and analyzed using an elemental analyzer coupled with an isotope ratio mass spectrometer. Fish muscle tissues were analyzed using a NA 1500 Series 2 (Carlo Erba, Milan, Italy) coupled with a Delta Plus XP with a Conflo III interface (Thermo-Finnigan, Bremen, Germany). All other samples were analyzed using a Flash EA 1112 elemental analyzer equipped with the Smart EA option (Thermo Scientific, Milan, Italy), coupled with a Delta V Advantage isotope ratio mass spectrometer with a Conflo IV interface (Thermo Scientific, Bremen, Germany). This equipment can accommodate small sample sizes (0.1mg). These samples were analyzed at the Littoral, Environment and Societies Joint Research Unit stable isotope facility (University of La Rochelle, France). The Smart EA option enables analysis of samples with a large range of carbon and nitrogen concentrations. Intercalibration was done between both isotope mass spectrometers. Results are expressed in δ notation as deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) following the formula: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Stable isotope statistical analyses

Isotopic compositions of macrofauna were compared seasonally using non-parametric Kruskal-Wallis rank sum tests to investigate patterns that may be introduced based on seasonal or salinity-related fluctuations in isotopic composition (Peterson 1999; Fry 2002; Lorrain et al. 2002). Stable isotope data were compared across regions and salinity regimes using Wilcoxon signed rank tests. Isotopic compositions of fish were correlated with water quality measurements using Spearman rank correlations. Fish were grouped by salinity regime and the spread of $\delta^{13}C$ and $\delta^{15}N$ values were compared using Levene's test for equality of variances (R package "car"; Fox and Weisberg 2011).

Stable isotope data were implemented into a mixing model (R package SIMMR; Parnell 2016) to determine and compare Black Drum dietary patterns under different salinity regimes. Stable isotope values of Black Drum collected in the BBC were separated into hypersaline and normal estuarine salinity groups (based on salinity conditions prior to collection), and a mixing model was created for each group. Models were run for 10,000 iterations with the first 1,000 iterations discarded. SIMMR models use Bayesian statistics to determine probability distributions of possible dietary items. Four possible dietary items were included in the models based on mean values of macrofauna: suspension feeders in the BBC, deposit feeders in the BBC, suspension feeders in the Laguna Madre, and deposit feeders in the Laguna Madre. A trophic enrichment factor (TEF) is used to account for changes in $\delta^{13}C$ and $\delta^{15}N$ between dietary items and consumers, and mean values from the literature were used (3.4 ± 1‰ for $\delta^{15}N$ and 0.4

± 1.3‰ for $\delta^{13}C$; Post 2002). 95% credibility intervals (CI) of dietary inputs are reported, and means, 95 and 25% CI are displayed in figures.

RESULTS

Benthic community characterization

Water quality measurements

Mean salinity in the BBC ranged widely from a high of 53.9 ± 2.6 (mean ± standard deviation) to a low of 15.8 ± 4.4 during the 14 quarterly sampling events (Figure 4). Hypersaline conditions were observed from March 2014 to March 2015, followed by a shift to normal estuarine salinity conditions in June 2015 (15.8 ± 4.4) corresponding with a major flooding event in the watershed. Salinity in the BBC increased gradually for the remainder of the sampling period, with hypersaline conditions returning 15 months later, in September 2016. Salinity in the Laguna Madre fluctuated less than in the BBC, increasing from 25.7 in June 2015 to 47.5 in July 2017. Laguna Madre pH values also fluctuated less (8.11 to 8.45) than in the BBC (7.87 ± 0.25 2014). Dissolved oxygen was higher on average in the Laguna Madre (8.06 ± 2.34 mg/L) than in the BBC (6.75 ± 1.44 mg/L for comparable period). to 8.78 ± 0.05). Minimum pH corresponded with the 2015 flooding event (7.87 ± 0.24), and the maximum pH (8.78 ± 0.05) was recorded during a hypersaline period in the complex (June 2014)

A PCA of pH, salinity, DO and temperature explained a cumulative 79.2% of variation in PC1 (44.3%) and PC2 (34.8%) (Figure 5). Salinity and pH vectors were closely coupled, while temperature and dissolved oxygen had strong opposing trends. All vectors were elongated, indicating that each represented a large portion of environmental variation. Although there was minimal variation in water quality between sites within the BBC, seasonal groupings were apparent. Winter samples clustered together, while summer samples had similar temperatures but variable salinity and pH.

Benthic community

The most abundant taxa within the BBC were polychaetes *Streblospio benedicti* (2567 m^{-2}) and *Capitellidae* spp. (1141 m^{-2}), as well as bivalves *Mulinia lateralis* (608 m^{-2}). *M. lateralis* also accounted for the majority of the total biomass (70.3%, 2.5 g m^{-2}). Polychaetes *Exogone dispar* (5048 m^{-2}) and *Capitellidae* spp. (6345 m^{-2}), and Oligochaete worms (4570 m^{-2}) dominated the Laguna Madre numerically, but polychaetes *Maldanidae* spp. (16.8%, 2.4 g m^{-2}), bivalves *Mulinia lateralis* (5.5%, 0.8 g m^{-2}), and a single Holothuroidean (36.9%, 5.3 g m^{-2}) collected in June 2016 made up the largest proportions of biomass. Nonmetric multidimensional scaling (nMDS) and SIMPER grouping showed that macrofaunal communities in the Laguna Madre grouped separately from those in the BBC by all groupings (Figure 6), while all BBC macrofaunal communities were at least 30% similar to one another. With 60% similarity grouping, 3 BBC sites grouped separately from other sites in the complex. A temporal nMDS of BBC macrofaunal communities (Figure 7) showed that 2014 sampling events were similar, with a shift in communities after the 2015 flooding event. The benthic community showed a further shift in late 2016 as hypersaline conditions returned to the system, resulting in a third grouping distinct from the previous hypersaline regime.

The BIO-ENV analysis indicated that the best water quality descriptors of macrobenthic community structure were concurrent pH and change in salinity (calculated by subtracting the previous salinity measurement from the current salinity measurement) (Rho = 0.119). Within the BBC, macrofaunal abundance was positively correlated with concurrent salinity (Table 1), while biomass and salinity showed a strong negative relationship (Table 1).

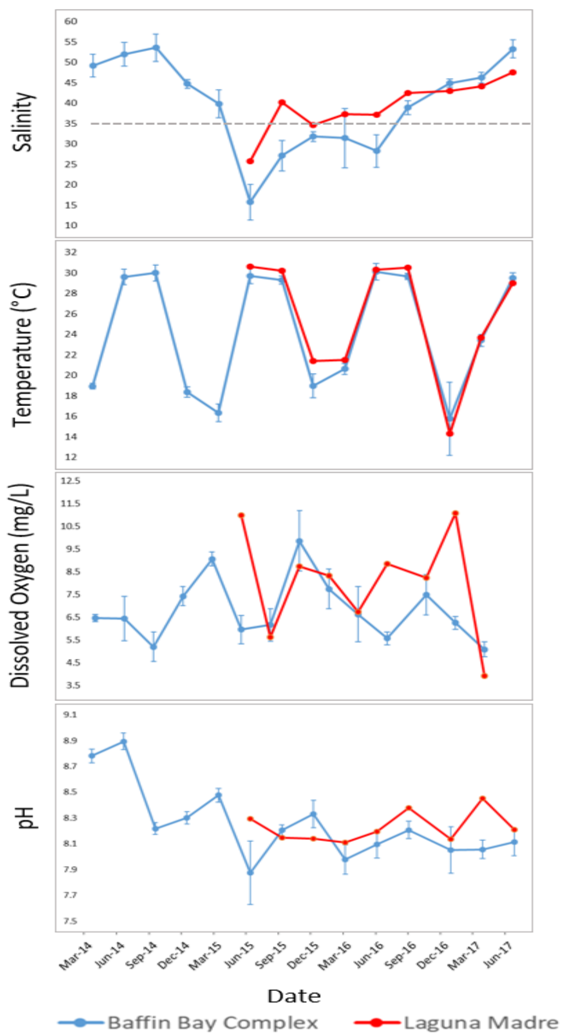

Figure 3. Salinity, temperature, dissolved oxygen, and pH in the Baffin Bay complex and the Laguna Madre from March 2014 to July 2017. BBC data are presented as a mean of values across the complex, with error bars indicating complex-wide standard deviation. In the plot of salinity, a dashed horizontal line (at 35) indicates the threshold for hypersalinity.

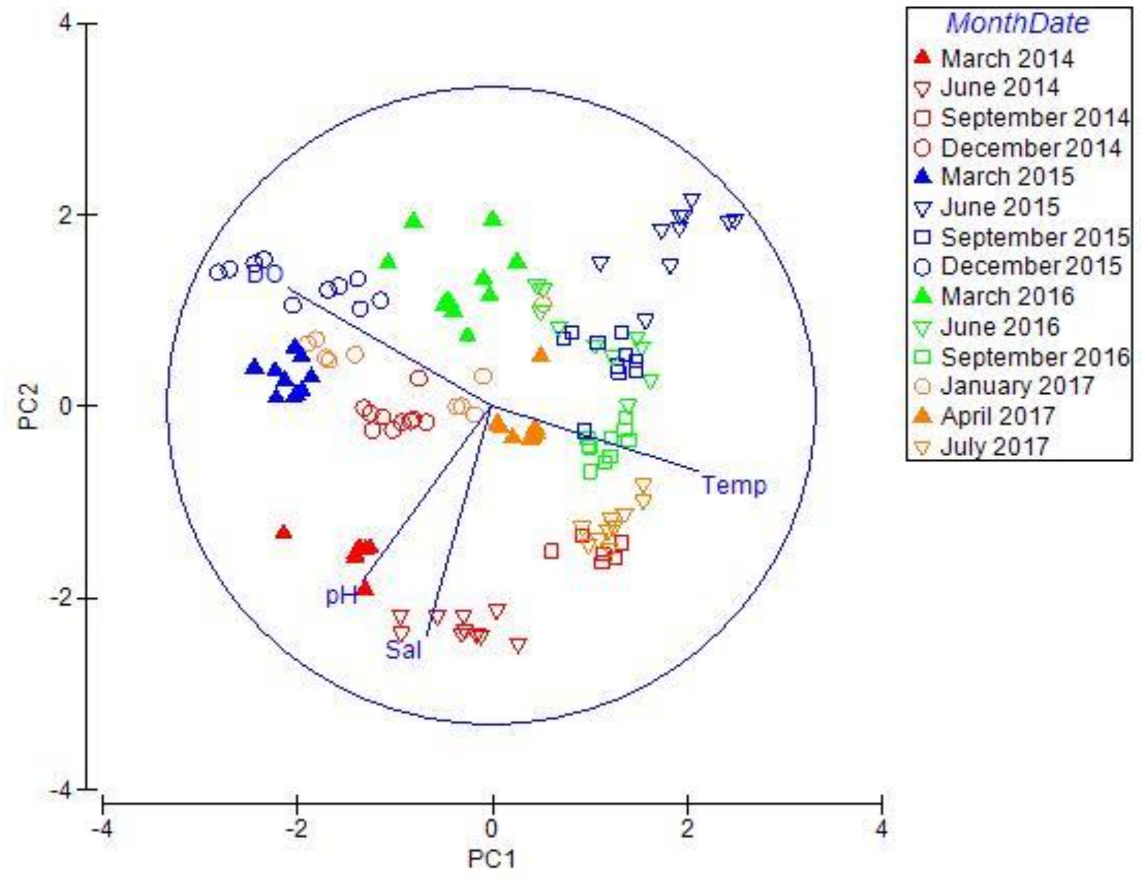

Figure 5. Principal Components Analysis (PCA) plot showing water quality variation in the Baffin Bay complex. Sampling year is represented by color and season is denoted by shape.

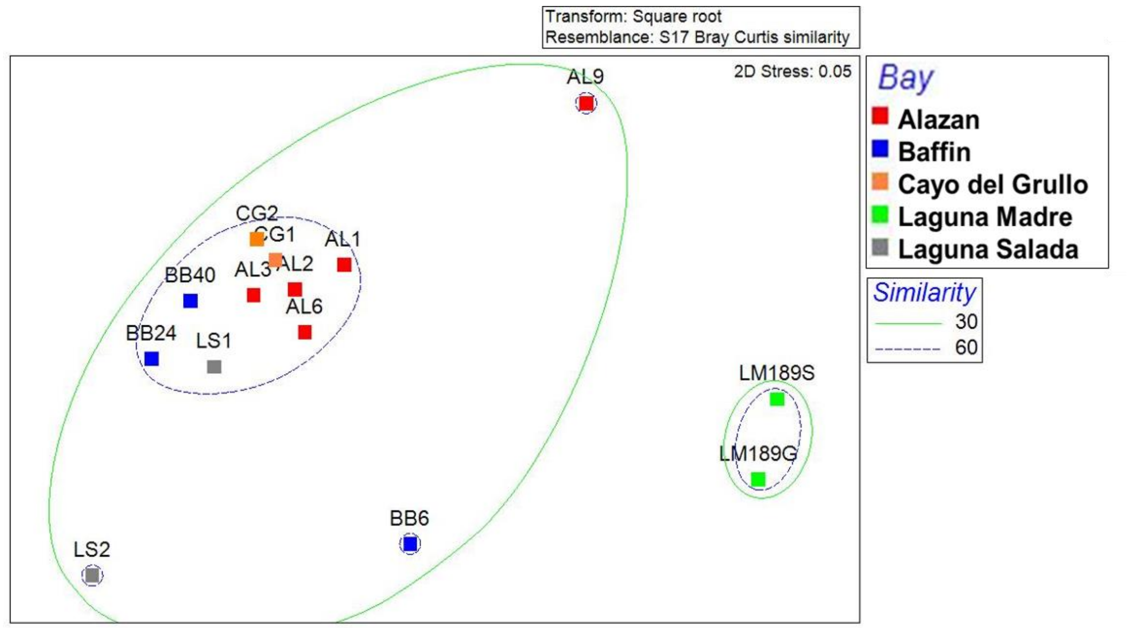

Figure 6. Non-metric multidimensional scaling plot of macrofaunal community composition in the Baffin Bay complex and the Laguna Madre averaged by site (June 2015- July 2017). Colored squares represent location of samples used for analysis by tertiary bay. Circles represent similarity groupings from cluster analysis.

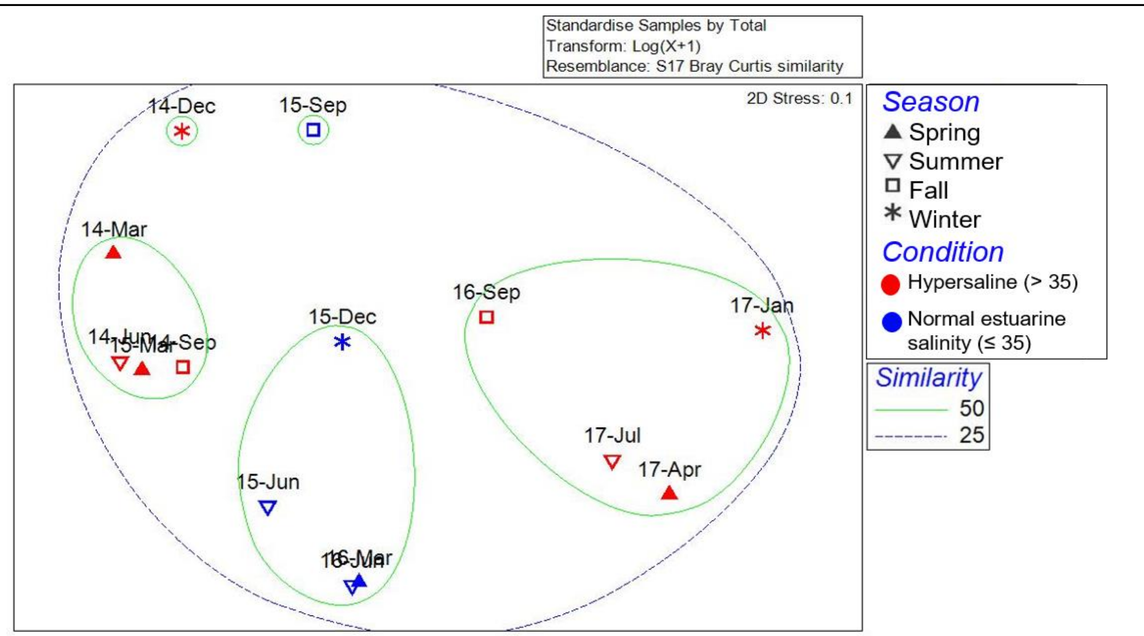

Figure 7. Non-metric multidimensional scaling plot of macrofaunal community structure in the Baffin Bay Complex utilizing benthic data collected March 2014- July 2017. Ten long-term sampling sites were included in analyses. Season of sampling is indicated by shape, and complex-wide mean salinity during sampling is indicated by color (hypersaline period in red, normal estuarine salinity conditions in blue).

Table 1. Spearman rank correlation coefficients among macrofaunal community measurements and water quality parameters. Analyses included 10 BBC sites (AL1, AL2, AL3, CG1, CG2, LS1, LS2, BB6, BB24 and BB40) which were consistently sampled from June 2014 to July 2017. Significant results are indicated by shading.

Variable (unit)		Salinity	Change in Salinity	Temperature (˚C)	pH	Dissolved Oxygen(mg/L)
Biomass (g m^{-2})	rho	-0.293	-0.386	0.015	-0.201	0.233
	p	0.003	<0.001	0.881	0.043	0.018
Abundance (n m^{-2})	rho	0.385	0.101	-0.157	0.085	0.069
	p	<0.001	0.313	0.116	0.394	0.488
Hill's Diversity (N1)	rho	0.242	0.298	-0.036	-0.218	0.003
	p	0.014	0.002	0.719	0.028	0.979
Species Richness (S)	rho	0.261	0.268	-0.030	-0.212	0.017
	p	0.008	0.006	0.764	0.032	0.869
Bivalvia Abundance (n m^{-2})	rho	-0.159	-0.371	0.028	-0.218	0.099
	p	0.109	<0.001	0.783	0.027	0.321
Crustacea Abundance (n m^{-2})	rho	0.165	0.360	-0.088	-0.407	-0.094
	p	0.097	<0.001	0.378	<0.001	0.345
Gastropoda Abundance (n m^{-2})	rho	0.361	0.044	-0.032	0.565	0.132
	p	<0.001	0.664	0.753	<0.001	0.188
Polychaeta Abundance (n m^{-2})	rho	0.322	0.112	-0.109	0.333	0.136
	p	<0.001	0.265	0.275	<0.001	0.172

Macrofaunal biomass was also negatively correlated with the change in salinity, indicating that both lower salinities and large decreases in salinity increase macrofaunal biomass. All community metrics showed strong relationships with some measure of salinity, and most had significant relationships with pH. Macrofaunal biomass was significantly lower under hypersaline conditions (1.7 ± 3.1 g m^{-2}) than in normal estuarine salinity conditions (4.0 ± 5.6 g m^{-2}, $p = 0.001$). Abundance during the two periods was not significantly different ($p > 0.2$), however, diversity and species richness were both significantly higher under high salinity conditions ($p \leq 0.05$). Macrofaunal abundance, biomass, diversity and species richness were all significantly higher in the Laguna Madre than in the BBC for the time period where both were sampled ($p \leq 0.04$, Table 2, Figure 8).

Higher taxonomic groupings of macrofaunal taxa exhibited strong but diverse trends in relation to salinity and other water quality variables within the BBC (Table 1). Bivalves (primarily *M. lateralis*) drove trends in macrofaunal biomass while polychaetes (primarily *S. benedicti and Capitellidae sp*.) comprised the majority of macrofaunal abundance (Figure 8).Some taxa were affected by measured salinity, while others responded to the direction and magnitude of salinity change. Gastropods and polychaetes increased with measured salinity (Table1). Bivalves had a negative relationship with the change in salinity while crustaceans exhibited an opposite trend (Table 1). pH values had significant effects on all groups; gastropods

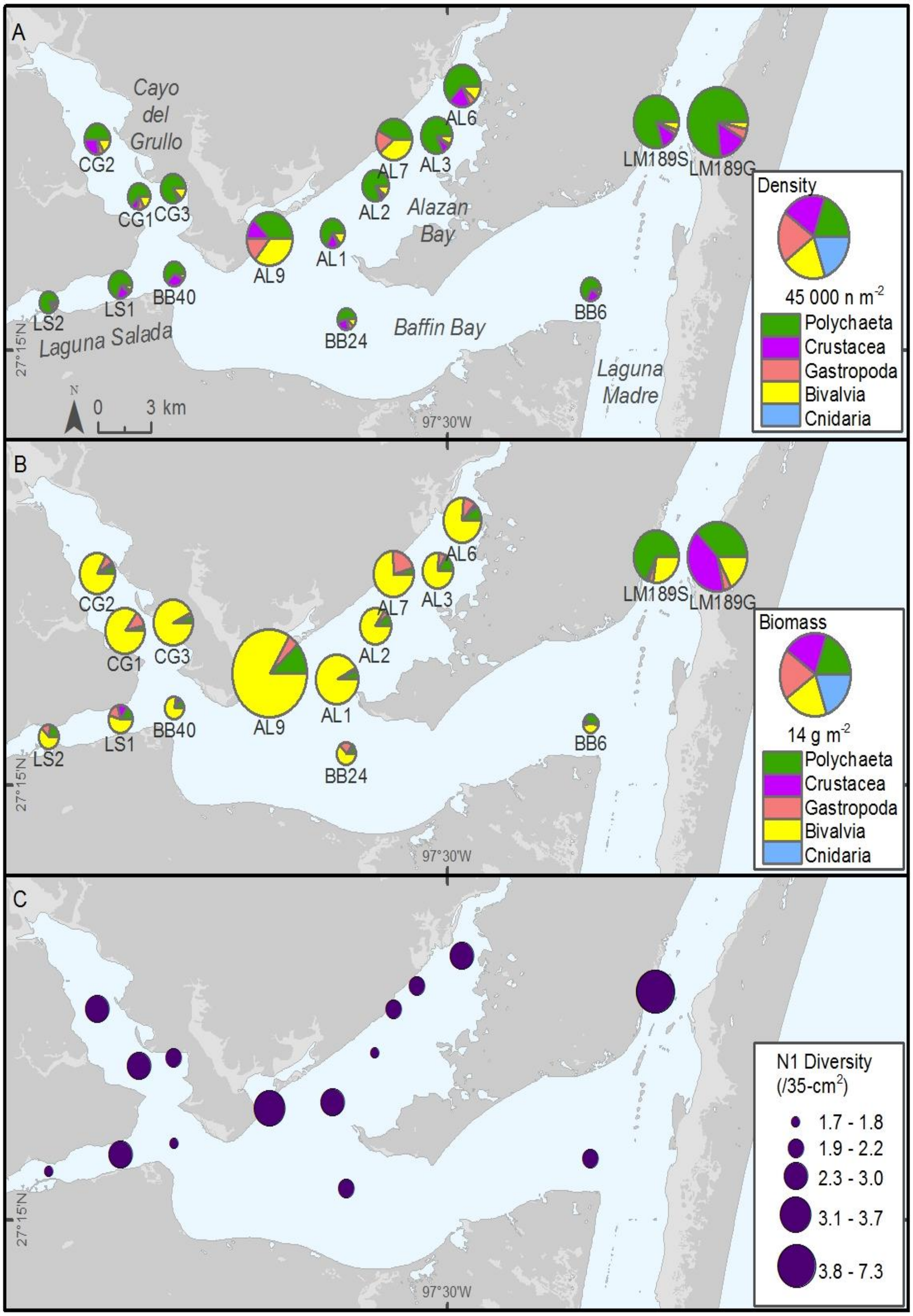

Figure 8. Maps of mean macrofaunal abundance/ density (A), biomass (B), and diversity (C) by station in Baffin Bay and the Laguna Madre from March 2014 to July 2017.

Table 2. Comparison chart of macrofaunal community metrices (mean ± SD) measured from benthic cores collected June 2015 to July 2017. Analyses included 12 Baffin Bay Complex sites and 2 sites in the Laguna Madre.

Variable (unit)	Baffin Bay Complex	Laguna Madre
Biomass (g m^{-2})	3.92 ± 4.22	14.27 ± 17.65
Abundance (n m^{-2})	4343 ± 1459	29215 ± 13146
Hill's Diversity (N1)	2.79 ± 0.89	7.82 ± 1.35
Species Richness (S)	5 ± 2	21 ± 13

and polychaetes increased with pH while bivalves and crustaceans decreased. There was no significant relationship between temperature and any benthic community metrics.

Salinity was significantly negatively related to the W-statistic (measure of disturbance) from the ABC curves ($p = 0.002$, adj $R^2 = -0.14$) for sites within the BBC (Figure 9), indicating that higher salinity corresponds with more abundant but smaller organisms (abundance > biomass). This trend was most prevalent in sites within the main body of Baffin Bay (adj $R^2 = -0.45$) and Alazan Bay (adj $R^2 = -0.13$), and was not significant in the Laguna Madre ($p > 0.4$). The change in salinity also had a significant negative correlation with W-statistics ($p \leq 0.007$, adj $R^2 = -0.12$), but pH, temperature and dissolved oxygen had no significant relationships with W-statistics

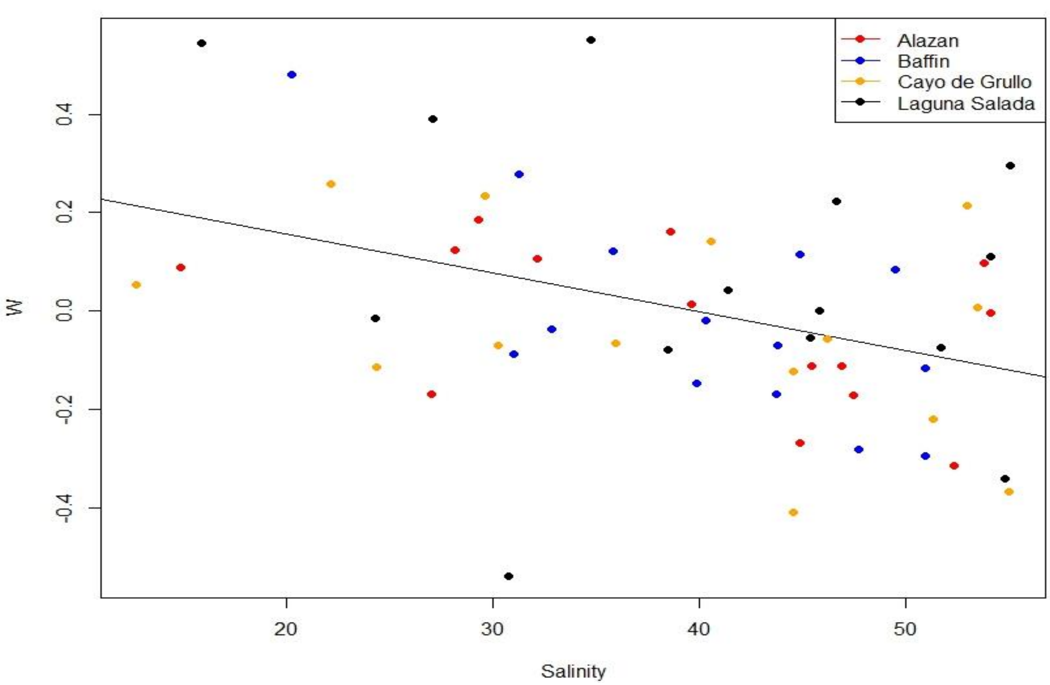

Figure 9. Linear regression of W statistic (a measure of disturbance) and salinity in the Baffin Bay complex. Individual samples are represented by circles and sample location (bay) is denoted by color. W statistic values can range between -1 (indicating a grossly disturbed system) and +1 (indicating a pristine system).

Assessment of trophic interactions

Benthic macrofauna

One hundred and sixty-one live macrofaunal specimens including 42 taxa were collected from the BBC and Laguna Madre for isotopic analysis in 9 seasons. $\delta^{13}C$ values were consistently more depleted in the BBC than the Laguna Madre while $\delta^{15}N$ values were more enriched (Figure 10). $\delta^{13}C$ values of suspension feeders were stable over time for both the BBC (from -24.3 to -16.8 ‰) and Laguna Madre (from -20.1 to -15.5 ‰) ($p > 0.2$). Deposit feeders in the BBC also had stable carbon isotope values (from -21.6 to -17.9, $p > 0.1$), however deposit feeders in the Laguna Madre had $\delta^{13}C$ values that fluctuated seasonally ($p = 0.02$), with both fall seasons being more enriched in ^{13}C compared to other seasons.

Pogonias cromis tissue and stomach content

A total of 299 Black Drum ranging in size (total length) from 357 to 725 mm (mean 463 ± 76 mm), were collected from February 2014 through August 2017. 91% of these individuals had stomach contents, 41.5% (by weight) of gut materials were identifiable (Figure 11), with the remainder composed of unidentifiable, partially digested material. The primary distinguishable material in gut contents of fish collected in the Baffin Bay Complex was Bivalvia (primarily shell hash), which made up 30.9% of all gut content, and 95.0% of identifiable content. Primary identifiable Baffin Bay Complex Black Drum stomach contents also included 2.8% *Anomalcardia auberiana* shells, 1.5% seagrass, and 1.2% *Mulinia lateralis* shells. Laguna Madre Black Drum identifiable stomach contents also contained primarily Bivalvia (74.9%), as well as 8.9% seagrass, 7.0% Crustacea, 4.8% Gastropoda, and 4.1% Polychaeta. The proportions of crustaceans and gastropods in stomach contents of Black Drum collected in the Laguna Madre were significantly greater than in the BBC ($p < 0.01$). Similar to benthic cores, under normal estuarine salinity conditions in the BBC, Black Drum stomach contents had a higher percent composition of Bivalvia (normal salinity = 98.7%, hypersalinity = 88.8%, $p < 0.01$) and lower percent composition of Gastropoda (0.0% and 0.3%, $p = 0.02$).

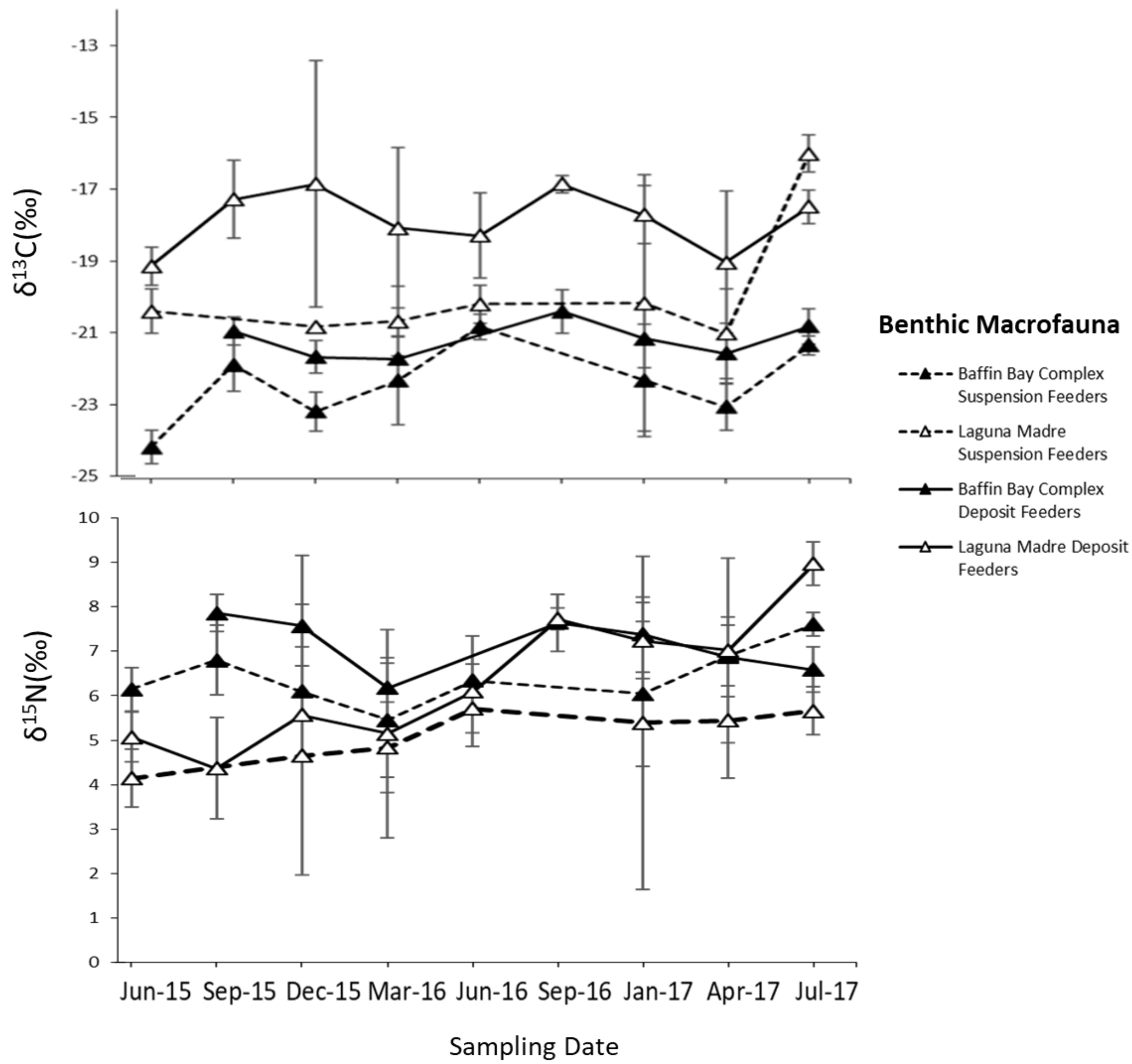

Figure 10. Isotopic composition of benthic macrofauna (Black Drum prey resources; deposit and suspension feeders) in the Baffin Bay complex and the Laguna Madre. Seasonal values for suspension and deposit feeders were omitted when a single organism was collected.

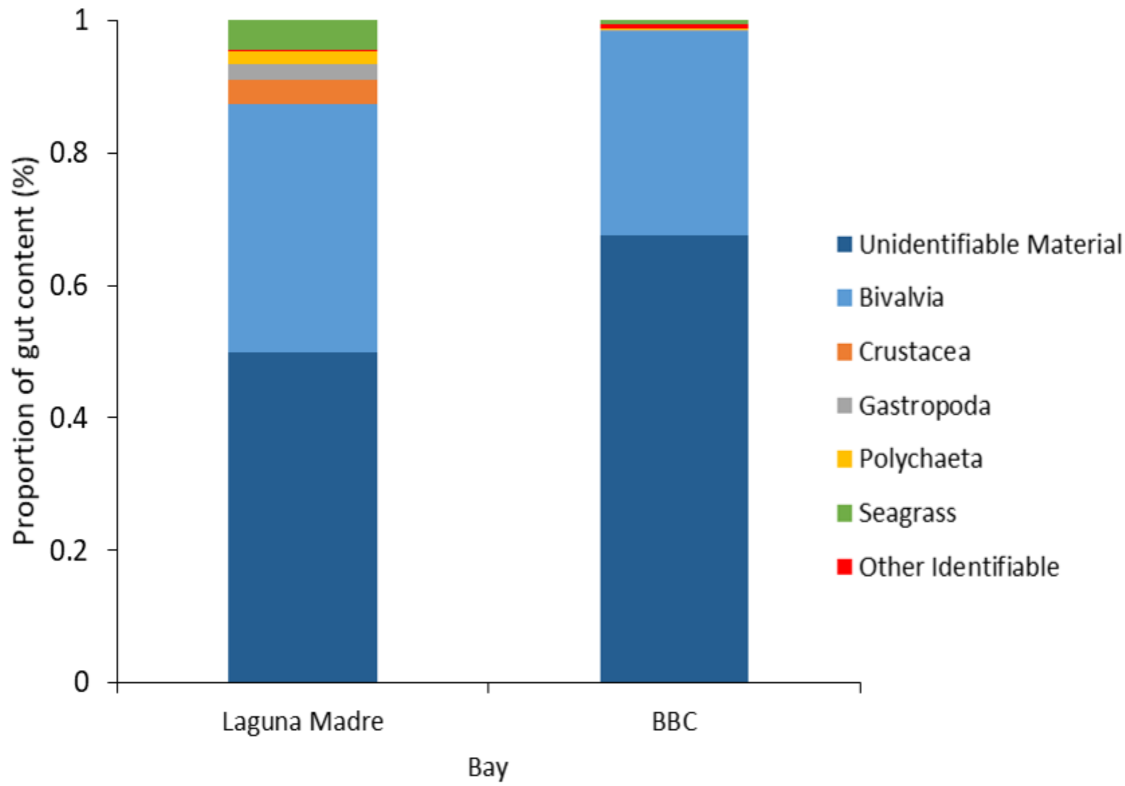

Figure 11. Proportion of food items (wet weight, mg) found in Black Drum gut contents collected in the Baffin Bay complex (BBC) and the Laguna Madre from March 2014 to August 2017.

Table 3. Summary of isotopic analyses of Black Drum muscle tissue (‰, mean ± SD) collected in the Baffin Bay Complex and the Laguna Madre. Baffin Bay Complex samples are also compared under normal estuarine salinity (≤ 35) conditions, and hypersaline (> 35) conditions.

Variable	**Baffin Bay Complex**	**Laguna Madre**	**Baffin Bay Complex Normal**	**Baffin Bay Complex Hypersaline**
n	78	73	36	42
$\delta^{13}C$	-18.2 ± 1.9	-17.0 ± 2.0	-17.5 ± 2.2	-18.7 ± 1.4
$\delta^{15}N$	10.3 ± 1.1	10.2 ± 1.0	10.0 ± 1.1	10.6 ± 1.1

Stable isotope analyses were completed on muscle tissues of 151 Black Drum (Table 3). Black Drum caught in the Laguna Madre were more ^{13}C enriched than those in the BBC ($p < 0.01$, Table 3, Figure 12). Black Drum collected in the BBC were more ^{13}C enriched during periods with normal estuarine salinity conditions than those collected during hypersaline conditions ($p = 0.009$, Rho = -0.28, Figure 12); $\delta^{15}N$ values of Black Drum muscle tissue were more enriched under hypersaline conditions ($p = 0.003$, Rho = 0.26). $\delta^{13}C$ values of Black Drum collected during hypersaline conditions were significantly less variable than those collected during normal estuarine salinity conditions ($p = 0.003$, Figure 13). pH was negatively correlated with $\delta^{13}C$ values and positively correlated with $\delta^{15}N$ values of Black Drum in the BBC ($p \leq 0.02$, $\delta^{13}C$ Rho = -0.39 and $\delta^{15}N$ Rho = 0.25, Table 4). Temperature and DO did not have significant correlations with $\delta^{13}C$ or $\delta^{15}N$ values.

SIMMR mixing model results indicated that deposit feeders compose the majority of assimilated material (BBC deposit feeders from 2.9 to 64.6%, Laguna Madre deposit feeders from 24.5 to 80.6%; 95% CI ranges) in Black Drum diets. The model predicts that Black Drum collected in the BBC feed more heavily on resources in the BBC under hypersaline conditions (dietary proportion of deposit feeders from the BBC from 23.2 to 64.6%, Laguna Madre from 24.5 to 54.7%), but use food resources primarily in the Laguna Madre under normal estuarine salinity conditions (dietary proportion of deposit feeders from the BBC from 2.9 to 36.4%, Laguna Madre from 43.3 to 80.6%) (Figure 14).

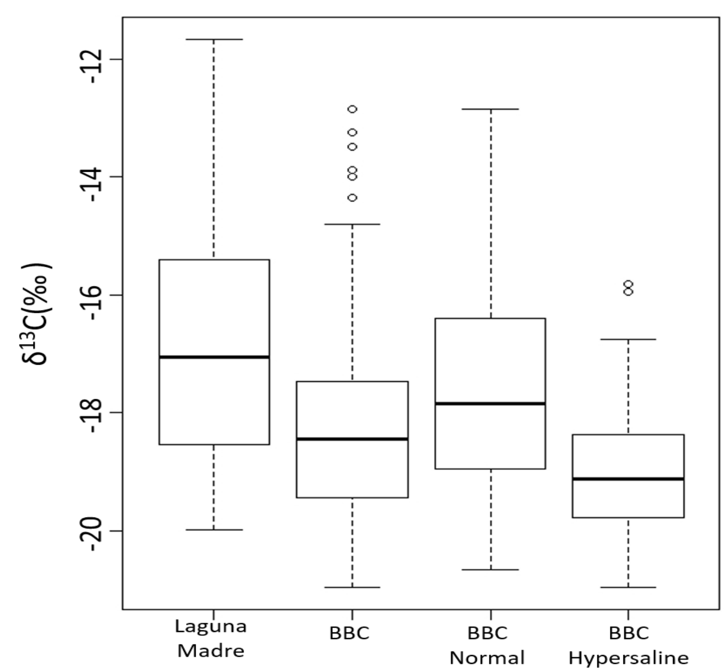

Figure 12. Carbon isotopic composition of muscle tissues from Black Drum collected in the Baffin Bay complex (BBC) and Laguna Madre for sampling dates April 2014 to August 2017. Baffin Bay Complex samples are also compared under normal estuarine salinity (≤ 35) conditions, and hypersaline (> 35) conditions.

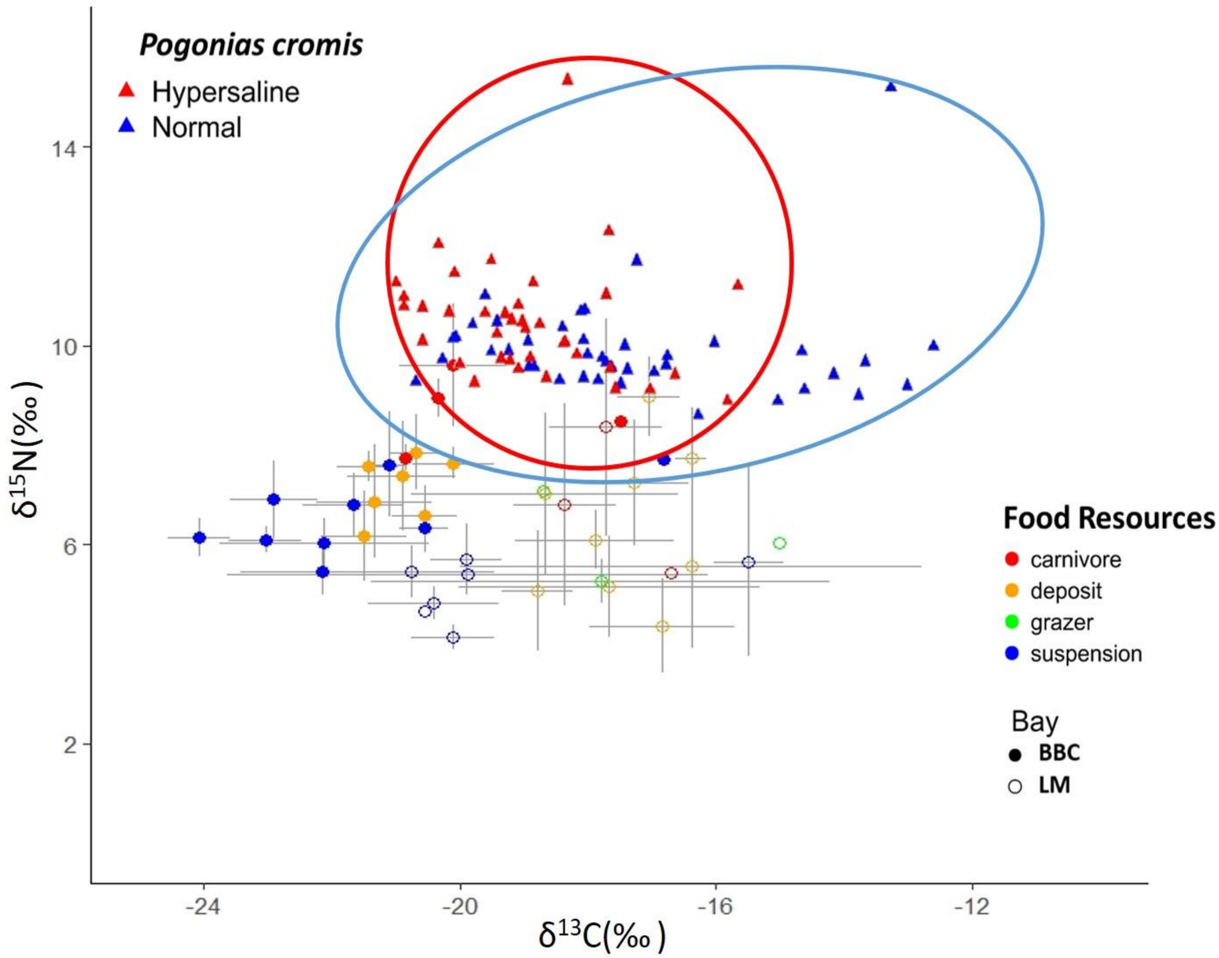

Figure 13. Stable isotope biplot of Black Drum food resources (circles), and muscle tissue (triangles) from the Baffin Bay complex (BBC) and the Laguna Madre (LM). Muscle tissues are encircled to indicate spread of $\delta^{13}C$ values under different salinity regimes (red=hypersaline (> 35), blue=normal estuarine salinity (≤ 35)).

Table 4. Spearman rank correlation coefficients showing relationship between isotopic compositions of muscle tissue from Black Drum collected in the Baffin Bay Complex and water quality parameters. Statistically significant results are indicated by shading.

Variable		Salinity	Change in Salinity	Temperature (˚C)	pH	Dissolved Oxygen(mg/L)
$\delta^{13}C$	rho	-0.293	-0.047	0.095	-0.391	0.160
	p	0.009	0.706	0.409	<0.001	0.193
$\delta^{15}N$	rho	0.257	0.051	-0.050	0.254	0.022
	p	0.022	0.677	0.644	0.025	0.857

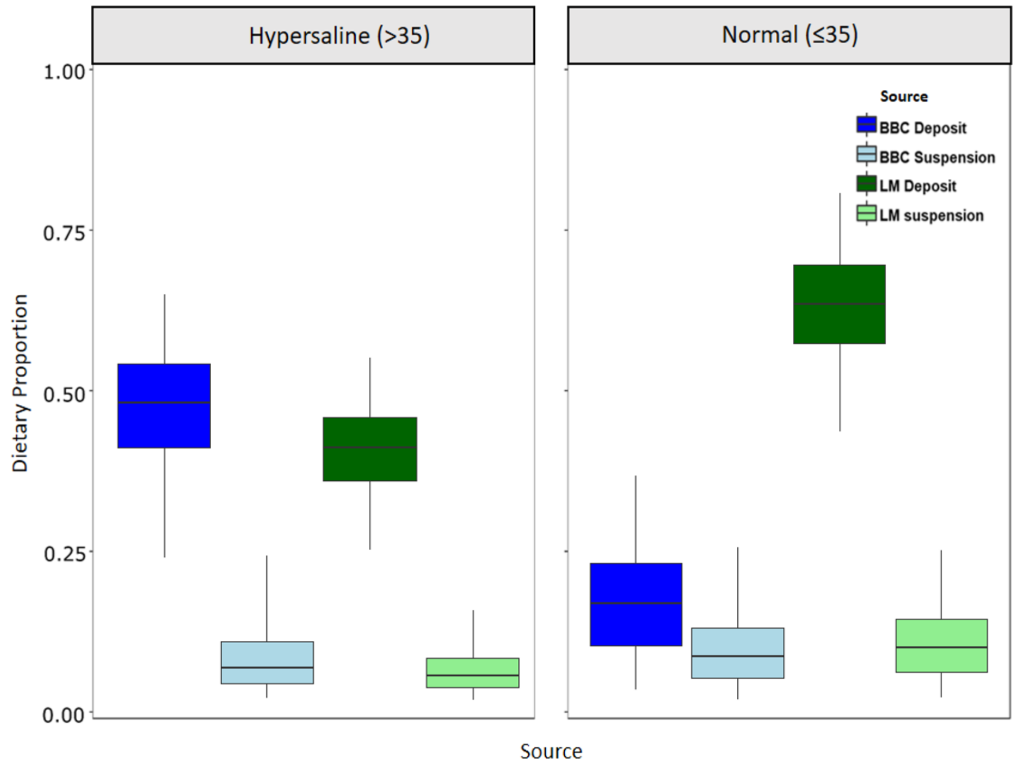

Figure 14. SIMMR mixing model results showing dietary proportions of benthic food resources from the Baffin Bay complex (BBC) and Laguna Madre (LM) assimilated into Black Drum muscle tissues under differing salinity regimes. Food resources are grouped by trophic group (deposit or suspension feeders), and bay collected (BBC or LM).

DISCUSSION

In the BBC, persistence of hypersalinity and frequent fluctuations in water quality lead to disturbed benthic communities with low diversity and biomass, and high abundance of small-bodied opportunistic species. These conditions undoubtedly have repercussions for higher trophic level organisms such as Black Drum in this system, including limited prey availability and altered foraging patterns. Water quality conditions in the BBC from 2014 to 2017 provided a unique opportunity to investigate salinity variation and resultant community dynamics. Fluctuations in freshwater delivery to estuaries are increasingly common both in South Texas and worldwide: Increased prevalence of drought and anthropogenic water use can result in increased salinity variation and instances of temporary or seasonal hypersalinity (Alongi 1990; Savenije and Pagès 1992; Largier et al. 1997; Brusca et al. 2005; Cyrus et al 2010). This variability in salinity and freshwater inflow can affect benthic productivity and act as a disturbance to estuarine systems directly (Montagna and Kalke 1995; Alber 2002; Palmer and Montagna 2015; Van Diggelen and Montagna 2016), or can further exacerbate conditions by triggering fluctuations in pH and dissolved oxygen (Kuentzel 1969; Buskey et al. 1998;

Scheltinga 2006). Understanding the cascading effects of these changes in water quality on estuarine systems is essential to their future management.

Macrofauna community composition within the BBC is reflective of the high levels of salinity variability observed there. Because diversity is typically low in the BBC (mean N1 = 2.13), the addition or loss of a single species causes significant changes in community structure, making alternative methods like the W-statistic more useful tools for investigating stability of this system. The most abundant macrofauna species in the complex are opportunists characteristic of disturbed communities (*S. benedicti*, *M. ambiseta*, *M. lateralis*; Grassle and Grassle 1974; Pearson and Rosenberg 1978; Alongi 1990; Dauer 1993; Ritter and Montagna 1999). *M. lateralis* in particular display highly variable life cycles because of their ability to colonize disturbed areas, grow rapidly, and survive a wide range of salinity and temperature (Breuer 1957; Calabrese 1969; Montagna et al. 1993). These bivalves had a disproportionate effect on biomass in the BBC: A large increase in *M. lateralis* abundance and biomass following the 2015 low-salinity event drove many of the trends in macrofaunal community structure (higher biomass, but lower diversity and species richness). During this comparatively low-salinity period, biomass of benthic macrofauna in the BBC was uncharacteristically similar to that of the Laguna Madre (Simmons 1957; Hedgpeth 1967; Montagna and Kalke 1995; Street et al. 1997) and dominated by the (temporarily) high abundance of *M. lateralis*. Macrobenthic biomass displays year-to-year variability in the BBC, but is typically far below that of the Laguna Madre (Kim and Montagna 2012). Laguna Madre macrobenthic communities were generally more representative of undisturbed environments with high diversity and abundance of larger, longer-lived individuals (Slobodkin and Sanders 1969; Dauer 1993; Street et al. 1997).

Isotopic analyses of Black Drum muscle tissues indicate that they use resources from both the BBC and Laguna Madre under normal estuarine salinity conditions, but become more restricted to the BBC under hypersaline conditions. Fish collected under normal estuarine conditions exhibited wide variation in $\delta^{13}C$ values indicating that, as a group, they assimilated a variety of prey resources. Conversely, Black Drum collected in the BBC under hypersaline conditions had lower variation in $\delta^{13}C$ values and were more ^{13}C depleted (similar to BBC resources) than those collected under normal estuarine conditions. Although potential food resources, particularly *M. lateralis*, are most abundant in the BBC under normal estuarine conditions, isotope data indicate Black Drum move into the Laguna Madre to forage on a more diverse prey base in the absence of salinity stress.

Varying Black Drum movement and resource use in response to salinity is likely related to the increased cost of osmoregulation with increasing hypersalinity. Osmotic regulation is energetically costly, but its energy cost is difficult to quantify: Estimates of metabolic cost range widely (10-60%, Boeuf and Payan 2001; Soengas et al. 2007; Brauner et al. 2013). Gonzalez and Mcdonald (1992) proposed that swimming activity may be limited by osmotic stress, and Swanson (1998) showed significant reduction in activity rates of *C. chanos* (Milkfish) subjected to hypersalinity. Although Simmons and Breuer (1962) hypothesized that fish come into the BBC to feed and are able to leave when food resources become scarce there, current isotopic analyses suggest otherwise. Additionally, results of a recent telemetry study conducted in the BBC demonstrate a strong negative relationship between Black Drum movement and salinity (Ajemian unpublished data). This effect could make it possible for fish to become ‘trapped’ in the BBC, even when food resources in the complex are scarce, leading to events similar to the widespread emaciation witnessed in 2012.

Results of the mixing models further support the idea of differential movement patterns, and a second important but non-traditional idea about Black Drum diet in the BBC: Suspension-feeders are omnipresent at low levels in the diets of these fish, but deposit-feeders make up the majority of assimilated content. These results indicate that deposit feeders, such as the *Maldanidae* spp. polychaetes found in large proportions in the Laguna Madre, may be more important than previously thought in the diets of Black Drum. While populations of *M. lateralis* and other suspension-feeding bivalves vary widely with salinity (Breuer 1957; Dalrymple 1964; Flint and Younk 1983; Montagna and Kalke 1995; Kim and Montagna 2012), deposit-feeders like polychaetes are always present in the BBC and Laguna Madre, providing a more consistent food source. Traditional (non-SI) Black Drum stomach content analyses were reflective of macrofaunal biomass in the BBC and Laguna Madre, but with a strong bias toward mollusks likely due to differential digestion rates (Hyslop 1980; Grubbs et al. 2013). Many historical papers identify *M. lateralis* and similar bivalve species as primary/preferred Black Drum food items (Pearson 1929; Breuer 1957; Darnell 1961; Sutter et al. 1986; Grubbs et al. 2013), but isotopic analyses lead to questions about this notion. Previous assessments of Black Drum diet have relied on these traditional assessments, which supply a ‘snapshot’ of diet. These studies have been used historically to establish a baseline, but make distinguishing consumption and assimilation, and determining long-term trends in movement difficult.

The BBC is a unique system with a host of salinity-related water-quality issues (e.g. algal blooms and resultant low-dissolved oxygen; fluctuations in pH). Though there are many reports on salinity tolerance of Black Drum and other euryhaline fish (Gunter 1961; Hedgpeth 1967; Skadhauge and Lotan 1974; Whitfield et al. 1981), few consider hypersaline conditions and/or behavior of these fish at the limits of their salinity tolerance. Most current research documents fish distribution (in the field) or survival (in the laboratory), but little is known about behavior under adverse conditions. In the BBC, hypersaline conditions lead to limited availability of prey for higher-trophic level organisms, and may also impede movement of these organisms, preventing them from seeking resources in the Laguna Madre or elsewhere. Understanding the impacts of salinity change on benthic prey availability, and trophic interaction dynamics, are critical to determining the ecosystem-scale effects of salinity variability.

Conclusions

Estuaries are vital ecosystems subject to frequent hydrological variation (Gaston et al. 1998; Sparks and Spink 1998). Estuarine systems serve as critical fisheries habitat, with the majority of all commercial fish species being estuarine-dependent for some portion of their lives (Schelske and Odum 1962; Houde and Rutherford 1993; Potter and Hyndes 1999; Beck et al. 2001; Barbier et al. 2011; Hyndes et al. 2014; Sheaves et al. 2015). The BBC supports a large commercial Black Drum fishery (Grubbs et al. 2013; Olsen 2016) which was compromised in a 2012 emaciation event thought to be linked to water quality conditions in the bay (Grubbs et al. 2013; Olsen 2015; Olsen 2016). The goal of this research was to better understand the effects of fluctuations in water quality on the functioning of a predominantly hypersaline estuarine system.

These results show that: 1) High salinity acts as a disturbance to macrofauna communities in the BBC; and 2) This disturbance cascades to higher trophic levels by limiting diet and movement of Black Drum, a commercially important fish species. Macrofauna community metrics in the BBC were primarily driven by *M. lateralis*, an opportunistic bivalve species considered to be important food items for Black Drum (Pearson 1929; Breuer 1957; Sutter et al. 1986; Grubbs et al. 2013). Isotopic analyses showed that Black Drum collected in the BBC primarily foraged on deposit-feeders in the Laguna Madre under lowered salinity conditions, despite high abundance of potential prey in the BBC, but foraged primarily in the BBC under hypersaline conditions, even though food resources in the system became scarce. Osmotic stress likely limited the movements of these fish, reducing foraging behavior outside of the BBC and leading to the 2012 event.

Though the Laguna Madre is a more diverse and stable system than the disturbance-driven Baffin Bay Complex, it likely does not serve as a refuge from adverse conditions if motile fauna cannot access it. We generally consider that fish and other mobile organisms are more resilient to disturbance than sessile organisms because they can actively avoid them (Renaud 1986; Menge and Sutherland 1987; Knott et al. 2009). Though Black Drum (and estuarine fish in general) are resilient to small-scale disturbances (Pihl et al. 1991; Breitburg 1996), disturbance at larger scales, such as long-term maintenance of hypersalinity and associated algal blooms, could cause recurrence of emaciation or fish-kills as have been seen in this and other systems (Pearson 1929; Whitfield and Bruton 1989; Paerl et al. 1999; Araujo et al. 2000). Events such as the drought that led to widespread Black Drum emaciation (and its opposite- the 2015 flooding event that led to a large reduction in salinity) are predicted to become more common with increased climate variability (Chiu and Kuo 2012; Stocker et al. 2013). These findings highlight a need for ecosystem-scale research on hydrological variability and a more robust understanding of resultant trophic interactions in estuarine systems.

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