

ECOSYSTEM RESILIENCE FOLLOWING SALINITY CHANGE
IN A HYPERSALINE ESTUARY

A Thesis

by

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This thesis meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Salinity variability can act as a disturbance to benthic macrofauna communities in estuarine systems, which has indirect effects on higher trophic levels. 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. 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 *Pogonias cromis*, Black Drum, a commercially important benthic predator. In 2012, *P. cromis* 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. 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. Salinity was the best predictor of changes in macrofauna biomass, abundance, and diversity in Baffin Bay, with community biomass and diversity primarily driven by the opportunistic bivalve species, *Mulinia lateralis*. The difference in primary producers in the phytoplankton-dominant Baffin Bay and seagrass-dominated Laguna Madre causes isotopically distinct organic matter and benthic food resources. Isotopic analyses of muscle tissues indicate that *P. cromis* use resources from both Baffin Bay and the Laguna Madre under normal estuarine salinity (≤ 35) conditions, but are more constrained to Baffin Bay under hypersaline (> 35) conditions. 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.

DEDICATION

To Dot and Doc who would have been especially proud today.

Mrs. Dorothy Lucille Miller, 'Dot' (1923-2015)

Dr. Wendell King Loomis, 'Doc' (1923-2015)

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INTRODUCTION

Estuarine systems 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; Nagelkerken 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 1984; 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 fish and motile invertebrates 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. 2014). Unlike the benthic community, 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 1984; 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 (Peterson and Fry 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.

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). Baffin Bay 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. The BBC supports a large *Pogonias cromis* (Black Drum) fishery, supplying the majority of all commercial *P. cromis* 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 the BBC, 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 BBC. Reports of emaciated *P. cromis* in the BBC during severe drought in 2012 raised major concern amongst industry, state officials, and the public (Grubbs et al. 2013; Olsen 2015), but little was known about *P. cromis* food resources or movement patterns, challenging the identification of potential drivers (Grubbs et al. 2013). This study links 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. The objectives of this study are to: 1) describe the effects of extreme salinity change on the benthic community of the BBC and 2) determine how salinity change affects the trophic structure in the complex, using *P. cromis* as an indicator species.

MATERIALS AND METHODS

Study area

The BBC (248 km²) is comprised of Baffin Bay proper and three tertiary arms: Laguna Salada, Cayo del Grullo and Alazan Bay (Figure 1). This shallow ($\leq 2\text{-}3$ 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, Figure 1), which feed into the BBC's tertiary arms.

The Laguna Madre is a shallow ($\leq 1\text{-}2$ 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 January 2017 (Long-term sites, Figure 1). An additional four stations were sampled in the LM and BBC (two each, Additional sites, Figure 1) quarterly from June 2015 to January 2017. 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 obtained from a past study (Mendenhall 2015). All later samples were collected and analyzed by the author.

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 cm² 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 μ m 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 °C for 24 hours, 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 and then rinsed in deionized water prior to being dried.

Sediment grain size analysis

One benthic core was collected annually at each benthic sampling site using a 35.4 cm² core tube to a depth of 10 cm for determination of sediment grain size. Analysis of 0-3 and 3-10 cm vertical sections followed standard geologic procedures (Folk 1966): A 20 cm³ subsample of each section was mixed with 50 ml hydrogen peroxide and 75 ml deionized water for 48 hours to allow organic material to be digested, then supernatant was removed. This mixture was wet-sieved using a vacuum pump and a Millipore Hydrosol SST filter holder fitted with a 62 µm stainless steel mesh screen to remove sand and rubble, which was then dried and weighed. Silt and clay fractions of sieved material were determined through pipette analysis, with respective portions dried and weighed. Percent of total mass for rubble/sand, clay, and silt was calculated for each site and depth interval. Paired t-tests were used to test for annual bay-wide variation.

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 January 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; Clarke and Warwick 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 2001). BIO-ENV was then used to relate these 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, then determines a subset of environmental parameters that maximize this correlation. Macro-benthic 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 SSOM and SPOM

Additional benthic cores were collected quarterly at six sites interspersed in the system ('Stable isotope sites' = CG2, LS2, AL9, BB40, LM189G and LM189S, Figure 1) for SI analyses of carbon and nitrogen of sediment surface organic matter (SSOM). The 0-3 cm depth section of one core per site and sampling period was retained for determination of the SI composition of SSOM. Sediment samples were sieved using a 500 μ m mesh to remove shell hash and macrofauna. The resulting <500 μ m material was retained and stored at -20°C until further processing. Samples were freeze dried (Labconco Freezone freeze-drier) and ground using a mortar and pestle. SSOM samples were acidified to eliminate inorganic carbon (Bunn et al. 1995): A portion of each sample was decarbonated by adding 1 mol.l⁻¹ HCl drop by drop until cessation of bubbling, then dried in a dry block heater, rinsed with deionized water, freeze-dried and re-ground into a homogenous powder before analysis. Acidified samples were used for stable isotope analysis of C, while raw samples were used for N analysis to prevent distortion to N values that the addition of HCl may cause (Bunn et al. 1995).

Surface water samples were collected quarterly for analyses of suspended particulate organic matter (SPOM). Water samples were sieved using a 250 μ m mesh in the field to remove detritus and large zooplankton, then 50ml were filtered onto pre-combusted (4 hours, 450°C) glass microfiber filters (GFF, Whatman) in the laboratory. Filters were dried in a drying oven at 50°C for 24 hours. Samples to be analyzed for carbon were decarbonated by contact with HCl

fumes in a vacuum-enclosed system. As for SSOM, acidified samples were used for stable isotope analysis of C, while raw samples were used for N analysis.

Stable isotope analyses of macrofauna

Two additional benthic cores were collected quarterly at each SI site for determination of isotope composition 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. Specimens were placed in artificial seawater for 24 hours to evacuate gut contents. Samples were frozen at -20°C until further processing. Shells were manually removed from mollusks. All samples were freeze dried and ground to a homogenous powder using a ball mill (Retsch MM 400).

*Analyses of *Pogonias cromis* tissues and stomach contents*

P. cromis 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 *P. cromis* collected by Texas Parks and Wildlife Department during fall and spring gillnet surveys. Fish were frozen in a -20 °C freezer until processing, which consisted of measuring total length and the removal of a dorsal muscle plug and stomach contents for further analyses. 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.

Unidentifiable material was combined with stomach liquids and centrifuged at 2,910 g for 5 minutes (VWR Clinical 200). Supernatant was discarded and isotopic compositions of unidentified stomach materials were used to account for resources that digest rapidly and cannot be accurately identified via sorting.

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 $\delta^{13}\text{C}$ values for dietary studies (Sardenne et al. 2015).

Determination of isotopic compositions

All samples were encapsulated in tin cups (except acidified SSOM samples which were packed in silver cups to avoid corrosion) 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) as 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 $\delta^{13}\text{C}$ and N_2 in air for $\delta^{15}\text{N}$) following the formula: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1] \times 10^3$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

Stable isotope statistical analyses

Isotopic composition of SSOM, SPOM, macrofauna, and stomach contents collected in the BBC and Laguna Madre 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). These data were then 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 *P. cromis* dietary patterns under different salinity regimes. Stable isotope values of *P. cromis* 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between dietary items and consumers, and mean values from the literature were used ($3.4 \pm 1\%$ for $\delta^{15}\text{N}$ and $0.4 \pm 1.3\%$ for $\delta^{13}\text{C}$; 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 \pm standard deviation) to a low of 15.8 ± 4.4 during the 12 quarterly sampling events (Figure 2). 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 43.0 in January 2017, compared to BBC salinities from 15.8 ± 4.4 to 44.9 ± 1.0 during the same period. In the Laguna Madre, pH values also fluctuated less (8.11 to 8.38) than in the BBC (7.87 ± 0.25 to 8.78 ± 0.05). Minimum pH corresponded with the 2015 flooding event (7.50 at site AL9), and the maximum pH (8.99) was recorded during a hypersaline period in Laguna Salada (site LS2, Figure 1) in June 2014. Dissolved oxygen was higher on average in the Laguna Madre (8.22 ± 1.7 mg/L) than in the BBC (7.13 ± 1.62 mg/L for complete sampling period, 7.04 ± 1.72 mg/L for comparable period).

A PCA of pH, salinity, DO and temperature explained a cumulative 81.4% of variation in PC1 (48.3%) and PC2 (33.1%) (Figure 3). 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 significant portion of environmental variation. Although there was minimal variation in water quality between sites within the BBC, seasonal groupings were apparent. All winter samples clustered together, while summer samples had similar temperatures

but variable salinity and pH; the largest difference in water quality measurements was between June 2014 and June 2015.

Sediment grain size analysis

Sediment grain size was measured in the BBC and the Laguna Madre in June of 2015 and 2016 (Figure 4.

). For the BBC as a whole, there was no significant change in composition of rubble, sand, or clay between years, but there was significantly less silt in 2016 than in 2015 samples ($p = 0.01$). Silt content was the highest at two sites (AL6: $58.6 \pm 1.9\%$ and AL3: $58.5 \pm 1.3\%$) closest to Petronila Creek, the bay's primary source of freshwater inflow. The highest rubble content was at the mouth of Alazan Bay (site AL9, $38.3 \pm 14.8\%$), while the largest proportions of clay were in Baffin Bay proper, sites BB24 ($64.7 \pm 18.8\%$) and BB6 ($50.5 \pm 14.6\%$). Within the BBC, sites with the highest sand content were AL9 ($44.3 \pm 16.5\%$) and LS2 ($36.8 \pm 0.2\%$). Laguna Madre sites were primarily composed of sand ($70.1 \pm 6.2\%$) and rubble ($17.1 \pm 5.0\%$).

Benthic community

The most abundant taxa within the BBC were polychaetes *Streblospio benedicti* (2728 m^{-2}) and *Capitellidae* spp. (841 m^{-2}), as well as bivalves *Mulinia lateralis* (522 m^{-2}). *M. lateralis* also accounted for the majority of the total biomass (73.2% , 2.4 g m^{-2}). Polychaetes *Exogone dispar* (1016 m^{-2}) and *Capitellidae* spp. (1040 m^{-2}), and Oligochaete worms (754 m^{-2}) dominated the Laguna Madre numerically, but polychaetes *Maldanidae* spp. (49.4% , 2.3 g m^{-2}), bivalves *Mulinia lateralis* (11.0% , 0.9 g m^{-2}), and a single Holothuroidean (6.8% , 6.8 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 (Figure 5), with all BBC macrofaunal communities at least 25% similar to one another. With 50% similarity grouping, BBC sites AL9 and BB6 grouped separately from other sites within the complex. Representation with superimposed sediment grain size data indicated that this difference may be related to sediment composition, particularly proportion of sand (Appendix 3.1). A temporal nMDS of BBC macrofaunal communities showed that communities were similar in 2014 and 2015 with the exception of the June 2015 sampling. However in 2016, there appears to have been a shift in macrofaunal community composition (Appendix 3.2).

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) ($Rho = 0.239$, Appendix 1). Within the BBC, macrofaunal abundance was positively correlated with concurrent salinity ($p < 0.003$, $r = 0.41$; TABLES

Table 1), while biomass and salinity had a significant negative relationship ($p < 0.003$, $r = -0.33$; TABLES

Table 1). Macrofaunal biomass was also negatively correlated with the change in salinity ($p < 0.001$, $Rho = -0.39$), indicating that both lower salinities and large decreases in salinity increase macrofaunal biomass. However, N1 diversity and species richness were both positively correlated with change in salinity ($p < 0.05$, $r = 0.27, 0.22$) as well as with dissolved oxygen ($p \leq 0.01$, $r = 0.27, 0.26$). Macrofaunal biomass was significantly lower under hypersaline conditions ($1.7 \pm 3.5 \text{ g m}^{-2}$) than in normal estuarine salinity conditions ($4.0 \pm 5.8 \text{ g m}^{-2}$, $p = 0.01$). However, abundance, diversity, and species richness were not significantly different ($p > 0.3$).

Macrofaunal abundance was significantly higher in the Laguna Madre ($33703 \pm 13803 \text{ m}^{-2}$, $p < 0.001$) than in the BBC ($5650 \pm 2278 \text{ m}^{-2}$), but biomass was not significantly different between bays for this time period ($p \geq 0.1$).

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). Some taxa were affected by measured salinity, while others responded to the direction and magnitude of salinity change. Gastropods and polychaetes significantly increased with measured salinity ($p < 0.001$, $Rho = 0.44, 0.52$), while bivalves decreased ($p = 0.003$, $Rho = -0.33$). Bivalves also responded to changes in salinity, increasing with salinity decrease ($p < 0.001$, $Rho = -0.42$), in contrast to crustaceans that increased with increases in salinity ($p = 0.004$, $Rho = 0.31$). Crustaceans, gastropods, and polychaetes had significant but variable relationships with pH ($p < 0.01$, $Rho = -0.42, 0.64, 0.33$).

Salinity was significantly negatively related to the W-statistic (measure of disturbance) from the ABC curves ($p < 0.0001$, $\text{adj } R^2 = -0.27$) for sites within the BBC (Figure 6), 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 ($\text{adj } R^2 = -0.50$) and Alazan Bay ($\text{adj } R^2 = -0.24$), and was not significant in the Laguna Madre ($p > 0.5$). The change in salinity also had a significant negative correlation with W-statistics ($p \leq 0.01$, $\text{adj } R^2 = -0.12$). pH and W-statistics had a significant positive relationship ($p \leq 0.01$, $\text{adj } R^2 = 0.13$). Temperature and dissolved oxygen had no significant relationship with W-statistics.

Assessment of trophic interactions

Organic matter sources

A total of 42 surface SSOM samples were collected in the BBC during 11 quarterly sampling trips from June 2014 to January 2017; 12 SOM samples were collected in the Laguna Madre during 6 samplings beginning in June of 2015 (Figure 7). Carbon and nitrogen isotope values for Laguna Madre SSOM were stable over time ($p > 0.1$), ranging from -19.4 to -16.0 ‰ and from 2.3 to 3.5 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Carbon isotope values for the BBC were also stable (from -22.5 to -20.1 ‰, $p = 0.06$), however nitrogen values fluctuated significantly ($p < 0.01$), with values generally more ^{15}N enriched preceding the 2015 low-salinity event. Laguna Madre sediments were consistently more enriched in ^{13}C and more depleted in ^{15}N than BBC samples ($p < 0.001$). SSOM $\delta^{13}\text{C}$ values in the Laguna Madre ranged from -19.4 to -16.0‰ (mean $-17.0 \pm 0.8\text{‰}$), compared to SSOM $\delta^{13}\text{C}$ values in the BBC ranging from -22.1 to -19.1‰ (mean $-20.9 \pm 1.0\text{‰}$). SSOM $\delta^{15}\text{N}$ values in the Laguna Madre ranged from 2.2 to 3.8‰ (mean of $2.9 \pm 0.4\text{‰}$) compared to SSOM $\delta^{15}\text{N}$ values in the BBC ranging from 4.1 to 10.2‰ (mean $5.7 \pm 1.2\text{‰}$).

SPOM was collected during 6 sampling dates from March 2015 to September 2016 (51 samples from 9 sites) in the BBC and on 4 sampling dates from December 2015 to January 2017 (4 samples with replication from one site) in the Laguna Madre (Figure 7). SPOM $\delta^{13}\text{C}$ values ranged from -28.2 to -20.1‰ (mean $-23.3 \pm 1.9\text{‰}$) in the BBC and from -25.4 to -21.0‰ (mean $-22.3 \pm 2.1\text{‰}$) in the Laguna Madre. SPOM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the BBC and the Laguna Madre were not significantly different from one another ($p > 0.1$). SPOM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values fluctuated in the BBC over time ($p < 0.001$), but were stable in the Laguna Madre ($p > 0.05$).

Benthic macrofauna

A total of 119 live macrofaunal specimens including 39 taxa were collected from the BBC and Laguna Madre for isotopic analysis in 7 seasons. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for suspension feeders averaged -22.1 ± 1.8 and $6.1 \pm 0.7\text{‰}$ in the BBC and -20.0 ± 1.3 and $5.1 \pm 0.7\text{‰}$ in the Laguna Madre, respectively (Figure 7). Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for deposit feeders were -20.8 ± 1.0 and $7.4 \pm 0.9\text{‰}$ in the BBC and -18.0 ± 1.1 and $5.8 \pm 1.5\text{‰}$ in the Laguna Madre. *Mulinia lateralis* were on average more ^{13}C depleted in the BBC than in the Laguna Madre (-22.0 ± 1.8 versus $-20.1 \pm 0.5\text{‰}$, $p < 0.01$). Other suspension feeders sampled in both BBC and Laguna Madre were also more ^{13}C depleted in the BBC ($p < 0.01$, Table 2, Table 3). Similar to *Mulinia lateralis*, deposit-feeding Capitellid polychaetes were on average more ^{13}C depleted in the BBC than in the Laguna Madre ($\delta^{13}\text{C} = -20.6 \pm 1.2\text{‰}$ versus $-18.7 \pm 0.3\text{‰}$, $p = 0.01$), as were other deposit-feeders collected in the Laguna Madre ($p = 0.01$, Table 2, Table 3). $\delta^{13}\text{C}$ values of suspension feeders were stable over time for both the BBC (from -24.8 to -16.8‰) and Laguna Madre (from -22.5 to -17.7‰) ($p > 0.2$). Deposit feeders in the BBC also had stable carbon isotope values (from -17.7 to -21.7 , $p > 0.1$), however deposit feeders in the Laguna Madre had $\delta^{13}\text{C}$ values that fluctuated seasonally ($p = 0.04$), with both fall seasons being more enriched in ^{13}C compared to other seasons.

Pogonias cromis tissue and stomach content

A total of 295 *P. cromis*, ranging in size (total length) from 356 to 725 mm (mean 458 ± 76 mm), were collected from December 2013 through March 2017. 87% of these individuals had stomach contents. Within these stomach contents, 33.5% (by weight) of materials were identifiable (Figure 8). The primary distinguishable material was Bivalvia (primarily shell hash). Baffin Bay Complex *P. cromis* stomach contents contained 97.5% Bivalvia, 1.5% seagrass, 0.7%

Polychaeta, 0.1% Crustacea, and 0.2% Gastropoda, by weight. Identifiable whole or half *Anomalcardia auberiana* and *Mulinia lateralis* comprised 2.8% and 1.2% of biomass, respectively. Laguna Madre *P. cromis* stomach contents also contained primarily Bivalvia (73.3%), as well as 11.5% seagrass, 9.1% Crustacea, 5.1% Polychaeta and 1.1% Gastropoda, with 1.1% and 0.8% *Anomalcardia auberiana* and *Mulinia lateralis*, respectively. The proportions of crustaceans and gastropods in stomach contents of *P. cromis* 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, *P. cromis* stomach contents had a higher percent composition of Bivalvia (normal salinity = 98.8%, hypersalinity = 95.2%) and lower percent composition of Gastropoda (0.1% and 0.3%), though these differences were not statistically significant. Isotopic analyses of *P. cromis* stomach liquids showed intermediate values between benthic food resources and *P. cromis* muscle tissues (Figure 9), although stomach liquids had a wider range of $\delta^{13}\text{C}$ values (-12.8 to -25.6 ‰, mean = -20.0 ± 2.7 ‰) than either benthic food resources or *P. cromis* muscle tissues.

Stable isotope analyses were completed on muscle tissues of 131 *P. cromis* (Table 4). *P. cromis* caught in the Laguna Madre were more enriched in ^{13}C than those in the BBC ($p = 0.008$, Figure 10). *P. cromis* collected in the BBC were more ^{13}C enriched during periods with normal estuarine salinity conditions than those collected during hypersaline conditions ($p = 0.01$, Rho = -0.29, Figure 10); $\delta^{15}\text{N}$ values of *P. cromis* muscle tissue were more enriched under hypersaline conditions ($p = 0.008$, Rho = 0.29). $\delta^{13}\text{C}$ values of *P. cromis* collected during hypersaline conditions were less variable than during normal estuarine salinity conditions ($p = 0.03$). pH was negatively correlated with $\delta^{13}\text{C}$ values and positively correlated with $\delta^{15}\text{N}$ values of *P. cromis* in

the BBC ($p \leq 0.01$, $\delta^{13}\text{C}$ Rho = -0.44 and $\delta^{15}\text{N}$ Rho = 0.31, Table 5). Temperature and DO did not have significant correlations with $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values.

SIMMR mixing model results indicated that deposit feeders compose the majority of assimilated material (BBC deposit feeders from 24 to 56%, Laguna Madre deposit feeders from 35 to 68%; 95% CI ranges) in *P. cromis* diets. The model predicts that *P. cromis* collected in the BBC feed more heavily on resources in the BBC under hypersaline conditions (dietary proportion of deposit feeders from the BBC from 25 to 74%, Laguna Madre from 15 to 60%), but use food resources primarily in the Laguna Madre under normal estuarine salinity conditions (dietary proportion of deposit feeders from the BBC from 8 to 50%, Laguna Madre from 35 to 80%) (Figure 11).

DISCUSSION

Benthic community composition

Salinity was found to be the best predictor of changes in macrofaunal community composition in the BBC. Although the BBC is a predominantly hypersaline estuary, it behaves similarly to other estuaries in Texas by some measures: Lower salinities in the BBC contributed to less disturbed conditions (indicated by higher W-scores), including increased macrofaunal biomass. Macrofaunal biomass has been shown to increase with salinity reduction across Texas bays (Kim and Montagna 2012). Change in salinity is a predictor of macrobenthic species diversity and richness in the BBC, as well as in systems that display more typical estuarine salinity gradients (e.g. Montague and Ley 1993; Attrill et al. 1996; Pollack et al. 2009; Palmer and Montagna 2015; Van Diggelen and Montagna 2016). Increases in salinity contributed to more diverse macrobenthic communities in the BBC, as shown in other studies (Ysebaert et al. 1993; Josefsen and Hansen 2004; Pollack et al. 2011). However, because salinity can act as a

stressor (Hedgpeth 1967; Buskey et al. 1998), increases in freshwater input can increase abundance and diversity for organisms at the limits of their tolerance (Montagna et al. 2002; Velasco et al. 2006; Lamprey and Armah 2008). In typical estuarine systems, increased diversity is related to the inclusion of marine species under higher-salinity conditions (Whitfield et al. 2012). In the BBC, this effect is caused by the dominance of *M. lateralis* and loss of gastropod species under low salinity conditions. Because diversity is typically low in the BBC (mean N1 = 1.88), 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.

Macrofauna community composition within the BBC is reflective of the high levels of salinity variability observed there. The most abundant macrofauna species in the complex (*S. benedicti*, *M. ambiseta*, *M. lateralis*) are opportunists characteristic of disturbed communities (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, as in other systems along the Texas coast (Breuer 1957; Dalrymple 1964; Flint and Younk 1983; Montagna and Kalke 1995). A large increase in *M. lateralis* abundance and biomass following the 2015 low-salinity event drove many of the trends in macrofaunal community structure in the BBC (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). Other taxa increased with salinity; gastropods (primarily *Acteocina canaliculata*, a marine species) were common in hypersaline samples, but only two individuals were found in salinities lower than 30. Similarly large fluctuations in *A. canaliculata* populations have been reported in the Chesapeake Bay, with highest abundances recorded with particularly high or low salinities (Holland et al. 1987).

Although the BBC and Laguna Madre have some macrobenthic taxa in common (i.e. *M. lateralis*, and *Capitellidae spp.*), 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). Many of the species observed in the Laguna Madre are used as indicators of pristine conditions. Syllidae polychaetes, the most numerically common taxa in the Laguna Madre, are typically associated with seagrass beds (Franke 1999) and are used as pollution sentinel species (Bellan 1982). The presence of deep-burrowing species such as Maldanidae polychaetes, which dominated macrobenthic biomass in the Laguna Madre, is also indicative of environmental quality and the absence of disturbance (Dauer 1993).

Over the course of this study, mean BBC-wide salinity fluctuation of nearly 40 was accompanied by large variation in pH (~1.5) and periodically low dissolved oxygen, which also had substantial effects on benthic community composition. While not directly correlated in this study, pH is influenced by salinity, and can be indicative of freshwater inflow (Scheltinga et al. 2006), and algal blooms (Kuentzel 1969). High salinity can also exacerbate brown tide algae, *Aureoumbra lagunensis*, which is common in the BBC (Buskey et al. 1998; Buskey et al. 2001;

Wetz et al. 2017), and can lead to depletion of dissolved oxygen as algae decay in mass quantities (Duarte et al. 2009). All of these factors contribute to make the BBC a highly-disturbed system, both within the time period of this research, and historically (Breuer 1957; Dalrymple 1964; Montagna and Kalke 1995; Buskey et al. 2001). Conditions in the Laguna Madre were more stable and suitable for benthic fauna than those in the BBC by multiple measures: Salinity and pH fluctuated less (both were consistently similar to that of seawater), and dissolved oxygen was typically higher. Seagrass beds likely increase dissolved oxygen concentrations (Onuf 2007) and have been shown to support recovery of macrobenthic abundance and diversity following disturbance in the Laguna Madre (Montagna et al. 2010).

While temporal benthic community composition in the BBC and Laguna Madre were primarily affected by water quality, macrobenthic spatial distribution was influenced by grain size, which can act as an additional stressor (Johnson 1970; Warwick and Uncles 1980; Mannino and Montagna 1997). W-statistics were lower (indicating higher disturbance) in areas with high silt/clay content (in sediments: close to Petronila Creek and in Baffin Bay proper). High proportions of fine-grain sediments can make conditions challenging for macrofauna, particularly suspension feeders (Rhoads and Young 1970). Significantly more silt was present in sediments in 2015 than in 2016 BBC samples. This increase is likely related to large freshwater inputs from the 2015 low-salinity event (Bolam et al. 2004; Hermand et al. 2005). Although the BBC benefitted from the lowered salinity caused by this event, increased silt content may have delayed the subsequent shift in macrofaunal community composition observed in 2016. Sites in the Laguna Madre had high sand and low silt content. In general, sites in the BBC with similar sediment composition to the Laguna Madre had the highest biomass within the study area.

Water quality conditions in the BBC from 2014 to 2017 provided a unique opportunity to investigate salinity variation and resultant community dynamics. There are few predominantly hypersaline estuaries worldwide (Javor 1989), but fluctuations in freshwater delivery to estuaries are increasingly common: Increased prevalence of drought and anthropogenic water use (Matson et al. 1997; Alber 2002; Foley et al. 2005; Seager et al. 2007; Chan and Wu 2015) 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; Montagna and Palmer 2012; 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). 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 opportunistic species. These conditions undoubtedly have repercussions for higher trophic levels in this and other systems (Nordby and Zedler 1991; Vega-Cendejas and Hernandez de Santillana 2004; Brusca et al. 2005; Grubbs et al. 2013; Olsen 2016).

Trophic interactions

SSOM $\delta^{13}\text{C}$ values in the BBC (mean = -20.9‰) and the Laguna Madre (-17.0‰) highlighted a larger influence of seagrass material (~ -10.0‰, Fry 2006) in the Laguna Madre. At the seasonal scale, a higher influence of seagrass material is also evident in fall as deposit feeders in the Laguna Madre are more enriched in ^{13}C . In the fall, seagrass input to sediments is higher due to a large volume of decomposing leaf litter following the growing season (Mateo and Romero 1997; Mateo et al. 2006). Despite fluctuations in SPOM $\delta^{13}\text{C}$ values for both the BBC

and Laguna Madre, $\delta^{13}\text{C}$ values for suspension feeders were stable over time as they tend to average the values of organic matter that they consume (Fry and Arnold 1982). Nitrogen values of SPOM and SSOM in the BBC were more ^{15}N enriched and variable—maybe reflective of terrestrial inputs to the watershed (McClelland et al. 1997; McClelland and Valiela 1998). SSOM $\delta^{15}\text{N}$ values in the Laguna Madre were more similar to those of nitrogen-fixing plants (i.e. seagrass; Peterson and Fry 1987). Distinction of these systems has been shown in previous studies: the difference in primary producers in the phytoplankton-influenced BBC and seagrass-dominated Laguna Madre causes organic matter and benthic food resources in each system to be isotopically distinct (Fry et al. 1977; Fry and Parker 1979; Street et al. 1997). This distinction allows inferences to be made about movements of higher-trophic level organisms like *P. cromis* between the two systems.

Isotopic analyses of muscle tissues indicate that *P. cromis* 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 $\delta^{13}\text{C}$ values indicating that, as a group, they assimilated a variety of prey resources. Conversely, *P. cromis* collected in the BBC under hypersaline conditions had lower variation in $\delta^{13}\text{C}$ values and were more ^{13}C depleted (similar to BBC resources) than those collected under normal estuarine conditions. Similarly, previous work in the BBC and Laguna Madre during hypersaline conditions found that fish and macrobenthos collected in the BBC were significantly more ^{13}C depleted than those in the Laguna Madre (Street et al. 1997). A telemetry project coinciding with the current study indicated *P. cromis* are seasonally constrained to the BBC at times of sharp salinity gradients (Ajemian, unpublished data). Other tagging studies of *P. cromis* in Texas indicate strong fidelity to individual bays, but with the

BBC and Laguna Madre considered as a single system (Osburn and Matlock 1984; Matlock and Weaver 1979; Marwitz 1986). Although food resources, particularly *M. lateralis*, are most abundant in the BBC under normal estuarine conditions, isotope data indicate *P. cromis* move into the Laguna Madre to forage on a more diverse prey base in the absence of salinity stress. Previous studies indicate that *P. cromis* are opportunistic predators, altering their diets to incorporate seasonal or environmental shifts in prey availability (Street et al. 1997; Blasina et al. 2010).

Results of the SIMMR isotope mixing models further support two important but non-traditional ideas about *P. cromis* diet in the BBC: 1) Suspension-feeders are omnipresent at low levels in the diets of these fish, but deposit-feeders make up the majority of assimilated content; 2) Fish leave the BBC to forage in the Laguna Madre when salinity conditions are normal. These results indicate that deposit feeders, such as the Maldanidae polychaetes found in large proportions in the Laguna Madre, may be more important than previously thought in the diets of *P. cromis*. 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) *P. cromis* 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 *P. cromis* 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 *P. cromis* diet (Breuer 1957; Darnell 1961;

Peters and McMichael 1990; Blasina 2010) 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.

Isotopic results were similar to Street et al. (1997) in that there is a clear distinction between BBC and Laguna Madre $\delta^{13}\text{C}$ values for organic matter and macrofauna. However, the current difference between comparable resources in the two bays was consistently near 1.5‰ while the previous authors recorded distinctions near 3.0‰. Samples from both the BBC and Laguna Madre in previous studies were more ^{13}C enriched than current samples (Fry et al. 1977; Fry and Parker 1979; Street et al. 1997). A portion of this difference could be due to location and timing of sampling: previous studies of the Laguna Madre used sites further North than the current sampling location (Fry et al 1977; Fry and Parker 1979; Street et al. 1997), and Fry et al. (1977) noted that sediment $\delta^{13}\text{C}$ values became increasingly negative as they approached the BBC. Street et al. (1997) sampled during a period with negligible freshwater inflow, so the influence of terrestrial organic matter (and associated $\delta^{13}\text{C}$ values ~ 28 ‰) was limited in comparison to those from the large inflows seen in this study. Anderson et al (1992) found long-term sediment $\delta^{13}\text{C}$ values in the area fluctuated ~ 4.0 ‰, representing tradeoffs of phytoplankton and seagrass inputs to these systems over time, which likely represents another cause of this dissimilarity.

Varying *P. cromis* 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 (Brauner et al. 2013): 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 *P. cromis* 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.

The Baffin Bay complex 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), but salinity variation and other water quality changes are becoming increasingly common globally (Chiu and Kuo 2012; Stocker et al. 2013). Though there are many reports on salinity tolerance of *P. cromis* 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 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. 1999; 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 *P. cromis* 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 *P. cromis*, 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 *P. cromis* (Pearson 1929; Breuer 1957; Sutter et al. 1986; Grubbs et al. 2013). Isotopic analyses showed that *P. cromis* 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 throughout 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 *P. cromis* (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 (Simmons 1929; Whitfield and Bruton 1989; Paerl et al. 1999; Araujo and Williams 2000). Events such as the drought that led to widespread *P. cromis* 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 other estuarine systems.

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TABLES

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 January 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	-0.329	-0.388	0.060	0.197	0.185
	p	0.003	<0.001	0.595	0.076	0.097
Abundance (n m ⁻²)	rho	0.412	0.101	-0.163	0.173	0.143
	p	<0.001	0.366	0.145	0.120	0.200
Hill's Diversity (N1)	rho	-0.011	0.271	-0.056	-0.060	0.264
	p	0.922	0.014	0.618	0.590	0.017
Species Richness (S)	rho	0.028	0.218	-0.026	-0.048	0.263
	p	0.804	0.049	0.816	0.670	0.017
Bivalvia Abundance (n m ⁻²)	rho	-0.330	-0.428	0.084	-0.132	0.175
	p	0.003	<0.001	0.452	0.236	0.116
Crustacea Abundance (n m ⁻²)	rho	-0.167	0.312	-0.059	-0.425	0.109
	p	0.133	0.004	0.598	<0.001	0.330
Gastropoda Abundance (n m ⁻²)	rho	0.442	0.033	-0.072	0.646	0.220
	p	<0.001	0.766	0.521	<0.001	0.047
Polychaeta Abundance (n m ⁻²)	rho	0.527	0.215	-0.068	0.331	<0.001
	p	<0.001	0.052	0.542	0.002	0.999

Table 2. Carbon isotopic composition (‰, mean ± SD) of benthic macrofauna and trophic guilds collected in the BBC and Laguna Madre from June 2015 to January 2017.

Trophic Group / Species	Baffin Bay Complex		Laguna Madre		Baffin Bay Complex Normal		Baffin Bay Complex Hypersaline	
	n	δ ¹³ C	n	δ ¹³ C	n	δ ¹³ C	n	δ ¹³ C
Carnivores	8	-19.6 ± 1.5	3	-18.1 ± 1.2	7	-20.3 ± 0.7	1	-17.5
<i>Acteocina canaliculata</i>	1	-17.5					1	-17.5
<i>Goniadidae sp.</i>	1	-20.7	1	-18.9	1	-20.7		
Nemertea	1	-19.5			1	-19.5		
<i>Onuphidae sp.</i>	5	-20.6 ± 0.4	2	-17.2 ± 0.8	5	-20.6 ± 0.4		
Deposit Feeders	20	-20.6 ± 1.1	45	-18.1 ± 1.3	12	-20.6 ± 1.5	8	-20.8 ± 0.6
<i>Ampharetidae sp.</i>			3	-18.3 ± 1.5				
Amphipoda	3	-21.0 ± 1.2	3	-17.6 ± 1.4			3	-21.0 ± 1.2
<i>Armandia agilis</i>			2	-17.6 ± 0.6				
<i>Capitella sp.</i>			3	-18.8 ± 0.3				
<i>Capitellidae sp.</i>	3	-20.6 ± 1.2	4	-18.7 ± 0.2	1	-22.0	2	-19.9 ± 0.3
<i>Cerithium lutosum</i>			3	-14.0 ± 2.7				
<i>Eunicidae sp.</i>	1	-20.4			1	-20.4		
<i>Goniadidae sp.</i>			1	-18.6				
<i>Grandidierella bonmeroides</i>			1	-17.9				
Holothuroidea			1	-19.5				
<i>Litopenaeus setiferus</i>	1	-17.9			1	-17.9		
<i>Maldanidae sp.</i>			11	-17.2 ± 0.5				
<i>Nereididae sp.</i>	1	-21.4	2	-17.8 ± 2.4			1	-21.4
<i>Notomastus sp.</i>			1	-18.0				
Oligochaeta			3	-18.4 ± 0.5				
<i>Orbiniidae sp.</i>	1	-21.7	1	-18.3	1	-21.7		
<i>Palaemonetes sp.</i>			2	-17.1 ± 1.9				
<i>Pectinariidae sp.</i>	7	-21.0 ± 0.4	1	-18.5	6	-21.2 ± 0.3	1	-20.6
Polychaeta	2	-20.7 ± 0.5			2	-20.7 ± 0.5		
<i>Spionidae sp.</i>			1	-20.0				
<i>Streblospio benedicti</i>			2	-19.1 ± 0.1				
Tanaidacea	1	-21.0					1	-21.0
Grazers			2	-16.9 ± 2.6				
<i>Astyris lunata</i>			1	-18.7				
<i>Erichsonella attenuata</i>			1	-15.0				
Suspension Feeders	24	-22.0 ± 1.3	17	-20.1 ± 1.7	18	-22.3 ± 1.5	6	-20.7 ± 1.6
<i>Amygdalum papyrium</i>			1	-20.7				
<i>Angulus texanus</i>			1	-17.2				

Trophic Group / Species	Baffin Bay Complex		Laguna Madre		Baffin Bay Complex Normal		Baffin Bay Complex Hypersaline	
	n	$\delta^{13}\text{C}$	n	$\delta^{13}\text{C}$	n	$\delta^{13}\text{C}$	n	$\delta^{13}\text{C}$
<i>Anomalcardia auberiana</i>	2	-23.6 ± 1.7	1	-17.8	2	-23.6 ± 1.7		
Cnidaria	1	-23.0			1	-23.0		
<i>Laevicardium mortoni</i>			1	-21.5				
<i>Lyonsia hyalina</i>	2	-21.8 ± 3.2	1	-22.5			2	-21.8 ± 3.2
<i>Mactrotoma fragilis</i>			1	-20.6				
<i>Mulinia lateralis</i>	18	-21.5 ± 2.3	7	-20.2 ± 0.4	14	-22.2 ± 1.3	4	-19.6 ± 3.9
<i>Serpulidae sp.</i>			1	-21.2				
<i>Tellina sp.</i>	1	-20.3	3	-19.3 ± 0.0	1	-20.3		

Table 3. Nitrogen isotopic composition (‰, mean ± SD) of benthic macrofauna and trophic guilds collected in the BBC and Laguna Madre from June 2015 to January 2017.

Trophic Group / Species	Baffin Bay Complex		Laguna Madre		Baffin Bay Complex Normal		Baffin Bay Complex Hypersaline	
	n	δ ¹⁵ N	n	δ ¹⁵ N	n	δ ¹⁵ N	n	δ ¹⁵ N
Carnivores	8	9.0 ± 1.0	3	6.8 ± 2.0	7	9.2 ± 1.1	1	8.5
<i>Acteocina canaliculata</i>	1	8.5					1	8.5
<i>Goniadidae sp.</i>	1	8.7	1	8.2	1	8.7		
Nemertea	1	10.5			1	10.5		
<i>Onuphidae sp.</i>	5	8.3 ± 0.9	2	5.4 ± 0.0	5	8.3 ± 0.9		
Deposit Feeders	20	7.9 ± 2.3	45	5.4 ± 1.3	12	8.0 ± 0.8	8	7.6 ± 1.1
<i>Ampharetidae sp.</i>			3	5.3 ± 0.1				
Amphipoda	3	6.8 ± 0.4	3	4.7 ± 1.2			3	6.8
<i>Armandia agilis</i>			2	6.4				
<i>Capitella sp.</i>			3	4.7				
<i>Capitellidae sp.</i>	3	7.9 ± 0.1	4	4.9 ± 0.0	1	7.8	2	8.0 ± 0.1
<i>Cerithium lutosum</i>			3	4.5 ± 1.4				
<i>Eunicidae sp.</i>	1	8.4			1	8.4		
<i>Goniadidae sp.</i>			1	7.6				
<i>Grandidierella bonneroides</i>			1	2.8				
Holothuroidea			1	5.2				
<i>Litopenaeus setiferus</i>	1	9.1			1	9.1		
<i>Maldanidae sp.</i>			11	7.2 ± 1.2				
<i>Nereididae sp.</i>	1	9.3	2	5.3 ± 1.3			1	9.3
<i>Notomastus sp.</i>			1	4.8				
Oligochaeta			3	6.5 ± 0.2				
<i>Orbiniidae sp.</i>	1	7.5	1	6.0	1	7.5		
<i>Palaemonetes sp.</i>			2	7.9 ± 0.7				
<i>Pectinariidae sp.</i>	7	7.0 ± 0.6	1	4.6	6	6.9 ± 0.6	1	7.4
Polychaeta	2	8.2 ± 0.5			2	8.2 ± 0.5		
<i>Spionidae sp.</i>			1	4.7				
<i>Streblospio benedicti</i>			2	4.2 ± 0.5				
Tanaidacea	1	6.5					1	6.5
Grazers			2	6.5 ± 0.7				
<i>Astyris lunata</i>			1	7.1				
<i>Erichsonella attenuata</i>			1	6.0				
Suspension Feeders	24	5.7 ± 0.6	17	5.1 ± 0.3	18	5.7 ± 0.7	6	6.3 ± 1.1
<i>Amygdalum papyrium</i>			1	5.4				
<i>Angulus texanus</i>			1	5.4				
<i>Anomalcardia auberiana</i>	2	6.0 ± 0.4	1	5.3	2	6.0 ± 0.4		
Cnidaria	1	5.9			1	5.9		
<i>Laevicardium mortoni</i>			1	5.1				

Trophic Group / Species	Baffin Bay Complex		Laguna Madre		Baffin Bay Complex Normal		Baffin Bay Complex Hypersaline	
	n	$\delta^{15}\text{N}$	n	$\delta^{15}\text{N}$	n	$\delta^{15}\text{N}$	n	$\delta^{15}\text{N}$
<i>Lyonsia hyalina</i>	2	5.5 ± 0.2	1	5.4			2	5.5 ± 0.2
<i>Mactrotoma fragilis</i>			1	4.7				
<i>Mulinia lateralis</i>	18	6.5 ± 0.7	7	5.1 ± 1.0	14	6.3 ± 0.6	4	7.1 ± 0.9
<i>Serpulidae sp.</i>			1	5.1				
<i>Tellina sp.</i>	1	4.8	3	4.6 ± 0.1	1	4.8		

Table 4. Summary of isotopic analyses of *P. cromis* muscle tissue (‰, mean \pm SD) collected in the Baffin Bay Complex and the Laguna Madre under normal and hypersaline conditions.

Variable	Baffin Bay Complex	Laguna Madre	Baffin Bay Complex Normal	Baffin Bay Complex Hypersaline
n	68	63	27	41
$\delta^{13}\text{C}$	-18.1 \pm 2.0	-17.2 \pm 2.0	-17.4 \pm 2.1	-19.03 \pm 1.4
$\delta^{15}\text{N}$	10.3 \pm 1.2	10.1 \pm 1.0	10.1 \pm 1.0	10.7 \pm 1.3

Table 5. Spearman rank correlation coefficients showing relationship between isotopic compositions of muscle tissue from *P. cromis* 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)
$\delta^{13}\text{C}$	rho	-0.293	-0.034	0.120	-0.435	0.160
	p	0.015	0.798	0.331	<0.001	0.229
$\delta^{15}\text{N}$	rho	0.286	0.051	-0.069	0.305	0.085
	p	0.018	0.706	0.577	0.011	0.524

FIGURES

Figure 1. 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.

Figure 2. Salinity (A), temperature (B), dissolved oxygen (C) and pH (D) in the Baffin Bay complex (BBC) and the Laguna Madre from March 2014 to January 2017. BBC data are presented as a mean of values taken across the complex, with blue shading indicating complex-wide standard error. In the plot of salinity, a horizontal line (at 35) indicates the threshold for hypersalinity.

Figure 3. Principal Components Analysis (PCA) plot showing water quality variation in the Baffin Bay complex. Year sampled is represented by color and season is represented by shape.

Figure 4. Map of Baffin Bay complex and Laguna Madre sampling sites with pie charts depicting mean sediment grain size from 2015-2016

Figure 5. Non-metric multidimensional scaling plot of macrofaunal community composition in the Baffin Bay complex and the Laguna Madre averaged by bay (June 2015- January 2017). Colored squares represent location of samples used for analysis by tertiary bay. Circles represent similarity groupings from cluster analysis.

Figure 6. 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.

Figure 7. Isotopic composition of sediment (SOM) and suspended particulate organic matter (SPOM), and benthic macrofauna (prey resources; deposit and suspension feeders) in the Baffin Bay complex (BBC) and the Laguna Madre. Benthic food resource collection began in June of 2015. Shading indicates sampling periods in which mean salinity in the BBC was ≤ 35 .

Figure 8. Proportion of identifiable food items found in *P. cromis* gut contents collected in the Baffin Bay complex (BBC) and the Laguna Madre from March 2014 to 2017. Gut contents were grouped for comparison by region and salinity regime.

Figure 9. Stable isotope biplot of *P. cromis* food resources (circles), stomach liquids (hollow triangles), and muscle tissue (solid triangles) from the Baffin Bay complex (BBC) and the Laguna Madre (LM). Muscle tissues are encircled to indicate spread of $\delta^{13}\text{C}$ values under different salinity regimes (red=hypersaline, blue=normal salinity).

Figure 10. Carbon isotopic composition of muscle tissues from *P. cromis* collected in the Baffin Bay complex (BBC) and Laguna Madre for sampling dates April 2014 to March 2017. Shading indicates sampling periods in which mean salinity in the BBC was ≤ 35 .

Figure 11. SIMMR mixing model results showing dietary proportions of benthic food resources from the Baffin Bay complex (BBC) and Laguna Madre (LM) assimilated into *P. cromis* muscle tissues under differing salinity regimes. Food resources are grouped by trophic group (deposit or suspension feeders), and bay collected (BBC or LM).

Figure 1.

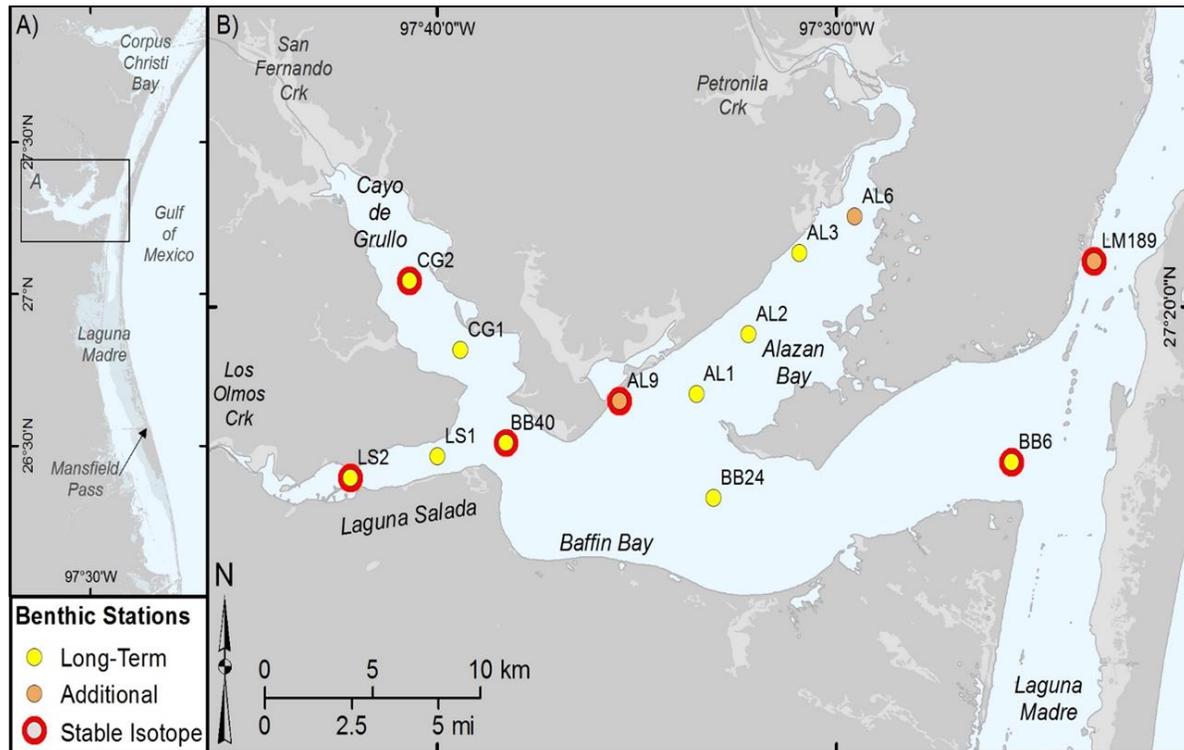


Figure 2.

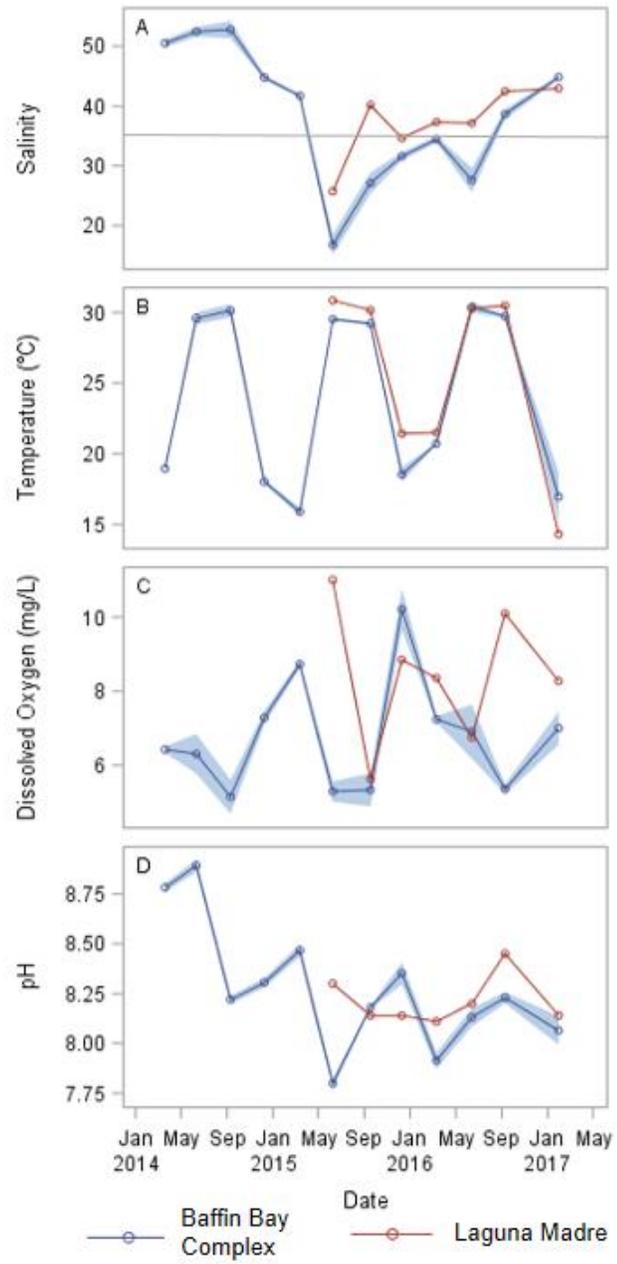


Figure 3.

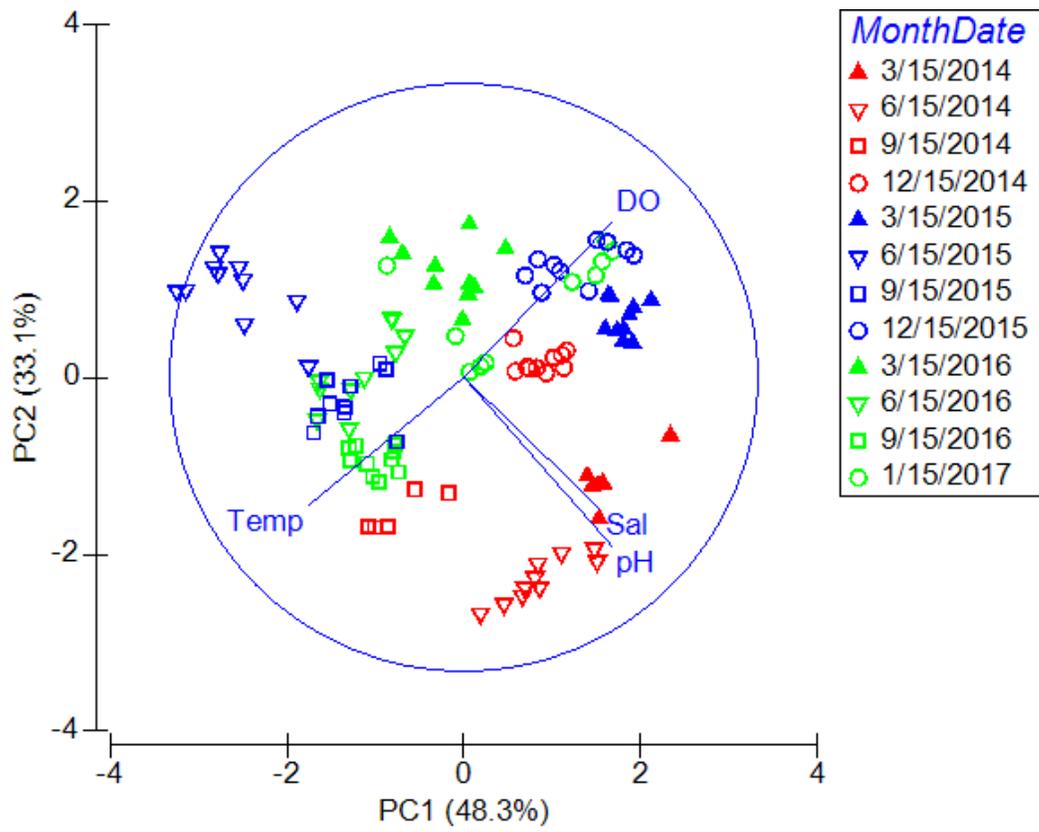


Figure 4.

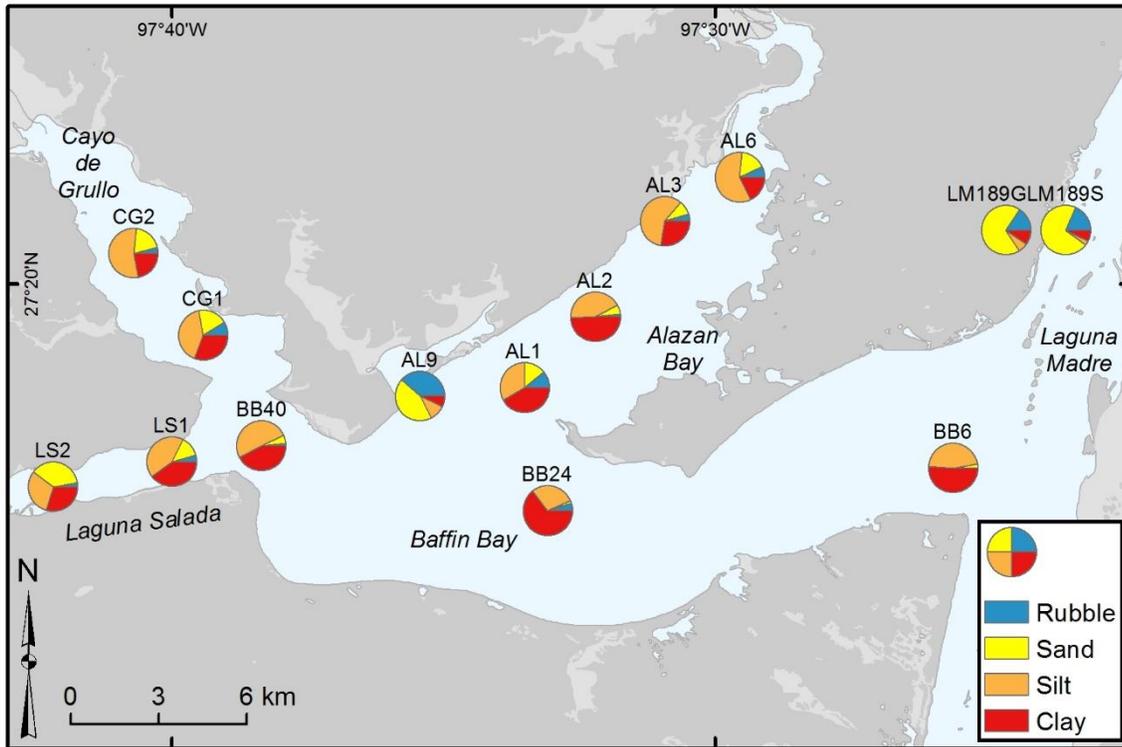


Figure 5.

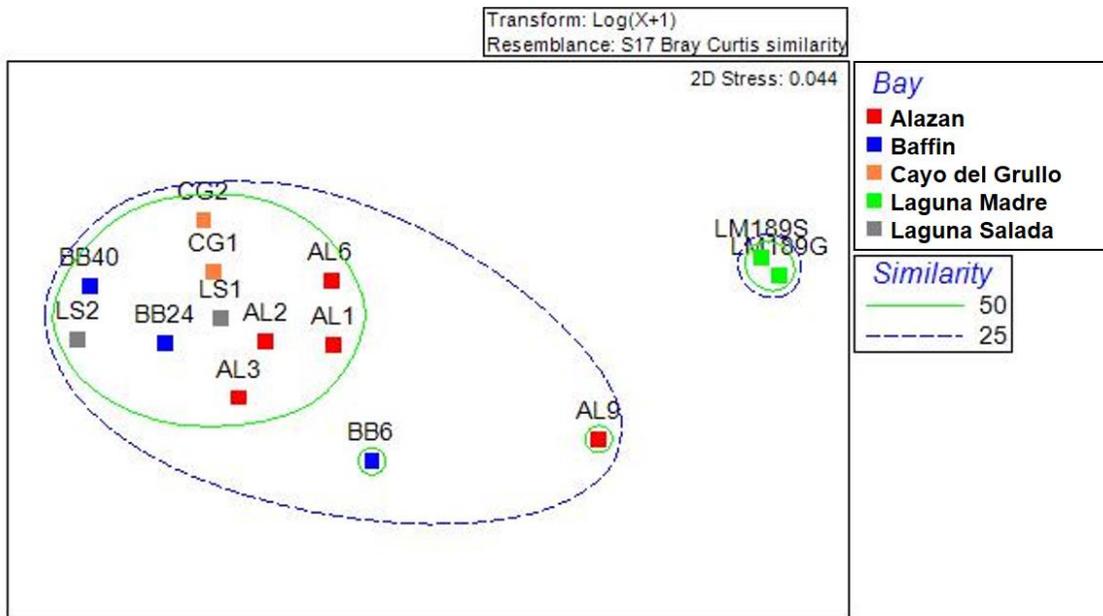


Figure 6.

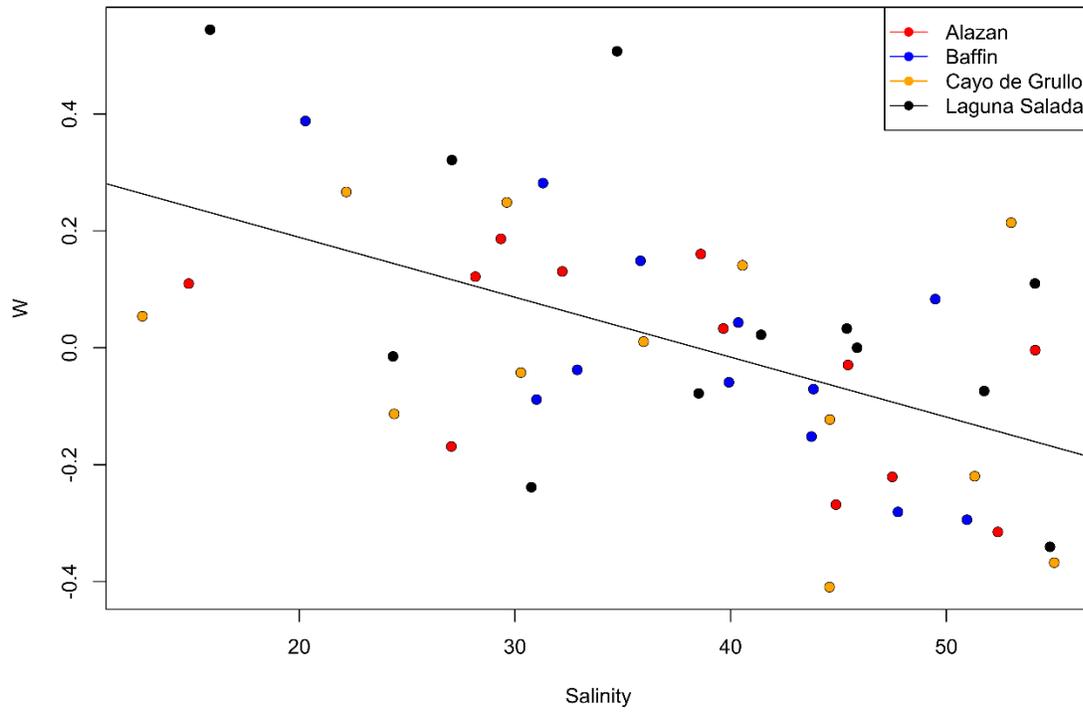


Figure 7.

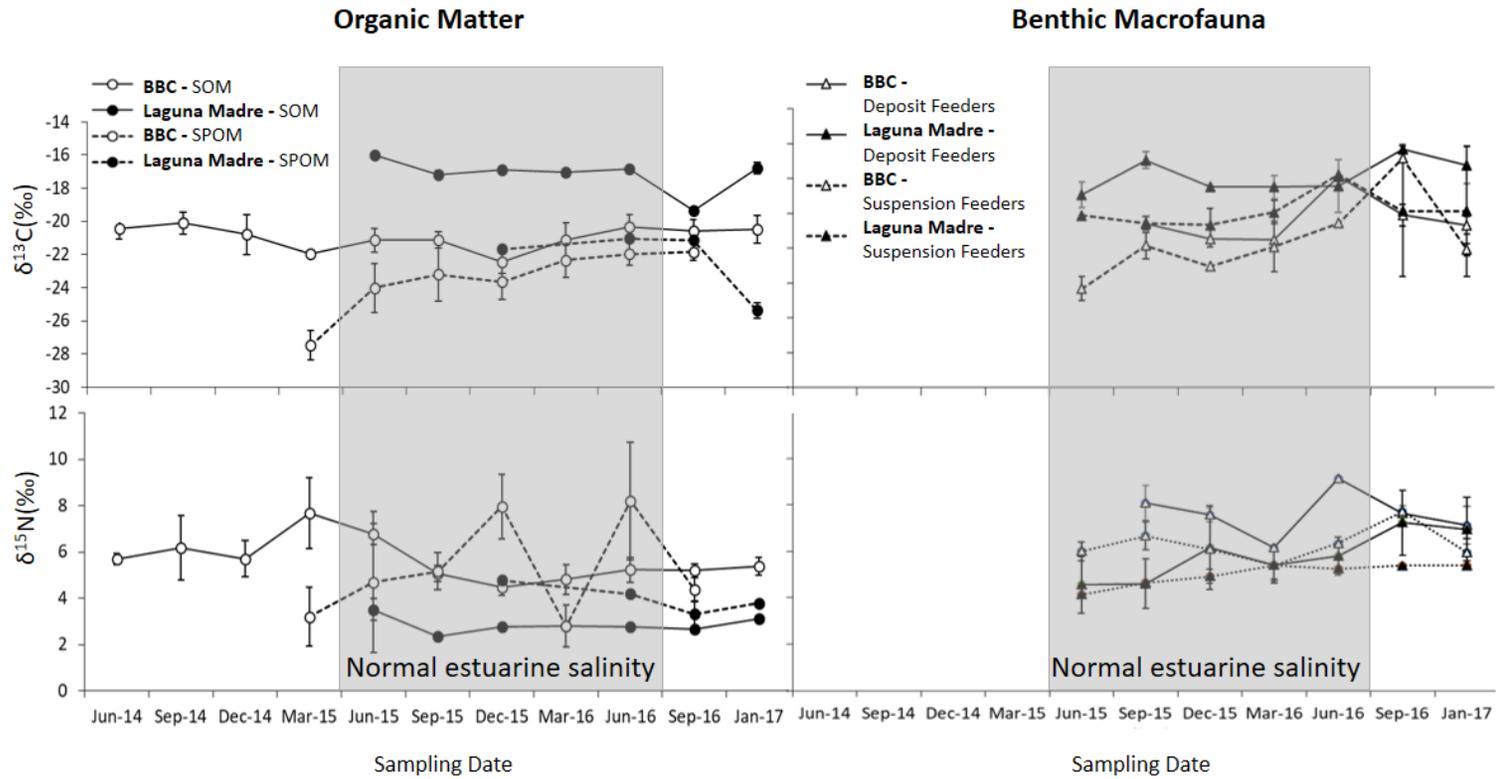


Figure 8.

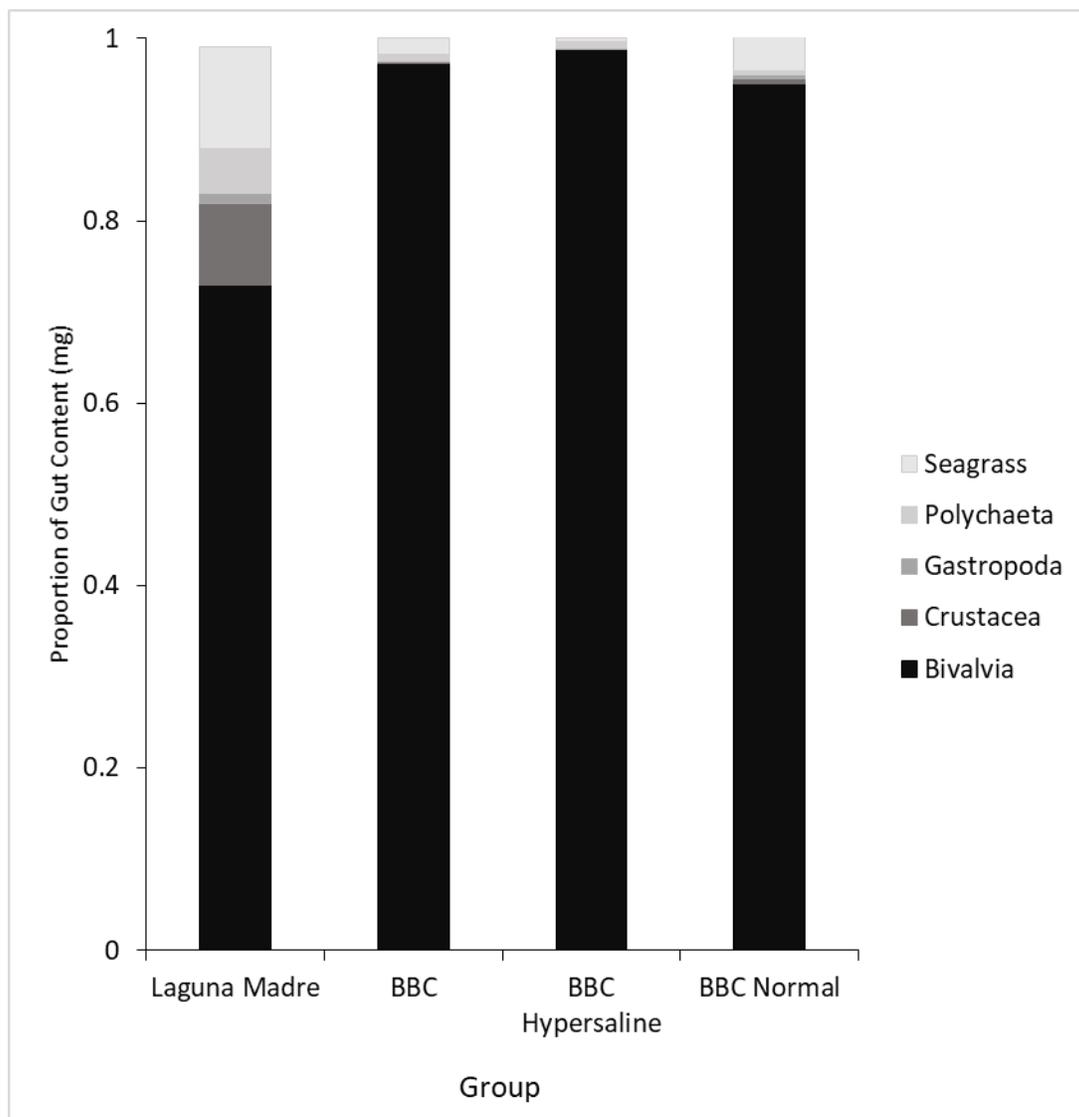


Figure 9.

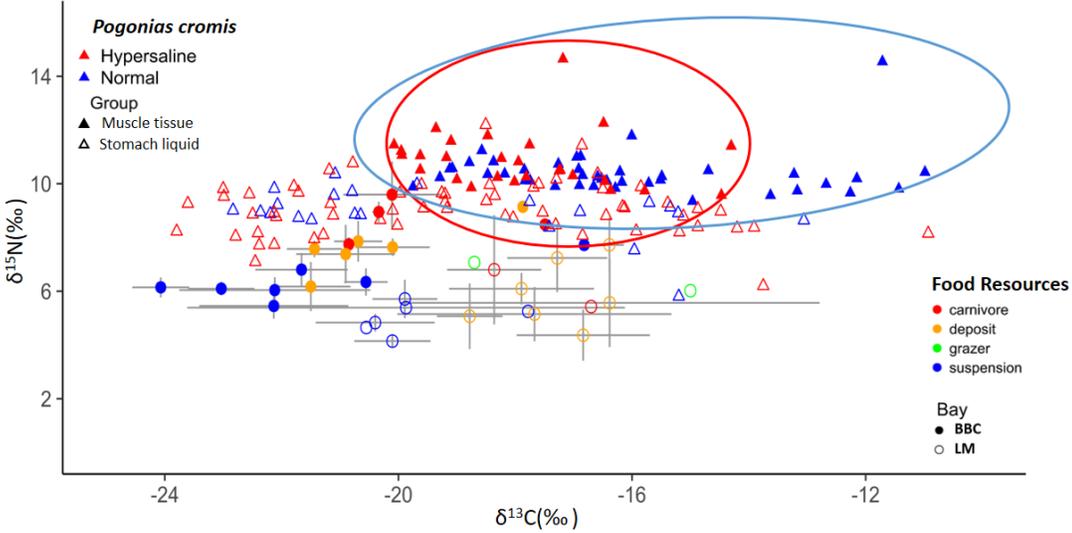


Figure 10.

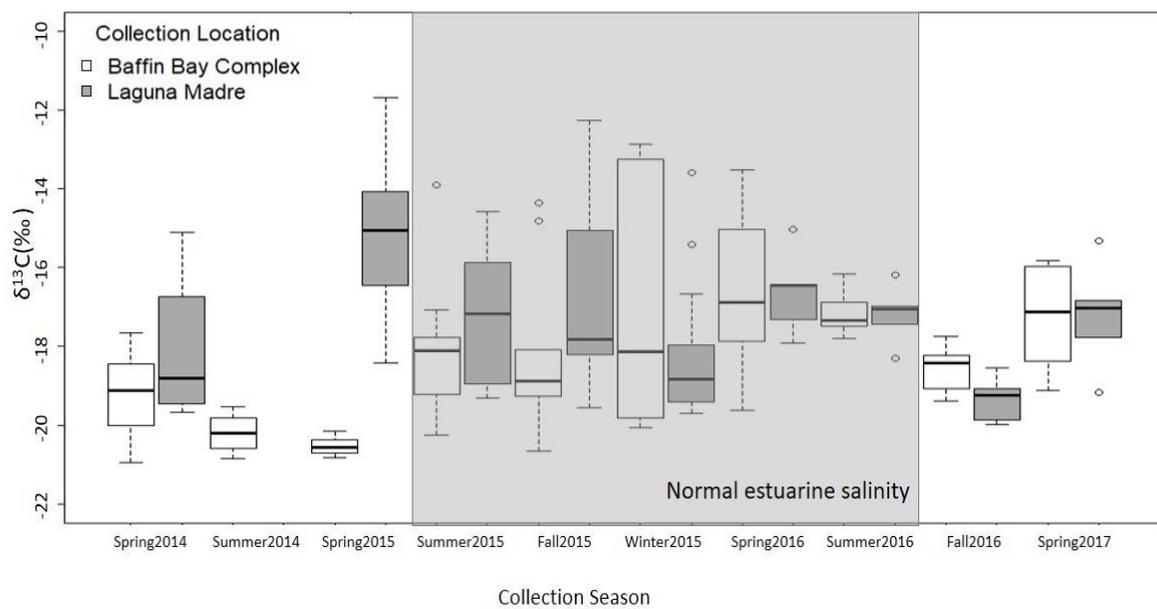
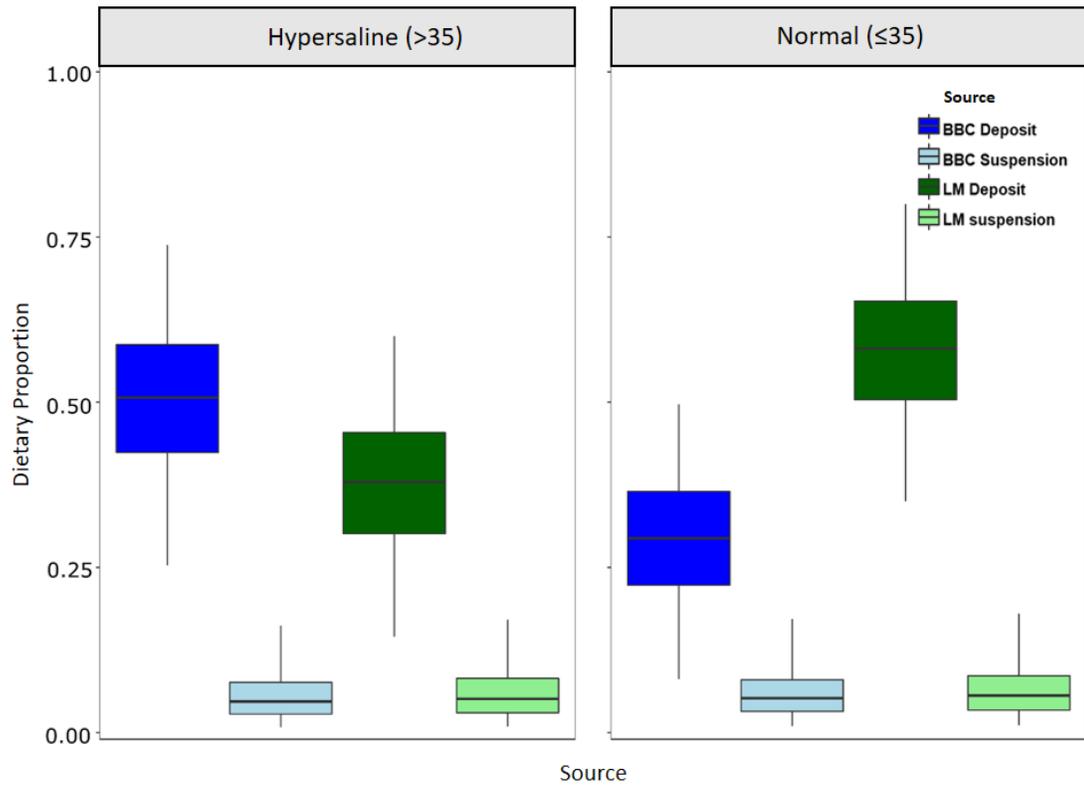


Figure 11.



APPENDICES

Appendix 1. Detailed results of BEST BIO-ENV procedure correlating water quality variables to macrofaunal community structure in the Baffin Bay Complex.

BEST

Biota and/or Environment matching

Data worksheet

Name: Data21
Data type: Environmental
Sample selection: 1-32,53-109,121-144
Variable selection: All

Resemblance worksheet

Name: Resem7
Data type: Similarity
Selection: 1-32,53-109,113-136

Parameters

Rank correlation method: Spearman
Method: BIOENV
Maximum number of variables: 5
Resemblance:
Analyse between: Samples
Resemblance measure: D1 Euclidean distance

Variables

1 Sal
2 changesal
3 Temp
4 DO
5 pH
6 secchi

Global Test

Sample statistic (Rho): 0.239
Significance level of sample statistic: 1%
Number of permutations: 99 (Random sample)
Number of permuted statistics greater than or equal to Rho: 0

Best results

No.Vars	Corr.	Selections
2	0.239	2,5
3	0.229	2,3,5
3	0.226	1,2,5
4	0.209	1-3,5
1	0.203	5
4	0.203	2,3,5,6
2	0.200	1,5
3	0.197	2,5,6
4	0.192	1,2,5,6
5	0.191	1-3,5,6

Outputs

Plot: Graph56

Appendix 2. Supplementary tables

Appendix 2.1. Taxa codes used to classify macrofauna collected in benthic cores and *P. cromis* stomach contents in Baffin Bay Complex and Laguna Madre samples.

Taxa Type	Taxa Code
Bivalvia	B
Bryozoa	BR
Crustacea	C
Cnidaria	CN
Echinodermata	E
Fish	F
Gastropoda	G
Mollusca	M
Nematode	ND
Nemertea	NE
Other	O
Oligochaeta	OL
Polychaeta	P
Pycnogonida	PY
Seagrass	SG
Sipunculid	S

Appendix 2.2. Mean macrofauna abundance (nm^{-2}) and biomass (gm^{-2}) of all species collected in benthic cores during sampling June 2014 to January 2017. BBC= Baffin Bay Complex, LM=Laguna Madre.

Taxa	Taxa Code	BBC nm^{-2}	LM nm^{-2}	BBC gm^{-2}	LM gm^{-2}
<i>Acteocina bidentata</i>	G	0	7	0.00	0.00
<i>Acteocina canaliculata</i>	G	74	41	0.00	0.07
<i>Acteon candens</i>	G	2	0	0.00	0.00
<i>Actiniaria spp.</i>	CN	9	68	0.01	0.00
<i>Ampeliscidae spp.</i>	C	62	0	0.00	0.01
<i>Ampharetidae spp.</i>	P	4	155	0.23	0.02
Amphipoda	C	108	1972	0.09	0.01
<i>Amygdalum papyrium</i>	B	5	34	0.04	0.02
<i>Anomalocardia auberiana</i>	B	291	189	0.05	0.17
<i>Armandia agilis</i>	P	19	621	0.13	0.00
Bivalvia	B	31	108	0.12	0.03
<i>Capitellidae spp.</i>	P	841	7111	0.44	0.05
<i>Caprellidae spp.</i>	C	5	0	0.00	0.00
<i>Cerithidae spp.</i>	G	1	108	0.16	0.00
<i>Chironomidae spp.</i>	O	1	0	0.00	0.00
<i>Columbellidae spp.</i>	G	0	7	0.00	0.00
Copepoda	C	41	642	0.01	0.02
<i>Crepidula convexa</i>	G	0	27	0.02	0.00
Crustacea	C	268	1209	0.04	0.01
Cumacea	C	22	34	0.00	0.00
<i>Dorveillidae spp.</i>	P	2	41	0.01	0.00
<i>Edotia spp.</i>	C	0	34	0.00	0.00
<i>Eulimastoma harbisonae</i>	G	50	7	0.00	0.03
<i>Eunicidae spp.</i>	P	0	14	0.00	0.00
<i>Exogone dispar</i>	P	4	5423	0.04	0.00
<i>Fargoa gibbosa</i>	G	29	0	0.00	0.01
Gastropoda	G	275	230	0.02	0.15
<i>Goniadidae spp.</i>	P	23	101	0.04	0.01
<i>Gyptis brevipalpa</i>	P	0	7	0.00	0.00
<i>Hargeria rapax</i>	C	2	0	0.00	0.00
<i>Holothuroidea</i>	E	0	7	6.77	0.00
Isopoda	C	0	81	0.01	0.00
<i>Laevicardium mortoni</i>	B	1	34	0.05	0.00
<i>Lyonsia hyalina</i>	B	7	0	0.00	0.01
<i>Mactrotoma fragilis</i>	B	7	41	0.21	0.02
<i>Maldanidae spp.</i>	P	1	1384	2.29	0.00

<i>Mitrella lunata</i>	G	2	0	0.00	0.00
<i>Mulinia lateralis</i>	B	522	601	0.93	2.44
<i>Mysidae spp.</i>	C	7	34	0.01	0.00
<i>Mytilidae spp.</i>	B	1	0	0.00	0.00
<i>Nassarius vibex</i>	G	1	0	0.00	0.03
Nemertea	NE	12	277	0.01	0.02
<i>Nemopsis bachei</i>	O	1	0	0.00	0.00
<i>Nereididae spp.</i>	P	3	20	0.02	0.00
Nudibranchia	G	0	7	0.00	0.00
<i>Odostomia spp.</i>	G	1	0	0.00	0.00
Oligochaeta	OL	9	5092	0.17	0.00
<i>Onuphidae spp.</i>	P	3	61	0.13	0.01
<i>Orbiniidae spp.</i>	P	24	486	0.11	0.01
Osteichthyes	F	0	7	0.00	0.00
Ostracoda	C	0	20	0.00	0.00
<i>Paraprionospio pinnata</i>	P	5	0	0.00	0.01
<i>Pectinariidae spp.</i>	P	15	81	0.07	0.02
<i>Perna perna</i>	B	0	7	0.00	0.00
<i>Phyllodoceidae spp.</i>	P	2	169	0.03	0.00
<i>Pista palmata</i>	P	1	7	0.00	0.00
Polychaeta	P	37	14	0.00	0.00
<i>Polydora cornuta</i>	P	1	41	0.00	0.00
<i>Porcellanidae spp.</i>	C	1	0	0.00	0.00
<i>Prionospio heterobranchia</i>	P	0	2060	0.10	0.00
<i>Prionospio pinnata</i>	P	3	14	0.00	0.00
Pycnogonida	PY	0	20	0.00	0.00
<i>Rissoella galba</i>	G	2	0	0.00	0.00
<i>Sabellidae spp.</i>	P	0	257	0.16	0.00
<i>Serpulidae spp.</i>	P	0	41	0.01	0.00
Sipunculid	S	0	81	0.59	0.00
<i>Sphaeromatidae spp.</i>	C	2	20	0.03	0.00
<i>Spionidae spp.</i>	P	1	95	0.01	0.00
<i>Streblospio benedicti</i>	P	2728	68	0.01	0.12
<i>Syllidae spp.</i>	P	0	2836	0.02	0.00
<i>Syllis cornuta</i>	P	0	0	0.00	0.00
Tanaidaceae	C	0	34	0.01	0.00
<i>Tellinidae spp.</i>	B	0	68	0.43	0.00
<i>Trypanosyllis gemmipara</i>	P	1	837	0.02	0.00
<i>Turbonilla spp.</i>	G	0	41	0.01	0.00
<i>Xanthidae spp.</i>	C	1	7	0.02	0.00

Appendix 2.3. Identifiable stomach contents from all *P. cromis* collected in the Baffin Bay Complex and the Laguna Madre from December 2013 to March 2017.

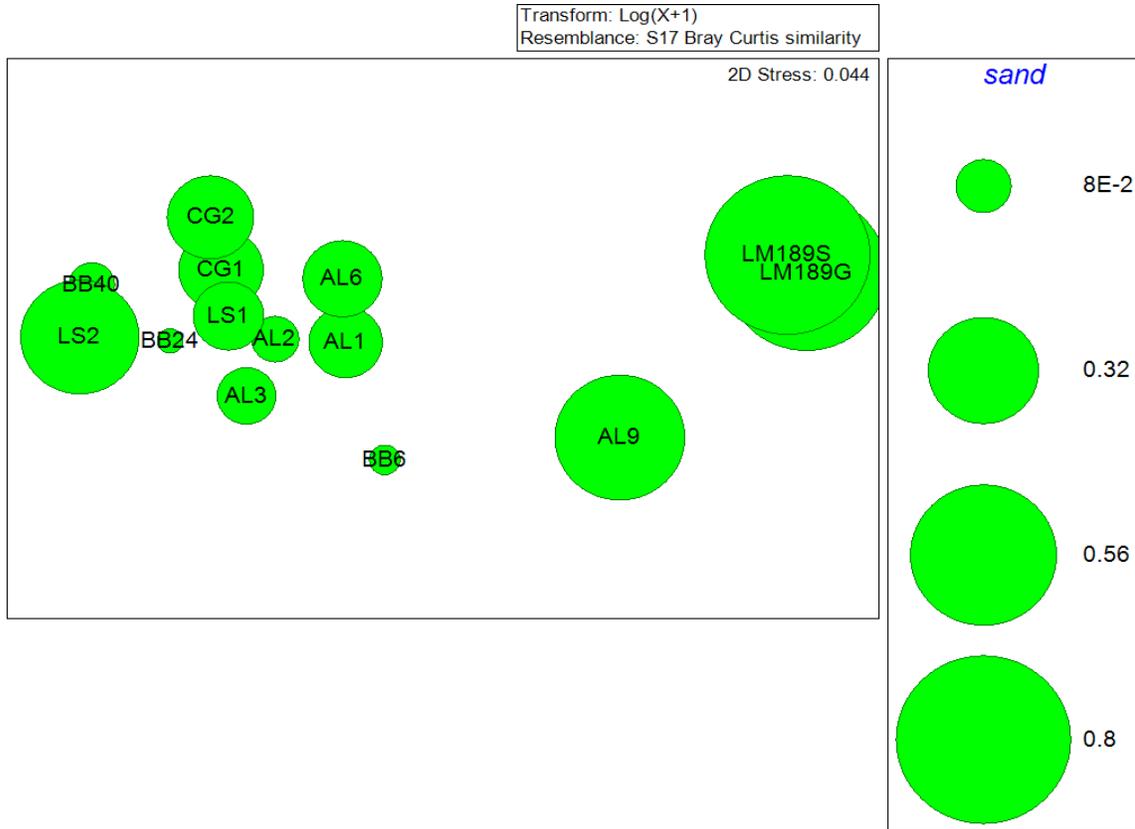
Species	Taxa Code	All Baffin Bay Fish		All Laguna Madre Fish	
		Frequency of Occurrence	Proportional Weight	Frequency of Occurrence	Proportional Weight
Bivalvia (unidentified)	B	0.59	0.91	0.67	0.71
<i>Anomalcardia auberiana</i>	B	0.20	0.03	0.35	0.01
<i>Amygdalum papyrium</i>	B	0.01		0.02	
<i>Atrina serrata</i>	B	0.01		0.03	
<i>Angulus tampaensis</i>	B	0.02		0.02	
<i>Chione cancellata</i>	B	0.01		0.02	
<i>Diplodonta semiaspera</i>	B	0.01		0.04	
<i>Laevicardium mortoni</i>	B	0.01		0.03	
<i>Mactrotoma fragilis</i>	B	0.01		0.12	
<i>Mulinia lateralis</i>	B	0.11	0.01	0.23	0.01
<i>Nuculana acuta</i>	B	0.01		0.03	
Gastropoda (Unidentified)	G	0.05		0.11	0.01
<i>Acteocina canaliculata</i>	G	0.02		0.04	
<i>Bittium varium</i>	G	0.01		0.06	
<i>Cerithium lutosum</i>	G	0.01		0.05	
<i>Caecum pulchellum</i>	G	0.01		0.02	
<i>Rissoina punctostriata</i>	G	0.01		0.02	
<i>Turbonilla elegans</i>	G	0.01		0.02	
Other Mollusca (Unidentified)	M	0.04	0.03	0.01	
Amphipoda	C	0.01		0.04	
Brachyura	C	0.03		0.12	0.09
Mysidae	C	0.01		0.02	
<i>Palaemonetes spp.</i>	C	0.01		0.02	
Pericarida	C	0.02		0.03	
<i>Portunidae spp.</i>	C	0.02		0.03	
Tanaidacea	C	0.01		0.02	
<i>Xanthidae spp.</i>	C	0.02		0.02	
Actinopterygii	F	0.04		0.09	

Nematoda	ND	0.04		0.07	
Oligochaeta	OL	0.02		0.02	
Polychaeta (Unidentified)	P	0.23	0.01	0.31	0.05
Serpulidae tubes	P	0.01		0.02	
Seagrass	SG	0.27	0.02	0.53	0.11
Bryozoa	BR	0.02		0.02	

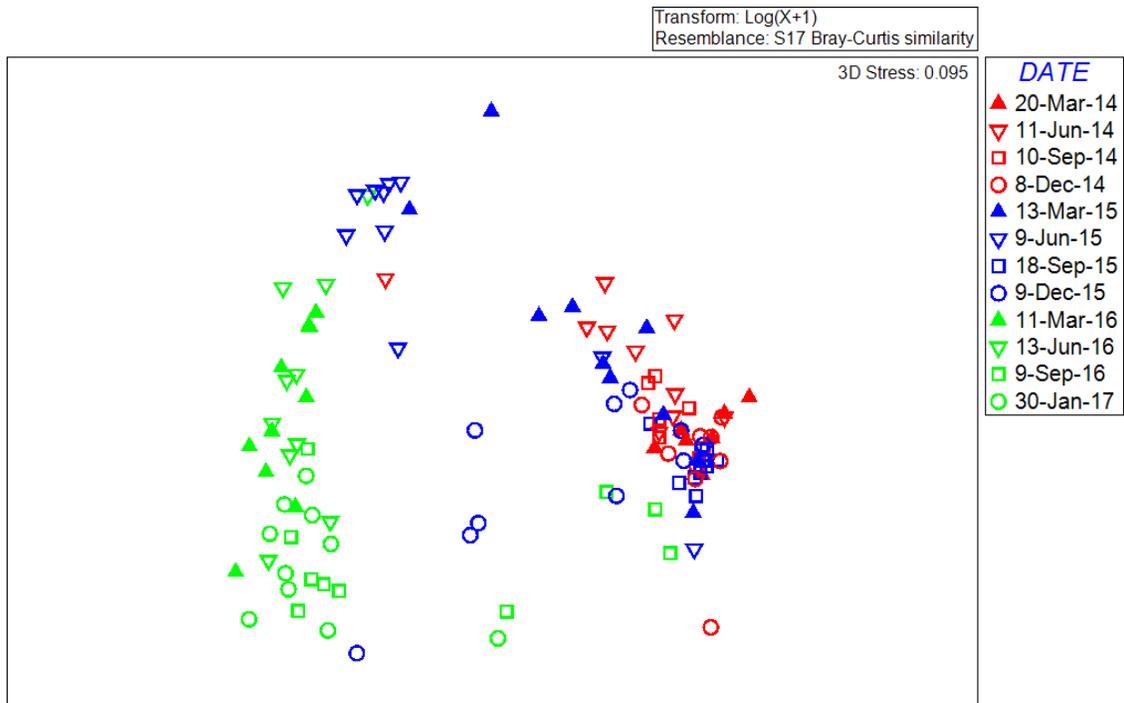
Appendix 2.4. Identifiable stomach contents from *P. cromis* collected in the Baffin Bay Complex from December 2013 to March 2017. *P. cromis* were collected under and are grouped by either normal (mean BBC-wide salinity ≤ 35) or hypersaline (mean BBC-wide salinity > 35) conditions.

Species	Taxa Code	Baffin Bay Normal Salinity		Baffin Bay Hypersalinity	
		Frequency of Occurrence	Proportional Weight	Frequency of Occurrence	Proportional Weight
Bivalvia (unidentified)	B	0.55	0.98	0.60	0.79
<i>Anomalcardia auberiana</i>	B	0.10	0.01	0.24	0.06
<i>Angulus tampaensis</i>	B	0.02			
<i>Mulinia lateralis</i>	B	0.10		0.09	0.02
Gastropoda (Unidentified)	G	0.02		0.05	
<i>Acteocina canaliculata</i>	G			0.01	
Other Mollusca (Unidentified)	M			0.07	0.07
Brachyura	C	0.02		0.01	
Pericarida	C			0.01	
<i>Portunidae spp.</i>	C			0.01	
<i>Xanthidae spp.</i>	C			0.01	
Nematoda	ND	0.02		0.03	
Oligochaeta	OL			0.01	
Polychaeta (Unidentified)	P	0.17	0.01	0.28	
Serpulidae tubes	P	0.00			
Seagrass	SG	0.18		0.30	0.04
Bryozoa	BR	0.02			

Appendix 3. Supplementary figures



Appendix 3.1. Non-metric multidimensional scaling plot of macrofaunal community structure in the Baffin Bay Complex and the Laguna Madre utilizing benthic data collected June 2015-January 2017 and averaged by site. Size of green circle represents proportion of sand in sediment composition from 2015-2016 grain size analysis.



Appendix 3.2. Non-metric multidimensional scaling plot of macrofaunal community structure in the Baffin Bay Complex utilizing benthic data collected March 2014-January 2017. Ten long-term sampling sites were included in analyses. Year of sampling is indicated by color, season is indicated by shape.