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Moving Forward in a Reverse Estuary: Habitat Use and Movement Patterns of Black Drum (*Pogonias cromis*) Under Distinct Hydrological Regimes

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Abstract

Understanding the effects of freshwater inflow on estuarine fish habitat use is critical to the sustainable management of many coastal fisheries. The Baffin Bay Complex (BBC) of south Texas is typically a reverse estuary (i.e., salinity increases upstream) that has supported many recreational and commercial fisheries. In 2012, a large proportion of black drum (*Pogonias cromis*) landed by fishers were emaciated, leading to concerns about the health of this estuary. In response to this event and lacking data on black drum spatial dynamics, a 2-year acoustic telemetry study was implemented to monitor individual-based movement and seasonal distribution patterns. Coupled with simultaneous water quality monitoring, the relationship between environmental variables and fish movement was assessed under reverse and "classical" estuary conditions. Acoustic monitoring data suggested that the BBC represents an important habitat for black drum; individuals exhibited site fidelity to the system and were present for much of the year. However, under reverse estuary conditions, fish summertime distribution was constrained to the interior of the BBC, where food resources are limited (based on recent benthic sampling), with little evidence of movement across the system. Out of eight environmental variables used to model fish movement using multiple linear regression, the only significant variable was salinity, which exhibited a negative relationship with movement rate. These findings suggest that prolonged periods of hypersalinity, which are detrimental to other euryhaline species due to increased osmoregulatory costs, reduce black drum distribution patterns and can limit the species' access to benthic habitats supporting abundant prey resources.

Keywords Fisheries · Estuarine systems · Telemetry · Movement · Habitat use

Introduction

Estuarine dependence and habitat connectivity in many fish populations is dependent on freshwater inputs into coastal estuaries (Able 2005). Freshwater inflow affects salinity, which plays a vital role in structuring estuarine fish assemblages (Barletta et al. 2005, Jenkins et al. 2015), and can affect the movement or distribution of individual species (Sakabe and Lyle 2010). However, previous research has historically focused on river-dominated (i.e., classical) estuaries where salinities decrease upstream. Although reverse estuaries, where salinities decrease downstream, occur worldwide (de Silva Samarasinghe and Lennon 1987; Mikhailov and Isupova 2008), information regarding the population dynamics of fish in these systems is lacking (Vorwerk et al. 2009).

Texas' Upper Laguna Madre (ULM; Fig. 1) is a predominantly hypersaline lagoon that receives minimal freshwater discharge from surrounding terrestrial sources (Tunnell and Judd 2002). The ULM is separated from the Gulf of Mexico by Padre Island, one of the world's most extensive barrier island systems (Tunnell and Judd 2002). This physiography, combined with the semi-arid climate of the region, produces persistent reverse estuarine conditions within the ULM. The Baffin Bay Complex (BBC) is a 248-km^2 ecosystem stemming from the ULM (Fig. 1) and comprises Baffin Bay proper, Alazan Bay, Cayo de Grullo, and Laguna Salada sub-regions (Fig. 1c). Depending

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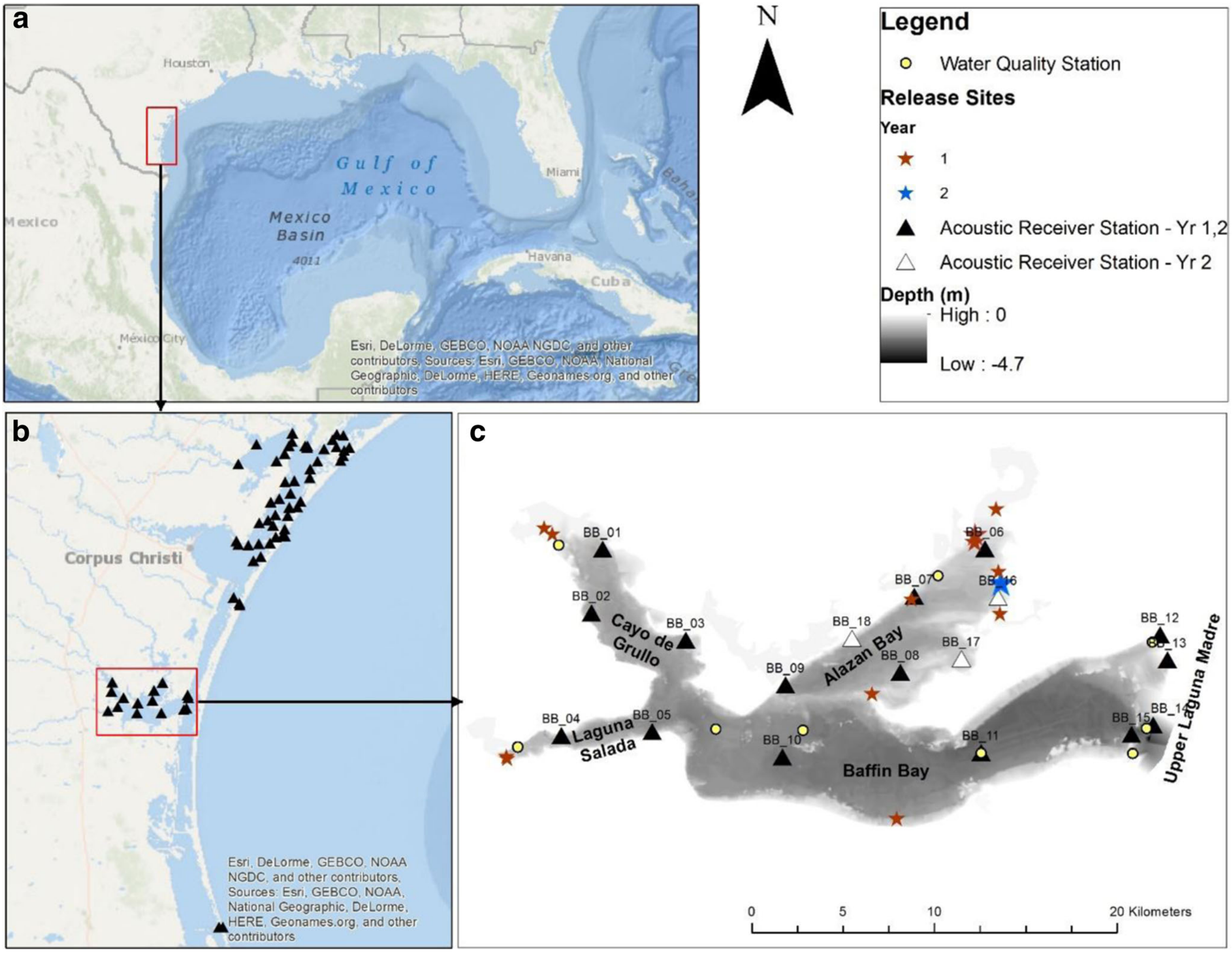

Fig. 1 Map of the study region including an overview of the location relative to the Gulf of Mexico (**a**), south Texas and the larger Texas Acoustic Array Network (**b**), and a zoomed in map of the Baffin Bay Complex (**c**). Acoustic receiver stations for years 1 and 2 (white triangles) and year 2 additions (black triangles) are overlain onto a digital elevation model depicting the bathymetry of the complex. Fish release locations are shown for year 1 (maroon stars) and year 2 (blue star)

on rainfall levels, freshwater inflow to BBC is delivered at highly variable rates via ephemeral discharges from Petronila, San Fernando, and Los Olmos creeks and submarine groundwater discharges (Uddameri et al. 2014). Salinities twice that of seawater can be encountered shoreward near inland creeks and tributaries of the BBC. While relatively isolated from large population centers, the BBC is not devoid of anthropogenic pressures; the estuary has been trending towards eutrophication with more persistent blooms of brown tide phytoplankton (*Aureorumba lagunensis*) (Wetz et al. 2017).

Despite these unique characteristics, the region supports recreational and commercial fishing. For example, the BBC is particularly popular for black drum, *Pogonias cromis* (Cornelius 1984). While the black drum is euryhaline and found throughout Texas bay systems and nearshore areas of the Gulf of Mexico, fishery-independent monitoring data indicate that the BBC supports the highest black drum abundances along the entire Texas coast, with levels steadily increasing since the 1980s and stabilizing over the last decade (Olsen 2014). Black drum of this region also reach sexual maturity at 2–3 years compared to 4–6 years in individuals from other regions of Texas (Bumguardner et al. 1996), suggesting substantial resources are available to promote early reproductive development. The diet of black drum from this region includes a wide variety of benthic invertebrates such as bivalves and polychaetes (Mendenhall 2015). Spawning is widespread among bays, inlet passes, and nearshore regions of the Gulf of Mexico and primarily occurs during early to late winter (February to March), although split spawning has been suggested with a second period occurring between May and June (Simmons and Breuer 1962; Nieland and Wilson 1993). While mark-recapture data indicate that fish generally return to their original location after spawning, there is no information as to whether this behavior applies to fish from the BBC.

In 2012, a large proportion of black drum landed by both recreational and commercial fisheries of the BBC exhibited abnormal physical characteristics. These included below average weights and transparent tissue morphology (Olsen et al. 2014). The factors explaining these abnormal characteristics could be numerous and are unknown, but are likely due to some degree of resource limitation. For example, black drum catch rates over time indicate abundances have stabilized at maximum levels in the BBC, which has been proposed as the population reaching its carrying capacity (Olsen et al. 2014; Olsen 2016). With few predators to control black drum populations in the hypersaline waters of the ULM and hypothesized regional fidelity (Osburn and Matlock 1984), it is plausible that these abundance levels may have led to intra-specific competition for resources.

Alternatively, or perhaps coincidentally, altered water quality may have played a role in black drum physiological ecology or access to food resources. For example, experimental studies suggest that hypersalinity can increase osmoregulatory costs in euryhaline fishes, which respond by reducing metabolic rate and thus activity levels (Swanson 1998; Aragão et al. 2010). Such responses may lead to reduced ability to encounter profitable habitats. Intermittent hypoxia, which has been observed in Baffin Bay in recent years (Wetz et al. 2017 data), has also been shown to concentrate demersal sciaenid fish in suboptimal (prey-deficient) habitats (Eby et al. 2005). Such an array of potential mechanisms warrant an understanding of the dynamics of black drum habitat use in this estuary, including the impact of environmental conditions on residency and movement patterns, as suggested by Olsen (2016).

In this study, individual-based movement and distribution patterns of black drum were monitored using acoustic telemetry over a 2-year period in the BBC. Our goal was to improve our scientific understanding of how this fishery species uses the BBC seasonally and under various environmental conditions in order to retrospectively identify potential drivers of the emaciation event in 2012. Because the monitoring period straddled 2 years of divergent levels of freshwater input, there was opportunity to compare fish movement patterns under distinct regimes (i.e., reverse vs. classical estuary), which in turn revealed differential use patterns important to managing this fishery.

Methods

Specimen Collection and Tagging

Between spring 2014 (April 23–May 20) and 2015 (April 19), 36 total adult black drum were collected for acoustic tagging procedures (Table 1). Individuals were captured using 15.2 cm monofilament gillnets (30 min maximum soak) as well as opportunistic hook-and-line sampling. All individuals were measured for total length (TL, 0.1 cm), weighed (to nearest 0.1 kg), and fitted with a yellow or green dart tag (Floy Tag, Inc.) with an identification number and contact information to report recaptures. Fish in suitable condition (no bleeding, no deep hooking, normal coloration, etc.) underwent surgery for implantation of a Vemco © V13 coded acoustic transmitter following a university-approved animal use protocol (AUP #09-14, Texas A&M University-Corpus Christi). Transmitters (model# V13-1H-069 k-1) had a 45-s nominal delay (range = 30–90 s) and transmitted on high power, resulting in a battery life of 362 days. During surgery, fish were submerged and inverted within a tank containing aerated ambient seawater. A small incision (2.0 cm) was made into the peritoneal cavity offset from the ventral mid-line for transmitter placement. Once the transmitter was inserted, the incision was closed with two interrupted Vicryl sutures using surgeon's knots (Reese Robillard et al. 2015). Fish were revived alongside the capture vessel and allowed to swim freely once signs of full recuperation were evident. In 2014, individuals ($n = 25$, mean TL = 43.1 ± 2.2 cm) were released in various sub-regions of the BBC (but predominantly Alazan Bay), while 2015 deployments ($n = 11$, mean TL = 48.4 ± 0.7 cm) were restricted to Alazan Bay (Fig. 1c). There were no significant differences in mean TL of acoustically tagged individuals between sampling years (Two-sample t test, $t = -1.529$, $d.f. = 34$, $P = 0.136$).

Acoustic Monitoring

In April 2014, an array of 15 moored acoustic receivers (Vemco VR2W) was deployed throughout the BBC to remotely monitor presence and absence of acoustically tagged black drum (Fig. 1). Due to the large size of the BBC, the array was arranged in a broad "fisheries" format to maximize coverage in various sub-regions (Heupel et al. 2006). Acoustic receivers were either mounted to vertically set PVC poles secured to the sediment (shallow regions < 1.5 m depth; $n = 10$) or attached to channel markers in regions of deeper depths and inlet passes (> 3.0 m; $n = 5$). In both cases, receivers were oriented with hydrophone transducers pointed towards the surface at approximately 0.5 m off the bottom. An additional three receivers were added to Alazan Bay in April 2015 to enhance coverage in this larger sub-region. Throughout the study period, a larger array of acoustic receivers was in place in several adjacent regions outside of BBC (Fig. 1b) to monitor individuals that left the system and to establish potential connections with other water bodies along the south Texas coast (Corpus Christi Bay, Mansfield Pass, Packery Channel, and Aransas Pass). This broader scale array, the Texas Acoustic Array Network (TEXAAN), had the ability to track animals on the order of 100 s of kilometers if necessary. Data were downloaded from BBC receivers at approximately 4-month intervals beginning in August 2014 and ending in April 2016.

Table 1 Summary information for all individuals collected and acoustically tagged throughout the study

Capture date	Collection gear	Total length (mm)	Weight (kg)	Tag ID	Last detection date	Detection periods (days)	Total detections	Sub-regions detected				
								AL	BB	CDG	LS	LM
4/23/2014	GN	538	2.20	1	5/3/2014	10	312					X
4/23/2014	GN	505	1.70	2	5/10/2014	18	48		X			
4/23/2014	GN	460	1.40	3	4/9/2015	351	135	X	X			X
4/23/2014	GN	375	0.70	*NA*	*NA*	*NA*	0					
4/23/2014	GN	476	1.40	4	4/29/2014	7	174		X			X
4/23/2014	HL	362	0.70	*NA*	*NA*	*NA*	0					
4/23/2014	GN	478	1.75	5	4/25/2014	3	33		X			
4/24/2014	GN	514	2.30	6	4/25/2014	1	14				X	
4/25/2014	GN	367	0.75	7	4/26/2015	367	4041	X	X	X		
4/25/2014	GN	461	1.50	8	4/26/2014	1	67		X			
4/25/2014	GN	347	0.70	9	12/19/2014	238	3843		X		X	
5/14/2014	GN	372	0.70	10	3/31/2015	322	8820	X	X	X	X	
5/15/2014	HL	369	0.75	11	11/6/2014	175	225	X				
5/15/2014	HL	418	1.00	12	4/23/2015	343	1168	X			X	
5/15/2014	HL	391	0.85	13	5/15/2015	365	2316	X	X	X		X
5/15/2014	GN	412	1.10	14	3/13/2015	302	2133	X	X			X
5/15/2014	GN	371	0.80	15	8/24/2014	102	1011	X				
5/15/2014	GN	351	0.60	16	5/15/2014	1	28	X				
5/15/2014	GN	354	0.70	17	5/17/2015	367	2783	X	X	X	X	X
5/15/2014	GN	375	0.75	18	9/21/2014	130	1078	X	X	X	X	
5/15/2014	GN	888	11.10	19	5/19/2015	369	237	X	X	X	X	X
5/15/2014	GN	345	0.75	20	5/16/2014	2	176			X		
5/15/2014	HL	370	0.70	21	2/25/2015	287	2198	X		X	X	
5/20/2014	GN	489	1.75	22	5/20/2014	1	7	X				
5/20/2014	GN	382	0.75	23	5/24/2014	4	38	X	X			
4/19/2015	GN	495	2.50	24*	9/13/2015	147	2012	X				
4/19/2015	GN	506	2.00	25	4/20/2016	368	10,642	X	X	X	X	
4/19/2015	GN	472	1.70	26	4/21/2016	369	6435	X	X	X	X	X
4/19/2015	GN	508	2.00	27	10/28/2015	193	2075	X	X	X	X	
4/19/2015	GN	503	2.00	28	4/1/2016	349	1773	X	X			X
4/19/2015	GN	441	1.70	29	4/19/2016	367	10,648	X	X	X	X	X
4/19/2015	GN	471	1.75	30	4/14/2016	362	7350	X	X	X	X	X
4/19/2015	GN	487	1.90	31	4/20/2016	368	7345	X	X	X	X	X
4/19/2015	GN	494	1.90	32	9/13/2015	148	4238	X	X	X	X	
4/19/2015	GN	440	1.40	33	2/11/2016	298	7456	X	X	X	X	X
4/19/2015	GN	502	2.20	34	4/12/2016	360	3341	X	X			X

Two individuals collected and tagged on 4/23/2014 were never detected and therefore were not given a Tag ID

*An individual whose transmitter was recycled from the previous year after recapture of tag 1

Range tests were performed on two representative receiver stations (one shallow PVC mount, one deep channel marker) to evaluate system performance. During the test, a range test tag (20 s burst interval) was deployed at various intervals from the acoustic receivers from 50 to 1000 m. Each interval was tested for approximately 5 min. Acoustic receivers were downloaded immediately afterwards and expected detections were compared to actual detections. Following Kessel et al. (2014), the proportion of detections received was then plotted against the distance between the range test tag and the receiver to estimate an effective range at 50% detection probability (Kessel et al. 2014).

Black drum acoustic data were imported to a database and plotted on a time-series to examine temporal movement patterns among various sub-regions of the BBC. The first analysis entailed an examination of individual-specific residency days at the various receiver sites. A residency day was considered a day in which a receiver received greater than two detections. Given the non-parametric nature of the data set and violations of normality, variation in residency was pooled by region (Alazan Bay, Baffin Bay, Cayo de Grullo, Laguna Salada, and Upper Laguna Madre) and statistically compared with a Kruskal-Wallis test.

To evaluate impacts of season on fish mobility, all net individual rates of movement were estimated. Given the non-overlapping detection ranges of the receivers due to the widely spaced array configuration, movement rates were calculated for each individual from consecutive detections between two different receivers. Distance traveled was assumed to be the shortest path between stations, which was divided by the difference in time (i.e., days) between the last detection at the first receiver and the first detection at the second receiver. In cases where there was no direct line-of-sight between two receivers (i.e., land impedance), minimum paths were manually drawn and calculated in ArcGIS 10.0 (ESRI, Inc.). For each individual, a minimum rate of movement (ROM_{min}) was determined for each month of the study. These indices were compared among months and monitoring years using two-way ANOVA, with individuals as replicates. Due to increased numbers of receivers (i.e., BB-16:BB-18) in Alazan Bay in year 2, these data were not used for these statistical analyses for consistency.

Water Quality Data

Water quality sampling was conducted on a monthly basis at nine sites in Baffin Bay (Fig. 1c). At each site, a profile of salinity, temperature, conductivity, dissolved oxygen, and pH was obtained by lowering a YSI ProPlus sonde at 0.5 m increments through the water column. Discrete samples were collected for chlorophyll *a* and turbidity. For determination of chlorophyll concentrations, a known volume of water sample was gently (≤ 5 mmHg) filtered through Whatman 25 mm GF/F filters that were then stored frozen until analysis. Chlorophyll *a* was extracted from the filters by soaking for 18–24 h in 90% HPLC-grade acetone at − 20 °C, after which chlorophyll *a* was determined fluorometrically with a Turner Trilogy fluorometer without acidification. Turbidity was determined from water samples that were collected and analyzed within 24 h according to EPA Method 180.1 (EPA 1993).

A multiple linear regression analysis was conducted to evaluate the relationship between various environmental parameters and black drum movement. Independent variables (averaged between surface and bottom samples and across the BBC) used in the regression model included temperature, salinity, dissolved oxygen, monthly rainfall, mean chlorophyll *a*, turbidity, and pH. The dependent variable was monthly mean ROM_{min} values from across the BBC. Prior to analysis, data were checked for linear model assumptions of normality and homogeneity of variances. If multicollinearity was encountered (i.e., variance inflation factor > 5), variables were removed systematically from the model and the test was rerun until no multicollinearity was reported. An α value of 0.05 was used for statistical significance.

Results

Environmental Conditions

Monthly water quality sampling revealed dynamic environmental conditions that varied considerably over the project period (Fig. 2). In the first sampling year, the BBC was hypersaline (> 40 psu, Fig. 2a) and exhibited reverse estuarine conditions; salinities increased upstream from the mouth of the system at the Upper Laguna Madre to the tributaries and ranged from 40.2 to 63.6. In August 2014, water temperatures exceeded 30 °C throughout the BBC (Fig. 2b). This month was also characterized by the highest mean salinities (54.7), with two upstream stations exceeding 60 in Alazan Bay and Laguna Salada. A strong cold weather event in November 2014 brought surface water temperatures below 12 °C, although this was short-lived (Fig. 2b). Salinities remained stable through winter followed by a considerable decrease over 4 months beginning in March 2015 and lasting until June 2015. This drop was concomitant with heavy rainfall in the region ranging from 277 to 487% higher than normal, ending multi-year drought conditions (http://www.weather.gov). During this period, the salinity gradient reversed and increased in a downstream manner towards the Upper Laguna Madre, inverting the system to classical estuarine conditions. In June 2015, salinities ranged from 16.6 to 52.6 lower than the previous year (Fig. 2a), with salinities recorded as low as 1.9 in Cayo De Grullo and as high as 26.2 in the Upper Laguna Madre. Salinities began to moderate from the late summer through fall and stabilized in winter of 2016. Another major rainfall event occurred in March 2016, which brought extreme changes in salinities to Cayo de Grullo and Alazan Bay.

Range Test

Shallow and deep acoustic receivers performed differently in range tests, but were slightly improved from ranges previously classified in the region (Payne 2011). For the receiver in shallow water (1.0 m), detection efficiency was 100% at 300 m, and then sharply dropped to 0% from 500 to 1000 m. As such, effective range (50% detection probability) was estimated at 400 m for shallow receivers. For receivers on channel markers in deep water (4.0 m), detection efficiency declined more linearly with distance from transmitter. Transmissions were

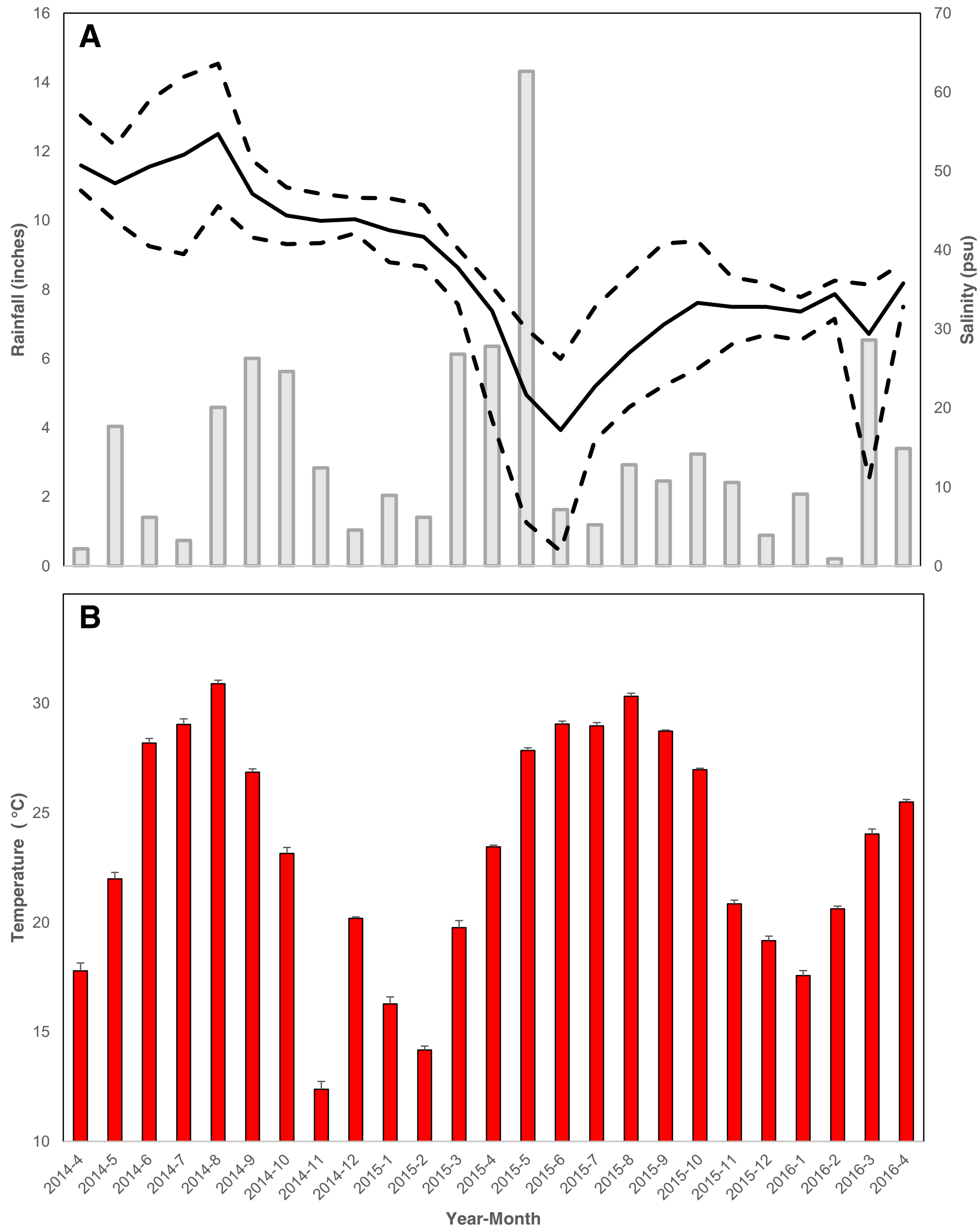

Fig. 2 Plots of monthly environmental conditions across the Baffin Bay Complex. **a** Rainfall from Corpus Christi (source: weather.gov) are depicted by bars, while line plots indicate mean (solid black) and maximum and minimum (dashed black) salinity. **b** Monthly mean temperature and standard error

detected out to 750 m, with an effective range of approximately 550 m.

Year 1 Detection Patterns

Over the course of an entire year of monitoring, 23 of 25 (92%) of acoustically tagged black drum were detected for a total of 30,351 detections across the 15 receiver stations. Detection period (from the first to last detection within the array) ranged from 1 to 369 days. Tags 1, 4, 5, 6, 8, 16, 20, 22, and 23 were all detected for less than 10 days (Table 1), and two individuals released in Alazan Bay on 23 April 2014 were never detected. The fish with tag 1, which was immediately detected along Upper Laguna Madre receivers at the mouth of the BBC and nowhere else thereafter, was the only individual recaptured by a recreational angler (on 25 November 2014). The remaining individuals were detected across multiple embayments in the BBC. The station receiving the greatest number of detections in year 1 was BB_03, which was situated in the southeastern portion of Cayo De Grullo. While six individuals were detected at this station, nearly all detections (i.e., 95%) came from two individuals, which were primarily detected in the region during summer months. Other regions of high activity (> 2000 detections) included a Laguna Salada station (BB_05) and Alazan Bay stations BB_06–07. The greatest number of tagged individuals was recorded at BB_06–07 ($n = 11$), although these stations were situated closest to the release sites in Alazan Bay.

In year 1, many individuals conducted inter-bay movements throughout the BBC, although only two individuals were detected in all five regions. The majority of these habitat transitions, and thus wider detection distributions, occurred in spring and fall of 2014 (Fig. 3). Inter-bay movements were overall minimized and restricted to within the three major tributaries during the summer, when large amounts of detections were recorded at the interface of Cayo De Grullo and Laguna Salada (Fig. 4a) with generally no animals detected at Upper Laguna Madre or Baffin Bay sites between June and September (Fig. 3). During October and November, Baffin Bay "proper" use appeared to increase, with fish distribution beginning to spread eastward. No individuals were detected on acoustic receivers situated along the Texas coastal-bend area, outside the BBC.

Year 2 Detection Patterns

In year 2, all 11 individuals tagged were detected by acoustic receivers for a total of 63,315 detections from 18 receiver stations. Among individuals, detection periods ranged from 147 to 369 days. Although released from the same site in Alazan Bay, with the exception of one individual that was fitted with a recovered transmitter, all tagged fish exhibited inter-bay movements beginning in May 2015. As in year 1, detections were considerably greater in the three major tributaries of the BBC compared to Baffin Bay proper and the Upper Laguna Madre. The greatest number of overall detections was recorded at station BB_16, which was adjacent to the release site. However, within the three tributaries, detection patterns were overall relatively homogenous compared to year 1.

In year 2, five of ten individuals fitted were detected across all sub-regions of the BBC, and three additional individuals were detected in all but one sub-region. Fish movement patterns were initially synchronized, with several individuals simultaneously leaving Alazan Bay and moving into Baffin Bay interior during early June and dispersing from thereon across Cayo De Grullo and Laguna Salada throughout the summer period with periodic exchanges between those sites and Alazan Bay (Fig. 3). Similar to the previous year, most of the summer activity was restricted to interior of the BBC, although spread over a much wider area (Fig. 4b). The fall period captured several individuals around Baffin Bay proper as well as the Laguna Madre. Departures from the BBC via the Upper Laguna Madre were likely for several individuals between fall 2015 and winter 2016, most of which appeared to return to the interior tributaries of the BBC via the Upper Laguna Madre by early spring. Similar to year 1, in year 2 no individuals were detected on acoustic receivers situated along the Texas coastal-bend area outside the BBC.

Residency and Movement Rates

Overall black drum residency varied significantly by region within the BBC throughout the study period (Kruskal-Wallis Test, $H = 46.670$; d.f. = 4, $P < 0.001$). Subsequent pairwise comparisons using Dunn's Method found significantly higher residency in Laguna Salada than Laguna Madre ($Q = 3.826$, $P = 0.001$), Baffin Bay proper ($Q = 3.734$; $P = 0.002$), and Alazan Bay ($Q = 3.146$; $P = 0.017$). Similarly, black drum residency was significantly higher in Cayo de Grullo than Laguna Madre ($Q = 3.515$; $P = 0.004$) and Baffin Bay proper

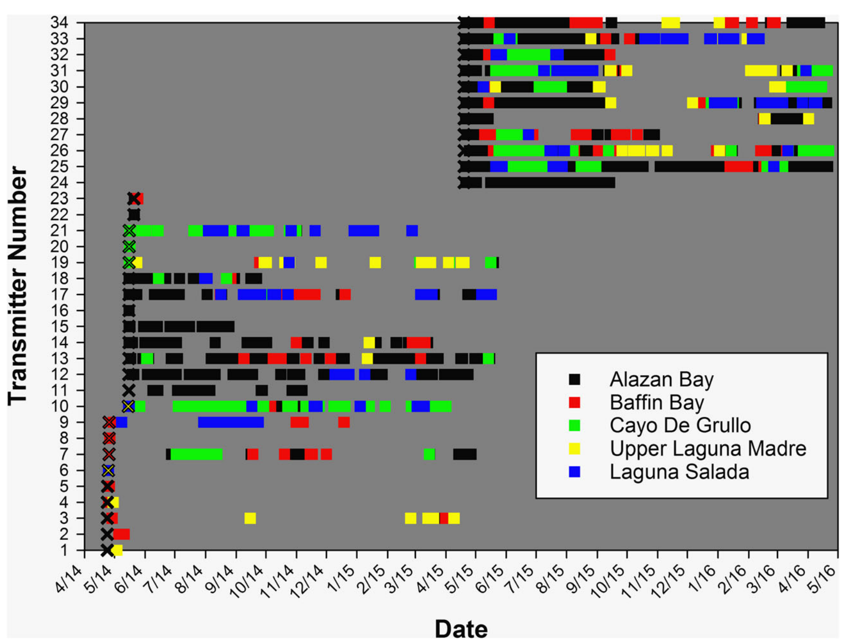

Fig. 3 Abacus plot of detection data by individual (transmitter number) over time. Color codes for sub-region categories are listed in the legend

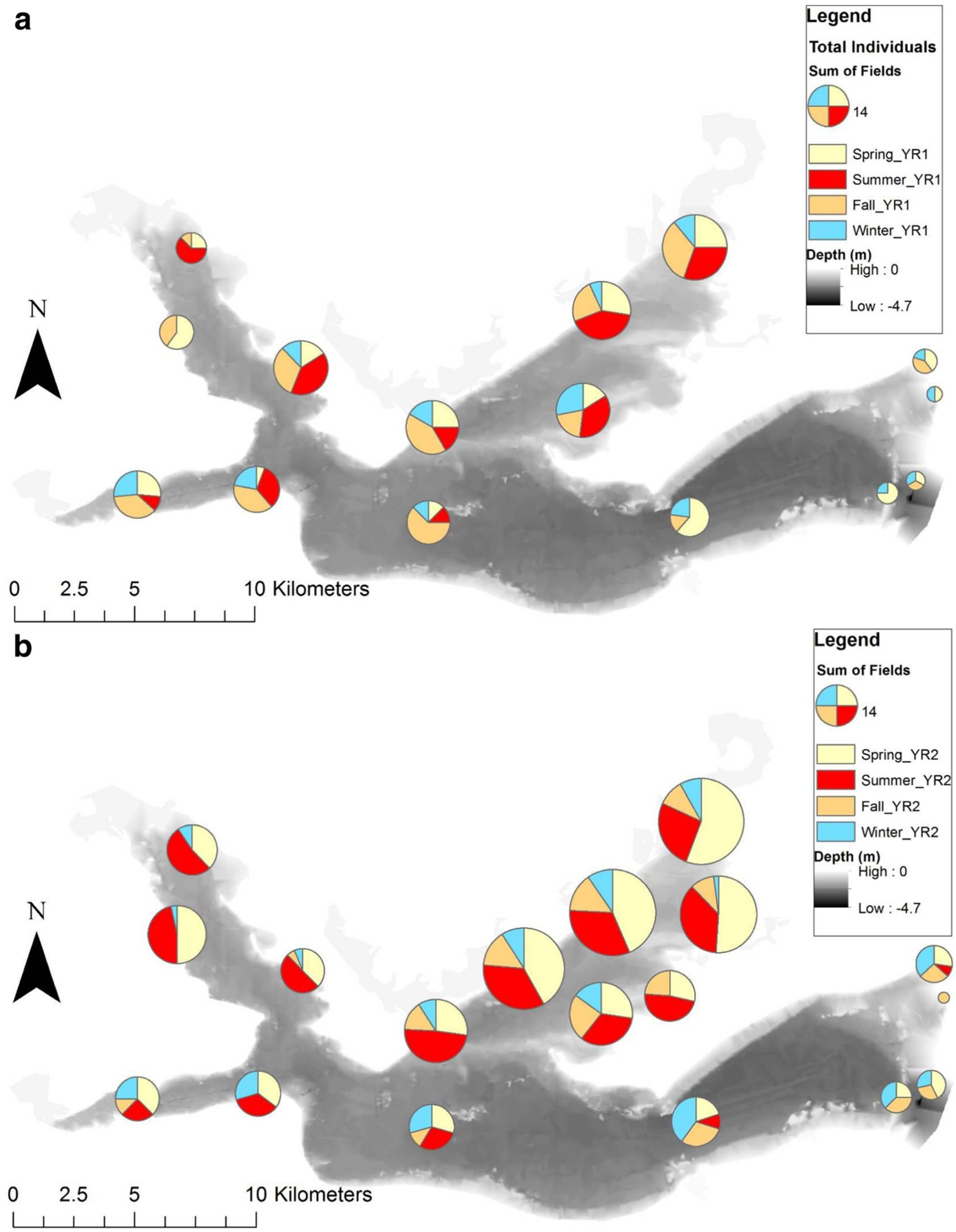

Fig. 4 Maps of numbers of tagged individuals detected by season for year 1 (**a**) and year 2 (**b**). White stars depict release sites (scaled to the number of fish). Pie charts are scaled to the number of detections (Note: Scales between years are not the same)

($Q = 3.415$; $P = 0.006$), but not Alazan Bay ($Q = 2.789$; $P = 0.053$). Residency was similar between Laguna Salada and Cayo de Grullo ($Q = 0.791$; $P = 1.000$) and all remaining pairwise comparisons.

Statistically significant interannual (two-way ANOVA, $F_{1,208} = 80.179$, $P < 0.001$) and monthly variability (two-way ANOVA, $F_{11,208} = 7.631$, $P < 0.001$) was observed in black drum minimum movement rates. However, a significant interaction effect was also found between these two factors (two-way ANOVA, $F_{11,208} = 5.324$, $P < 0.001$). Subsequent pairwise comparisons showed that ROM_{min} was significantly higher in year 2 than year 1 for the months of May, June, July, August, January, and March.

Plotted with various environmental variables, movement rates appeared to be positively correlated with rapid declines in salinity (Fig. 5). Subsequent multiple linear regression analysis found multicollinearity between two independent variables used in the original model: temperature (VIF = 11.470) and dissolved oxygen (VIF = 10.515). However, given the known response of dissolved oxygen to water temperature (and not vice versa), dissolved oxygen was removed from the regression model, which subsequently resolved multicollinearity. Further analysis showed that ROM_{min} was effectively explained by remaining model inputs ($R^2 = 0.634$, $F_{6,22} = 4.639$, $P = 0.007$); however, not all of the independent variables

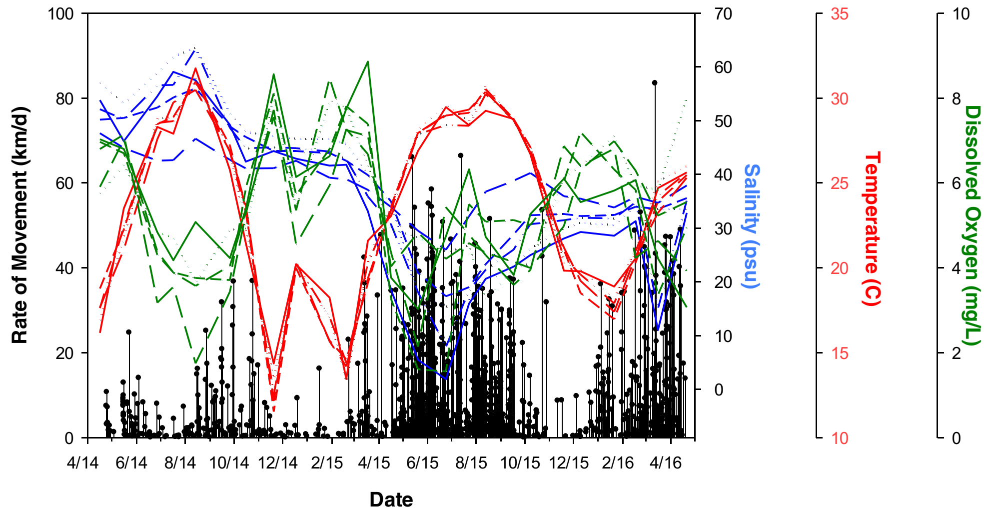

Fig. 5 Multiple scatter and line plots of Rate of Movement (black symbols with drop lines) of tagged Black Drum between acoustic receiver stations in relation to various environmental variables: salinity (blue lines), temperature (red), and dissolved oxygen (green). Separate lines within each variable indicate various water quality stations across the Baffin Bay Complex

were necessary with salinity appearing to account for the ability to predict ROM_{min} ($t = -3.119$, $P = 0.007$). The relationship between salinity and ROM_{min} was negative (Linear Regression, $y = -0.2736x + 17.676$, $R^2 = 0.5046$), with decreasing movement rates observed with increasing salinity (Fig. 6).

Discussion

Acoustic monitoring data indicate that the BBC, and in particular the three major tributaries (Alazan Bay, Laguna Salada, and Cayo de Grullo), represent important habitat for black drum. Although fish were not constrained to specific subregions and traversed the extent of the BBC, most individuals reaching the array's outer extent along the Upper Laguna Madre returned to the interior of the system at a later date. This finding supports historical observations of return migrations in this species along south Texas (Simmons and Breuer 1962) as well as acoustic telemetry studies of other sciaenid fishes, which commonly document site fidelity (Semmens et al. 2010; Reyier et al. 2011; Alós and Cabanellas-Reboredo 2012; Turnure et al. 2015). The lack of detections from the larger-scale acoustic array deployed outside of the BBC, which encompassed the three closest inlet passes with access to Gulf of Mexico waters (Aransas Pass, Packery Pass, and Mansfield Pass) suggests that fish may be restricted to the BBC and adjacent region of the Upper Laguna Madre. These findings are consistent with previous black drum mark-recapture (Osborn and Matlock 1984) and large-scale population genetic (Gold et al. 1994) studies, both of which indicate the possibility of a sub-population isolated from adjacent regions of the Texas coast. As with other estuarine fishes, this restricted range may render the black drum sub-population

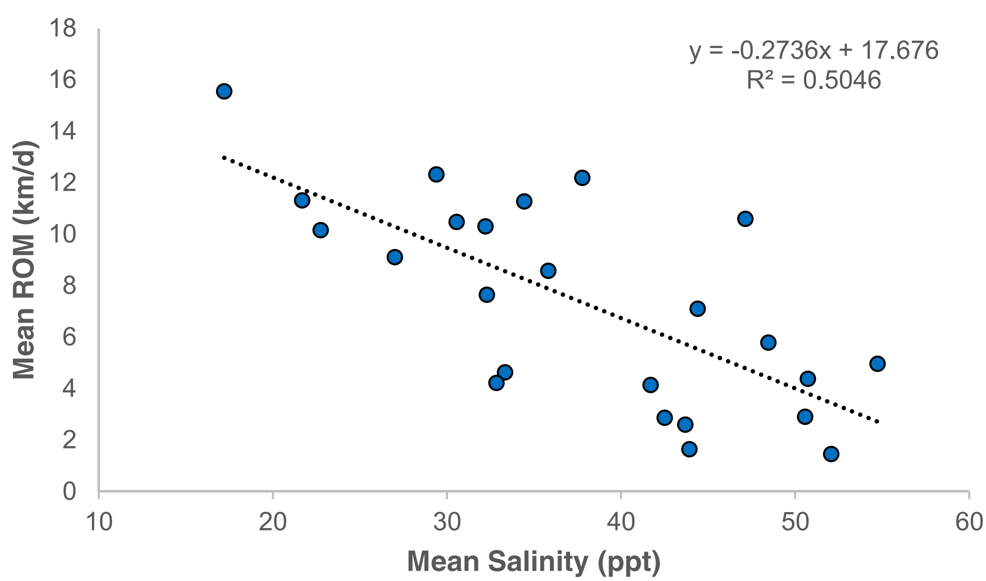

Fig. 6 Results of Linear Regression between monthly mean salinity and rate of movement (ROM) across all individuals

vulnerable to natural and anthropogenically induced disturbances such as hurricanes (Greenwood et al. 2006), cold weather events (Simmons and Breuer 1962; Stevens et al. 2016), and harmful algal blooms (Gannon et al. 2009). Future studies should investigate finer-scale population genetic connectivity as this information combined with the movement behaviors observed herein can guide future management of black drum.

Within the BBC, black drum exhibited comparatively lower residency and overall use of Baffin Bay proper and the Upper Laguna Madre regions when compared to the three tributaries. These findings suggest that larger and deeper portions of the system are used as movement corridors while shallower tributaries may be used for more prolonged activities such as feeding. Simultaneous sampling of benthic macrofauna in BBC has shown that, while seasonally variable, both abundance and biomass of black drum prey (bivalves and polychaetes) are consistently higher in the three major tributaries compared to Baffin Bay proper and Upper Laguna Madre interface (Mendenhall 2015). Additionally, animals collected from Baffin Bay proper possess higher incidence of empty guts compared to adjacent tributaries (Mendenhall 2015), suggesting food resources were scarcer in this portion of the BBC. Indeed, black drum are attracted to freshwater influxes from the creek extremities (Breuer 1957) where there is generally greater macrofaunal diversity following high inflow events (Montagna and Kalke 1992; Kim and Montagna 2009). Black drum movements and distribution may thus reflect dynamics in prey availability (Simmons and Breuer 1962) as has been shown for other benthic foraging fishes (Ajemian et al. 2012; Ajemian and Powers 2012).

Extended residency behavior in sciaenid fishes has also been linked to spawning (Alós and Cabanellas-Reboredo 2012). However, given the late-winter to early-spring spawning paradigm for black drum across the Gulf of Mexico (Saucier and Baltz 1993; Locascio et al. 2008; Locascio and Mann 2011), including Texas (Cody et al. 1985), spawning behavior appears unlikely to explain high summer residency in the BBC. The locations of tagged individuals in the BBC during the typical spawning period (February–April) were highly variable, indicating that spawning may have taken place either in multiple regions across the BBC, or in a localized region where there was insufficient acoustic coverage. Future investigations should consider finer-scale movement analyses as well as the incorporation of passive acoustics techniques to help resolve the location and timing of black drum spawning in predominantly hypersaline estuaries like the BBC.

River diversions and other anthropogenically induced reductions in freshwater inflow negatively affect a wide variety of estuarine fisheries species (Drinkwater and Frank 1994). Similar to the BBC, the Coorong coastal lagoon of southeastern Australia acts as a reverse estuary with extreme fluctuations in salinity (± 100). During periods of extreme drought, Smallmouth Hardyhead (*Atherinosoma microstoma*) experience major reductions in range relative to years with sufficient river flow (Wedderburn et al. 2016). Although a much longer-lived fish species in a different system, black drum appeared to similarly use less of the BBC in year 1 (extreme drought) compared to year 2 (wet). Wider use of the BBC, particularly during summer in year 2 (Fig. 4), was concomitant with lower salinities. The resulting expansion of habitat may have thus increased connectivity between the interior of the BBC and the Upper Laguna Madre. As such, freshwater inflows may play a major role in black drum interannual distribution and may have implications for trophic dynamics since prey resources are not homogenously distributed across this complex (Mendenhall 2015).

Experimental studies have found considerable salinity-induced physiological responses in euryhaline marine fishes. Both euryhaline Gilthead Seabream (*Sparus aurata*) and Senegalese Sole (*Solea senegalensis*) acclimated to seawater conditions (38 ppt) exhibit disproportionately higher metabolic response when exposed to hypersalinity (i.e., 55 ppt) than oligosaline conditions (5 ppt), suggesting a much higher energetic cost to acclimate to hypersaline water (Aragão et al. 2010). Young spotted seatrout (*Cynoscion nebulosus*), another sciaenid species with similar distribution to black drum, exposed to a range of temperatures (24, 28, 30, and 32 °C) and salinities (5, 10, 20, 35, and 45) exhibit increased routine metabolic rate with temperature. However, at higher salinities (> 35), oxygen consumption actually decreases once temperatures exceed 30 °C, which was attributed to reduced activity levels in these conditions (Wuenschel et al. 2004). Thus, despite being tolerant of wide ranges of salinities, black drum may cope with these similar conditions by minimizing movements, which would serve to conserve energy already being expended on metabolic activities associated with osmoregulation. This behavior has been observed in euryhaline milkfish (*Chanos chanos*), which have been shown to reduce maximal swimming performance at hypersaline conditions (55 ppt) presumably due to elevated osmoregulatory cost (Swanson 1998). Experimental studies of black drum physiological responses to salinity flux (both positive and negative) are needed to comprehend the movement patterns observed here, and are crucial to understanding the effects of long-term salinity dynamics on fish condition and behavior.

The BBC is a dynamic system that has historically cycled between reverse and classical estuarine conditions. This variability is linked to El Niño and La Niña climatic oscillations (Tolan 2007). This 2-year study demonstrates that important fishery species like black drum may be strongly influenced by local conditions (i.e., salinity), which influence both distribution and movement rates. The major black drum emaciation event observed in fall 2012 followed a summer of some of the highest salinities in the BBC in over a decade (Olsen 2016), which may have limited black drum home range to suboptimal regions deficient in prey (Mendenhall 2015). While Olsen (2016) showed that Baffin Bay fish appeared to be fully recovered (i.e., similar condition to fish from the Upper Laguna Madre) by spring 2014, this analysis was constrained to two seasons (fall and spring) when fish tend to have higher mobility and thus access to greater food resources. Future efforts should incorporate year-round monitoring to better understand the finer-scale temporal dynamics in fish condition that may still affect fisheries yet are not captured by seasonal fishery-independent surveys. Additionally, there is significant opportunity to assess the environmental impacts of the BBC's dynamic estuarine conditions on other euryhaline sciaenid fisheries species inhabiting this system: red drum, *Sciaenops ocellatus*, and spotted seatrout, *Cynoscion nebulosus*. The incorporation of these species may provide a more holistic view of ecosystem-wide dynamics of this estuary and perhaps explain why black drum are so numerous in this system. Additionally, these data, in conjunction with data on their benthic prey sources (e.g., Mendenhall 2015), may be crucial to understanding the consequences of both eutrophication in Baffin Bay (Wetz et al. 2017) as well as regional modifications to freshwater inflows on Texas' estuaries, which remains a major environmental issue in the region.

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