HABITAT USE AND MOVEMENT OF TARPON IN THE NORTHERN GULF OF MEXICO

A Thesis

by

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ABSTRACT

Atlantic tarpon (*Megalops atlanticus*) are capable of long-distance migrations (hundreds of kilometers) but also exhibit resident behaviors in estuarine and coastal habitats. The aim of this study was to characterize essential habitat(s) and identify migration pathways of tarpon in the northern Gulf of Mexico. Habitat use by tarpon was investigated using gillnet data collected by Texas Parks and Wildlife Department (TPWD) over the past four decades. Generalized additive models (GAMs) were used to identify environmental factors that have a significant role in tarpon presence and assess temporal trends in the occurrence of tarpon in this region, which have increased over the past four decades. Adult tarpon caught off Texas and Louisiana were tagged with acoustic transmitters (n = 44) to characterize spatial and temporal trends in their movements and migrations, and two distinct migratory contingents were detected. Tarpon tagged west of the Mississippi River delta off Texas migrated south in the fall and winter into areas of south Texas and potentially into Mexico, while individuals tagged east of the delta migrated into Florida during the same time period, suggesting the presence of two unique migratory contingent or subpopulations in this region. An improved understanding of the habitat requirements and migratory patterns of tarpon inhabiting the Gulf of Mexico is critically needed by resource managers to assess the vulnerability of each stock to fishing pressure and guide multi-state and multi-national conservation efforts to rebuild and sustain tarpon populations.

DEDICATION

To the fisherman in my family who introduced me to my passion; Martin “Bubba” See, Micheal Hartner, Jhon Hartner, and most importantly David Barry Stephens Jr., my father, who taught me about so much more than fishing while on the water.

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Contributors

This work was supervised by a thesis committee consisting of Dr. Jay Rooker (advisor) of the Department of Marine Biology, Dr. David Wells of the Department of Marine Biology, Dr. Wesley Highfield of the Department of Marine and Coastal Environmental Science, and Dr. Michael Dance of the Department of Oceanography & Coastal Sciences at Louisiana State University. The long-term gillnet data used for this study was provided by the Texas Parks and Wildlife Department.

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INTRODUCTION

Atlantic tarpon (*Megalops atlanticus*) are popular and highly targeted gamefish in coastal waters of the Atlantic Ocean (Ault, 2010; Mill, 2010; Ault & Luo, 2013). Their large size and acrobatic fight attract fishermen from all over the world, creating a multibillion-dollar recreational fishing industry (Ault, 2008; Luo et al., 2020). Tarpon occur from Senegal to Congo and Bermuda to Brazil in the eastern and western Atlantic Ocean, respectively (Robins et al., 1986; Ault & Luo, 2013). This species is capable of long-distance migrations, often displaying movements over hundreds of kilometers; however, resident behaviors are also evident with some individuals showing high site fidelity to estuarine and coastal areas (Luo et al., 2020). Well-developed seasonal migration patterns have been reported for tarpon with individuals often moving to higher latitudes in the late spring and early summer, and then migrating back to lower latitudes in the late summer and early fall (White & Brennan, 2010; Spotte, 2016). Although our understanding of tarpon migrations has improved in recent years (Luo et al., 2020), more spatially resolved data on their distribution, habitat requirements, and movements in certain geographic regions are lacking, compromising the ability of resource managers to protect and conserve migratory contingents or stocks within the larger Atlantic-wide population.

Coastal and offshore waters of the Gulf of Mexico (GoM) represent essential habitat for tarpon (Smith, 1980; Crabtree et al., 1992). Based on collections of tarpon larvae (leptocephali) and early juveniles in the U.S. waters from Florida to Texas, adult tarpon spawn in coastal and offshore waters of the GoM in the late spring and early summer (Crabtree et al., 1992, 1997; Shenker et al., 2002; Baldwin & Snodgrass, 2008; Graham et al., 2017). After a planktonic larval duration of approximately two to three months, juveniles inhabit estuaries and remain in these inshore nurseries for several years before moving back into coastal waters as sub-adults and adults (Robins, 1977; Geiger, 2000; Wells, 2003). Once sexually mature (approximately 10 years of age and 120 cm FL]), tarpon spend the majority of their time in coastal and offshore waters in the GoM but are known to enter tidal passes and move back into estuaries (Ault, 2008; Luo et al., 2008; Matich et al., 2017). Similar to other regions, seasonal migrations displayed by tarpon in the GoM appear to be temperature dependent (Childs et al., 2008; Luo & Ault, 2012). Luo et al. (2020) showed that seasonal migrations in the fall and winter to lower latitudes were well developed for tarpon in the GoM, with different migratory patterns displayed by tarpon tagged east and west of the Mississippi River. Tarpon west of the river delta (hereafter western stock) commonly crossed the Texas-Mexico border and overwintered in the southern GoM while tarpon east of the river delta (eastern stock) moved to south Florida during the same period (Luo et al., 2020). Some evidence of eastern and western population structure was observed with nuclear DNA markers (Ward et al., 2005), supporting the premise that two contingents or subpopulations exist in the GoM.

Historically, tarpon in the western GoM supported substantial recreational tarpon fisheries and between the 1920s and 1940s, Port Aransas, Texas was referred to as the “Tarpon Capital of the World” (Holt et al., 2005). This fishery collapsed in the 1960s and steep declines in tarpon landings were initially attributed to overharvesting (Winemiller & Dailey, 2002; Holt et al., 2005). However, corresponding reductions of juvenile tarpon landings led to speculation about recruitment failure due to the loss of nursery habitat or physiological stress related to water temperatures off Texas being near their physiological limits (Smith, 1980; Crabtree et al., 1995; Holt et al., 2005). Although mechanism(s) responsible for the decline of tarpon in this region are unknown, the primary impediment to managing the western stock is the lack of data on the habitat requirements and movements of individuals. This information is needed to create appropriate regulations to manage tarpon along their seasonal migratory routes, which is inherently challenging because tarpon commonly cross management boundaries during their seasonal migrations and regulations often differ between states and countries.

The aim of this study was to characterize habitat requirements and migratory pathways for tarpon from the northwestern GoM using historical catch data and conducting electronic tagging, respectively. Gillnet surveys from Texas Parks and Wildlife Department (TPWD) were used to describe spatial distributions of tarpon in Texas bays and estuaries over the past four decades. Since TPWD catch data includes multiple environmental parameters, multivariable models were used to identify environmental conditions that define essential habitats of juvenile and sub-adult tarpon in this geographic region. To complement catch data, acoustic telemetry was used to characterize the habitat requirements and movements of adult tarpon tagged both east and west of the Mississippi River Delta in the northern GoM. The use of acoustic telemetry afforded information on the migratory pathways of mature tarpon, which was then used to determine the degree of stock mixing and/or straying between eastern and western migratory contingents. Acoustic telemetry data also allowed for insights on timing of movements in recent years. The combination of catch data and electronic tagging used in this study will lead to an improved understanding of the habitat requirements and migratory pathways of tarpon in the northern GoM, which is critically needed by resource managers to assess the western stock's vulnerability and guide multi-state and multi-national conservation efforts to rebuild tarpon populations.

Objectives

1. Identify habitats and regions in the western GoM that represent essential (high quality) habitat of juvenile and subadult tarpon

H_1: Presence and relative abundance (catch per unit effort) of tarpon will be greater in bay systems with higher average annual water temperatures near or above the preferred 26°C threshold (Luo et al., 2020).

2. Quantify temporal shifts in presence and relative abundance of juvenile and subadult tarpon in the western GoM over four decades

   H_2: Given the preference for warmer water temperatures by tarpon, interdecadal shifts (increases in recent years) in water temperature will increase the presence and/or relative abundance of tarpon in northern bay systems along the Texas coast.

3. Characterize migratory patterns of adult tarpon collected in the western GoM using acoustic telemetry and identify temporal trends of observed movements

   H_3: Tarpon collected in the northern GoM will migrate southward along the coast in the early to mid-fall while northward movements will be observed in late spring to mid-summer. Movements crossing the Mississippi River Delta will be negligible because eastern and western stocks display different migratory patterns and are presumed to rarely mix.

METHODS

TPWD Gillnet Catch Data

Spatial and temporal patterns of habitat use by juvenile and subadult tarpon in bay systems along the Texas coast were assessed using a long-term gillnet monitoring survey conducted by TPWD. Spring (April-June) and fall (September-November) gillnet surveys were conducted within 10 major sampling areas identified by TPWD (Sabine Lake, Galveston Bay, Cedar Lakes, East Matagorda Bay, Matagorda Bay, San Antonio Bay, Aransas Bay, Corpus Christi Bay, Upper Laguna Madre, and Lower Laguna Madre) from 1980 to 2018. Due to irregular sampling effort and low tarpon catch numbers, surveys from Sabine Lake, Cedar Lakes, and East Matagorda Bay were removed from the dataset. The remaining areas were summarized into five major bay systems; Galveston Bay, Matagorda Bay, San Antonio Bay, Corpus Christi Bay (comprised of Corpus Christi Bay and Aransas Bay), and Laguna Madre (comprised of upper and lower Laguna Madre) (Figure 1). TPWD used a stratified clustered sampling design over the designated period, and set locations were randomly selected from a grid of one minute latitude by one second longitude cells. Gillnets were deployed within an hour of sunset and retrieved the next day within four hours of sunrise (Martinez-Andrade et al., 2009; Plumlee et al., 2018; Livernois et al., 2021. The monofilament gillnet used was 183 m in length and composed of four 45.7 m panels with differing stretched mesh sizes (76, 102, 127, and 152 mm). Gillnets were deployed perpendicular to the shoreline with the smaller mesh sizes closest to the shore. The date and time for each set was recorded along with environmental parameters including water temperature (°C), salinity (PSU), dissolved oxygen (mg l^{-1}), and turbidity (NTU). When retrieved, elapsed soak time was recorded, and tarpon, along with other species, were identified to the species level, measured (FL in mm), and enumerated.

Acoustic Telemetry

Adult tarpon were tracked using an array of Innovasea acoustic receivers (VR2W and VR2Tx) deployed in or near tidal passes, and in coastal waters from the Texas-Louisiana border to the Texas-Mexico border in the western GoM. The array is comprised of a series of acoustic gates with receivers positioned in coastal water outside five of the major bay systems included in the TPWD gillnet surveys (Sabine, Galveston, Matagorda, Corpus Christi, and Lower Laguna Madre), and one area off the coast of western Louisiana (Figure 2). At each location, receivers were deployed on a variety of structures including offshore rigs, pier pilings, submerged structures, or PVC pipe anchored into the sediment. In addition to receivers in coastal waters, receivers were positioned inside tidal passes (jetties) or in areas inside bays that are in close proximity to tidal passes to document potential estuarine-coastal movement of tarpon (Figure 2). Additionally, this study utilized other collaborative receiver networks in the GoM (e.g., Integrated Tracking of Aquatic Animals in the Gulf of Mexico, iTAG), and detection data from additional arrays complemented data from the network of acoustic receivers in the western GoM, providing additional insights on the larger-scale movements of tarpon (Figure 3). Receivers were serviced approximately every four months. Servicing included downloading data, removing biofouling on the external surface of receivers, and replacing batteries when required. Adult tarpon (>120 cm FL) were tagged internally with Innovasea V16-4H (69 kHz) acoustic transmitters programed with a 60-120 second random delay. This gave each transmitter an estimated battery life of approximately 1900 days. Tarpon were caught using conventional hook and line gear with artificial lures, popular in the northern GoM, for targeting tarpon. Heavy tackle was used in order to reduce fight time. Once reeled up next to the tagging vessel, tarpon were positioned on the starboard side by securing the mouth at one end directing it towards the bow of the vessel and attaching a tail rope to the caudal peduncle at the opposite end. The vessel maintained a slow speed (approximately 0.5 to 0.7 m sec^{-1}) to ensure that water passed through the mouth and over the gills of the tarpon and all fish remained in the water during the entire tagging process to increase survival rates (Edwards, 1998). Tarpon were then rotated ventral side up putting the fish in a state of tonic immobility (Henningsen, 1994; Kessel & Hussey, 2015). One to two scales were removed from the ventral side of the fish to allow for a small incision approximately 20 mm in length posterior and slightly dorsal of the pelvic fin. Incisions were slightly larger than the tag diameter size (16 mm), and Innovasea V16 transmitters were then inserted through the incision and into the peritoneal cavity of each tarpon. A suture was used to seal the surgery site using an Ethicon 4-0 monofilament suture in early deployments; however, no sutures were used in the later surgeries to minimize handling and surgery time and in turn reduce stress (Robillard et al., 2015; Keretz et al., 2018). Following the surgery, one scale was removed directly below the dorsal fin to allow for a conventional tag to be placed. This tag contained a unique identification number and contact information required to report any recaptured tarpon. Tarpon were tagged both east and west of the Mississippi River Delta to have representation from both the eastern and western stocks.

Data Analysis

TPWD gillnet data was used to characterize trends in the presence and relative abundance of juvenile and subadult tarpon in five major bay systems along the Texas coast, which represented approximately 95% of the number or tarpon caught in gillnet surveys. Catch per unit effort (CPUE) of tarpon was generated from gillnet catches and standardized to soak time (no. tarpon per 1,000 hours). CPUE was then used as the metric of relative abundance to investigate potential regional and inter-decadal variation in tarpon catches in the western GoM. In addition, tarpon presence/absence was used as dependent variables in estuary-specific generalized additive models (GAMs) parameterized with a suite of environmental parameters (independent variables) including season, decade, water temperature (°C), salinity (PSU), dissolved oxygen (mg l^{-1}), and turbidity (NTU) to identify habitat requirements and environmental drivers that influence the distribution and abundance of tarpon. The GAM modeling framework applied to gillnet data used a binomial distribution with a logit link and allowed for non-linear relationships that are common in ecology to be observed, and this modeling approach has been used successfully in other studies to determine fish-habitat relationships and identify key environmental drivers that influence habitat quality of many estuarine-dependent fishes (Furey & Rooker, 2013; Dance & Rooker, 2016; Livernois et al., 2021). A manual backwards stepwise selection procedure based on minimizing the Akaike Information Criterion (AIC; Akaike, 1974) using approximate p-values to help guide the selection process was used in order to select variables that would be included in final GAMs. Non-significant variables ($p > 0.05$) were removed one by one in order to determine whether their exclusion improved the AIC (Dance & Rooker, 2016; Dance & Rooker, 2019). This was done until only significant variables were retained in the final model. Percent deviance explained (DE) was calculated to assess the overall fit of the model (Sluis et al., 2021). Once the final model was determined, ΔAIC and ΔDE for each of the remaining variables was calculated by removing each variable individually and comparing the difference in AIC and DE values to values from the original model. Both ΔAIC and ΔDE were used to evaluate the importance of each retained variable.

Data generated from acoustic telemetry were used to assess the horizontal movement and migratory patterns of tarpon. Rate of movement (ROM) was calculated using known consecutive acoustic detections or satellite geolocations using ArcMap 10.7 and Geo Spatial Modeling

Environment (GME). All consecutive detections or movements used in ROM calculations were within 150 days of the previous detection in order to prevent using two detections from potentially opposing seasonal migrations (e.g., northern versus southern migrations) in the same calculation. Consecutive detections also had to be greater than 5 km in distance in order to exclude small-scale movements within spatially limited acoustic arrays (e.g., acoustic gates). Rate of movement was calculated by dividing the distance of the movement (shortest possible in water route) by the time elapsed for specific intervals during the tracking sequence (Dance & Rooker, 2015; Moulton et al., 2017). Each ROM estimate was classified as a “northern” or “southern” based on the direction (latitudinal change) of the observed track between consecutive detections. Rate of movement estimates for all tagged individuals were then averaged for each month and plotted to observe possible intra-annual trends in both ROM and directionality.

RESULTS

Overall, 407 tarpon (mean ± 1 SD: 67.90 ± 17.53 cm FL) were collected in TPWD gillnet surveys from 1980-2018 in five major bay systems investigated (Galveston Bay [n = 18], Matagorda Bay [n = 53], San Antonio Bay [n = 33], Corpus Christi Bay [n = 111], and Laguna Madre [n = 192]). Over the 38 years of sampling, 23,830 gillnet sets were conducted and tarpon were present in 344 (1.4%) of those sets. Regional variation in CPUE and percent frequency of occurrence (%F) was pronounced with higher values found in southern bay systems (Corpus Christi Bay CPUE[%F] = 1.20[1.5%], Laguna Madre = 2.02[2.2%]) relative to systems farther to the north (San Antonio Bay = 0.72[0.9%], Matagorda Bay = 1.15[1.3%], and Galveston Bay = 0.39[0.5%].

Pronounced seasonal and decadal trends in tarpon CPUE were observed along the Texas coast. Spring gillnet surveys had a mean decadal CPUE from 0.07 (1990-1999) to 0.08 (1980-1989) across all five major bay systems. Fall gillnet surveys resulted in mean decadal CPUE values two orders of magnitude higher than spring surveys, ranging from 1.68 (1990-1999) to 3.47 (2010-2018) (Figure 4). Matagorda Bay and Laguna Madre were the only bay systems that experienced increasing CPUE of tarpon across each of the four decades investigated; nevertheless, CPUE for the most recent survey period (2010-2018) in all five bay systems was highest or second highest among the decades sampled (Figure 5).

Regional Fish-Habitat Models

Galveston Bay

The final GAM for tarpon presence in Galveston Bay (AIC= 188.18; DE = 18.6%) retained three variables: decade (ΔAIC= 6.64; ΔDE= 5.9%), temperature (ΔAIC= 14.69; ΔDE= 8.7%), and salinity (ΔAIC= 8.13; ΔDE= 4.8%). Response plots indicated that tarpon presence in

Galveston Bay declined as salinity increased, with the highest presence found in fresh and brackish waters. The presence of tarpon in Galveston Bay also decreased with temperatures above 20˚C, with the additive effect becoming negative at approximately 27 ˚C (Figure 6). A significant inter-decadal trend was detected in the final model for Galveston Bay and the response plot showed that tarpon presence was highest in the earliest (1980-1989) and latest (2010-2018) survey periods (Figure 7).

Matagorda Bay

The final GAM model for tarpon presence in Matagorda Bay (AIC = 404.75; DE = 17.3%) included four variables: decade (ΔAIC= 12.75; ΔDE= 4.0%), season (ΔAIC= 39.73; ΔDE= 8.9%), temperature (ΔAIC= 5.09; ΔDE= 1.8%), and dissolved oxygen (ΔAIC= 9.01; ΔDE= 2.3%). Response plots indicated that tarpon presence in Matagorda Bay was positively correlated with dissolved oxygen levels. The presence of tarpon in Matagorda Bay also increased with increasing water temperature up to approximately 22°C, with the additive effect becoming negative above 28°C (Figure 6). Seasonal trends showed that tarpon presence in Matagorda Bay was notably higher in fall gillnet surveys, and response plots also denoted a significant inter-decadal trend for Matagorda Bay with tarpon presence increasing each of the four decades surveyed (Figure 7).

San Antonio Bay

The final GAM for tarpon presence in San Antonio Bay (AIC = 325.61; DE = 12.2%) consisted of two variables: season (ΔAIC= 30.15; ΔDE= 8.9%) and salinity (ΔAIC= 11.66; ΔDE= 4.2%). Response plots indicated that tarpon presence in San Antonio Bay was highest in fresh and brackish water, with tarpon presence declining as salinity increased (Figure 6). Tarpon presence in San Antonio Bay also showed seasonal trends, with fall gillnet surveys having significantly higher tarpon presence compared to spring gillnet surveys (Figure 7).

Corpus Christi Bay

The final GAM for Corpus Christi Bay (AIC = 903.71; DE = 15.0%) retained three variables: season (ΔAIC= 115.85; ΔDE= 11.1%), temperature (ΔAIC= 11.23; ΔDE= 1.5%), and salinity (ΔAIC= 10.42; ΔDE= 1.2%). Response plots indicated that tarpon presence in Corpus Christi Bay was highest in fresh and brackish conditions and declined as salinity increased. Response plots for water temperature showed that tarpon presence in Corpus Christi Bay began to decline at 22°C, with the additive effect becoming negative as temperatures approached 28°C (Figure 6). Seasonal trends for tarpon presence in Corpus Christi Bay were observed, with fall gillnets having markedly higher tarpon presence (Figure 7).

Laguna Madre

The final GAM for tarpon presence in Laguna Madre (AIC = 1251.70; DE = 14.1%) included three variables: decade (ΔAIC= 7.16; ΔDE= 1.0%), season (ΔAIC= 140.13; ΔDE= 9.8%), and salinity (ΔAIC= 30.55; ΔDE= 2.4%). Response plots for tarpon presence in Laguna Madre indicated higher levels of tarpon presence in fresh and brackish water but also in hypersaline conditions greater than 50 PSU (Figure 6). Significant seasonal trends were observed for tarpon presence in Laguna Madre with presence being higher for fall surveys. Response plots also denoted a significant inter-decadal trend in the Laguna Madre with tarpon presence increasing each of the four decades surveyed (Figure 7).

Acoustic and Satellite Telemetry

From 2018 to 2022, 44 tarpon were tagged with V16 acoustic transmitters in coastal waters off Texas and Louisiana. Tagged individuals ranged in size from 127 to 196 cm FL (mean

± 1 SD: 167 ± 20 cm FL). The majority of tarpon were tagged off the coast of Texas (n = 40) from Matagorda Bay to Galveston Bay with a smaller number tagged in Louisiana east of the Mississippi River Delta (n = 4) to serve as an outgroup potentially comprised of individuals from the eastern migratory contingent. All 44 individuals were tagged between the months of June to October.

Overall, 18 of the 44 acoustically tagged individuals were detected (40.9%), 16 tagged in Texas with the remaining two tagged in Louisiana east of the Mississippi River Delta. None of the tagged tarpon were detected moving across the Mississippi River Delta from the initial tagging location. Tarpon tagged in Texas displayed both northern and southern migrations along the coast with multiple detections recorded at each of the regional acoustic receiver locations (i.e., gates) along the coast (Figure 8). Individuals tagged east of the Mississippi River Delta displayed large-scale movements between Louisiana and Florida (Figure 8).

The majority of detections from tagged tarpon were recorded on receivers located in coastal waters, however a subset of individuals (n = 9) displayed estuarine-coastal connectivity. These individuals were detected in bay systems in Texas and Florida. Time spent within the bays varied, reaching as high as approximately two months for some individuals. Tarpon (ID 3023) tagged in coastal waters off northern Texas, moved into Galveston Bay six days after being tagged. The individual then spent 11 days in the bay, observed moving to the northern shoreline of the bay, before returning back to coastal waters. Tarpon (ID 2801) was tagged east of the Mississippi River Delta, off the Louisiana coast. The individual was detected moving south along the Florida coast before moving into a bay system inshore of Boca Grande. It remained in the bay for 55 days before detections concluded.

Rate of movement (ROM) estimates (distance between detections > 5km and elapsed time between detections < 150 days) ranged from 0.3 km day^{-1} to 35.6 km day^{-1}. Of the 45 ROM estimates generated from 18 tagged tarpon, 26 were classified as southern movements and occurred from September to March (Figure 10). The month with the highest mean ROM for southern movements by tarpon was November (23.8 km day^{-1}). The remaining 19 ROM estimates were classified as northern movements and occurred from April to August. Mean monthly ROM for northern movements by tarpon peaked in the month of June (20.0 km day^{-1}) (Figure 10).

DISCUSSION

Regional variation in the relative abundance (CPUE) and frequency of occurrence of tarpon was observed across estuaries in the western Gulf of Mexico, with the relative abundance from gillnet surveys being higher in more southern bay systems, suggesting that environmental conditions may be more favorable than bay systems to the north. The Texas coastline displays strong salinity and temperature gradients with salinity and temperature increasing with decreasing latitude or in more southern bay systems (Fujiwara et al., 2019). Tarpon are susceptible to cold water temperatures and often do not survive freeze events (Mace et al., 2017), and thus warmer southern bays generally experience higher winter temperatures and fewer freeze events, possibly leading to higher survival of juvenile tarpon. Apart from temperature, regional variation in salinity is also pronounced in Texas with elevated salinity typical of more southern bay systems. While tarpon can tolerate a wide range of salinity, early life stages (larvae) are typically collected in waters of higher salinity (~30-40 PSU; Zale & Merifield, 1989). As a result, higher salinity in southern bay systems may lead to increased survival of early life stages of tarpon inhabiting these regions, subsequently leading to higher numbers of juveniles and sub-adults. While physicochemical properties of southern bay systems may elevate habitat quality for early life stages of tarpon, the higher relative abundance of tarpon in these bay systems may be related to their proximity to spawning grounds. Luo et al. (2020) identified potential tarpon spawning locations off the coast of south Texas from Matagorda to Laguna Madre. The closer proximity of bay systems in the south to putative spawning grounds may result in higher larval supply and recruitment, and therefore influence regional patterns of abundance with more tarpon found in southern bay systems along the Texas coast.

Relative abundance of tarpon increased in all of the five major bay systems investigated since the 1990-1999 sampling period. Inter-decadal increases are evident in both northern and southern bay systems and most notable within the last decade of sampling (2010-2018) in this study. Increases in tarpon abundance across all Texas bays systems in the last decade of the survey may be associated with warming trends that have been noted as early as the 1970s and have accelerated over the last decade causing water temperatures to have increased across this entire region (Oviatt, 2004; Preston, 2004; Neilson-Gammon, 2020). Rising mean annual temperatures are driven almost completely by an increasing trend in higher winter minimum temperatures (Tolan & Fisher, 2009). The noticeable increase in tarpon abundance within the last decade (2010 -2018) may be indicative of range expansion by tropical, warm-water species (Sorte et al. 2010). Fujiwara et al. (2019) noted that warmer temperatures are capable of prompting poleward shifts in species ranges, leading to increases in the presence of tropical, warm-water species in sub-tropical environments. Similarly, increased northern ranges for tropical, warm-water species such as gray snapper (*Lutjanus griseus)* (Tolan & Fisher, 2009) and common snook (*Centropomus undecimalis)* (Purtlebaugh et al., 2020) have been reported, and it is plausible to assume that tarpon may be experiencing similar range expansion with warming conditions along the Texas coast. Moreover, prey items commonly consumed by tarpon such as Gulf menhaden (*Brevoortia patronus*), Atlantic croaker (*Micropogonias undulatus*), and white mullet (*Mugil curema*) have also experienced increased probabilities of occurrence in higher latitude bay systems due to climate change (Hare & Able, 2007; Ault, 2008; Fujiwara et al., 2019). Increases in prey availability and more suitable water temperatures experienced in the past few decades have likely produced more favorable environmental conditions for both juvenile and sub-adult tarpon, thus explaining observed increases in the relative abundance of tarpon across several bay systems (Matich, 2017).

Seasonal shifts in the relative abundance of tarpon was markedly higher in the fall gillnet survey compared to the spring, suggesting that either overwintering mortality or movement to areas not sampled with TPWD gillnets may be occurring. Numerous studies have assessed residency times of juvenile tarpon in estuaries with peak residency periods occurring from July to December (Rickards, 1966; Zerbi et al., 1999; Stein et al., 2016). In the present study, results show a similar trend with fall gillnet sampling season (September – November) coinciding with the period of peak residency observed in these previous studies. Winter mortality linked to sub-optimal temperatures (i.e., ‘winterkills’) has been observed for a variety of estuarine and marine fishes (Hurst, 2007), and thermal stress may be responsible for lower abundance of juvenile and subadult tarpon in the spring following a period of low winter temperatures in bays along the Texas coast. In addition to changes in winter survival, it is also possible that drops in water temperature may dictate the duration of estuarine habitat use by tarpon, especially in sub-tropical regions in the northern GoM. Temperature drops typically lead to fish searching for deeper waters for thermal refuge (Mace et al., 2017). In response, tarpon in search for thermal refuge may move to deeper regions of the bay or in tidal passes during the winter that are not sampled by TPWD gillnets, or even move to channel systems within the bays or jetties. Assuming they remain in these areas into the spring, this may result in lower CPUE values during the spring survey.

Similar to regional CPUE patterns observed across the bay systems sampled in Texas, generalized additive models (GAM) indicated that salinity and water temperature were important environmental factors affecting tarpon presence within most of the bay systems investigated.

Models developed for Galveston Bay, San Antonio Bay, Corpus Christi Bay, and Laguna Madre all showed increased tarpon presence in fresh and brackish water with presence decreasing as salinity increased across mesohaline of several bays up to a salinity of approximately 20 PSU. Although the Laguna Madre model showed a negative effect of salinity on tarpon presence starting at approximately 20 PSU, the response plot indicated an increase in tarpon presence at salinities greater than 50 PSU. This result is likely unique to the Laguna Madre since this bay system often becomes hypersaline with a mean salinity of approximately 31 PSU and salinities ranging up to 60-100 PSU at times of low rainfall levels (Smith, 1988). Previous studies have observed tarpon tolerating a wide range of salinities, from fresh to hypersaline environments (Crabtree et al., 1992; Luo & Ault, 2020); however, juveniles are often found in rivers, bays, and estuaries, highlighting the importance of fresh and brackish water habitats during the first year(s) of life (Crabtree et al., 1995; Adams et al., 2014). GAMs also revealed that tarpon presence generally increased at temperatures between 20-25°C, and this finding is in accord with the preferred temperature range of tarpon (20-26°C) reported in several other studies (Babcock, 1951; White & Brennan, 2010; Luo & Ault 2012; Spotte, 2016). While salinity and temperature were influential in explaining tarpon presence, dissolved oxygen was not deemed to be an important environmental factor in the majority of models, even though this factor is commonly found to restrict the distribution of many estuarine finfish species (Howell & Simpson, 1994; Breitburg et al., 2003). The limited influence of dissolved oxygen in final models is likely because tarpon can gulp air to facilitate respiration in areas of the bay with low dissolved oxygen levels (Babcock, 1951; Wells et al., 2003; Adams et al., 2014).

Collectively, migrations observed for acoustically tagged tarpon support the hypothesis of two distinct migratory contingents occurring in the GoM, which occur east and west of the

Mississippi River Delta. Similarly, Luo et al. (2020) suggested the presence of eastern and western migration routes for tarpon in the GoM based on findings from satellite tracking. In the present study, tarpon tagged east and west of the Mississippi River Delta often moved significant distances, but no individuals were observed crossing the delta. Seasonal migrations by tarpon to waters proximal to the Mississippi River Delta have been previously reported, and movement into this area is ostensibly associated with spawning and foraging behaviors (Dailey et al., 2008; Stein et al., 2016; Graham et al., 2017; Drymon et al., 2020). Nutrient loading from the Mississippi River enhances primary and secondary productivity, which is potentially the reason that tarpon and other large predators move into this region in the summer and fall (Grimes, 2001; Dailey et al., 2008; Drymon et al. 2020). Although nutrient loading from the Mississippi River increases primary and secondary productivity that enhances prey availability for tarpon, the inflow from the river creates strong gradients in physicochemical conditions that may serve as a barrier and restrict the movements of tarpon across this feature, ultimately limiting the exchange of tarpon on each side of the delta (Grimes & Finucane, 1991; Govoni & Grimes, 1992).

Movements of individual tarpon observed in this study from acoustic detections provided insights on habitat use and migration pathways of both eastern and western contingents. Some individuals were detected on the same receivers almost exactly a year apart from previous detections, suggesting fidelity and return migrations at approximately the same time of year. Many marine species follow common migration pathways with geographic routes that are repeated at similar times each year, and many of these recurring migrations are associated with spawning and foraging (Hunter et al., 2003; Schofield et al., 2010). Kurth et al. (2019) found evidence of migratory fidelity for tarpon, with individuals collected off Louisiana returning to the same coastal system each year. In addition to displaying common migration pathways in coastal waters, several tarpon tagged in this study were also observed moving from coastal waters back into estuaries, indicating a relatively high degree of estuarine-coastal connectivity for adult tarpon. Luo et al. (2020) found similar results using satellite tags with over 50% of the individuals tagged in coastal waters occasionally moving into estuaries and rivers. A possible benefit to returning to estuaries by adult tarpon could be to reduce parasites (Babcock, 1951; Westerdahl et al., 2014). Another potential motivation for adult tarpon moving into estuarine habitats may be associated with enhanced prey availability since primary and secondary productivity is often higher in these bay systems, which elevate the abundance of forage fish available to tarpon (Matich et al., 2017).

Rate of movement estimates of tarpon were used to quantify timing and directionality of observed movements. Mean monthly ROM estimates indicated that southern migrations started in September and lasted through March with the highest mean monthly ROM estimates occurring in November. Migrations are commonly driven by pronounced changes in environmental conditions (Secor, 2015), and November typically brings some of the first major cold fronts to the Texas coast. These fronts often affect tidal currents, water temperature, and water levels in estuarine and coastal systems, and these changes may initiate seasonal migrations of tarpon to more southern locations, subsequently leading to the observed increases in ROM estimates. Because tarpon are generally regarded as tropical, warm-water species, pronounced drops in water temperature apparently trigger the initiation of southward migrations. Similarly, a variety of other migratory species are known to migrate seasonally to reduce environmental variability experienced throughout the year (Secor, 2015). Numerous studies have associated tarpon movements to be closely related to the 26°C isotherm, indicating tarpon migrate north and south to inhabit preferred or optimal water temperatures (Babcock, 1951; White & Brennan, 2010; Spotte, 2016; Luo et al., 2020). Apart from maintaining optimal conditions for adults, tarpon migrations may also be associated with spawning with adults moving into areas that may serve as highly suitable habitats for early life stages of tarpon, which has been observed for other highly migratory species that return to warm, productive waters in the northern GoM to spawn (e.g., Rooker et al. 2007, 2013). Crabtree et al. (1992) used collections of tarpon larvae (leptocephali) to estimate the general location and timing of spawning for tarpon, with the latter occurring from late spring to late summer in Florida. In the present study, acoustically tagged tarpon were observed moving north along the coast of Texas from April through August, and these northward movements coincide with the presumed spawning season of tarpon. As mentioned previously, Luo et al. (2020) identified potential spawning locations in the northern GoM including an area from Matagorda Bay to the Lower Laguna Madre along the coast of Texas; however, the region north of Matagorda to the Mississippi River Delta was not deemed to be an important spawning area for tarpon. Based on detection data of tarpon during the presumed spawning periods mentioned above, the presence of tarpon in the northwestern GoM during this time frame may indicate that this region represents a new spawning area not previously known for tarpon. The collection of tarpon larvae and juveniles from northern bay systems in Texas (e.g., Galveston Bay, Sabine Lake) supports the hypothesis of spawning extending into northern areas in the northwestern GoM (TPWD, unpublished data). Return (i.e., northern) migrations occurred from April through August, peaking in June, and the observed timing of northern migration was similar to findings from satellite tagging tarpon in the GoM (Luo et al., 2020).

Results from this study suggest that Texas estuaries represent essential habitat for both juvenile and adult tarpon. Current warming trends will play a significant role in determining the distribution and abundance of tarpon in the northwestern GoM, with relative numbers of tarpon likely increasing over time to higher latitudinal zones in Texas as individuals expand their northern range. Movement data observed using acoustic telemetry provided more insight on the timing and migration pathways of tarpon, while also providing evidence for the presence of two distinct migratory contingents (east and west) divided at the Mississippi River Delta. Increased tagging effort on both the eastern and western side of the delta are needed to fully understand the nature of the stock structure and potential exchange between eastern and western contingents. Telemetry data from this study also demonstrated that tarpon move across state borders and the lack of detections in the winter after moving into coastal waters off Brownsville, Texas near the international border probably signifies that a fraction of the tarpon cross into territorial waters of Mexico. The movement of tarpon across state and federal borders where regulatory measures often differ indicates the strong need for cooperative management to sustainably manage the tarpon in the GoM.

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APPENDIX A

FIGURES

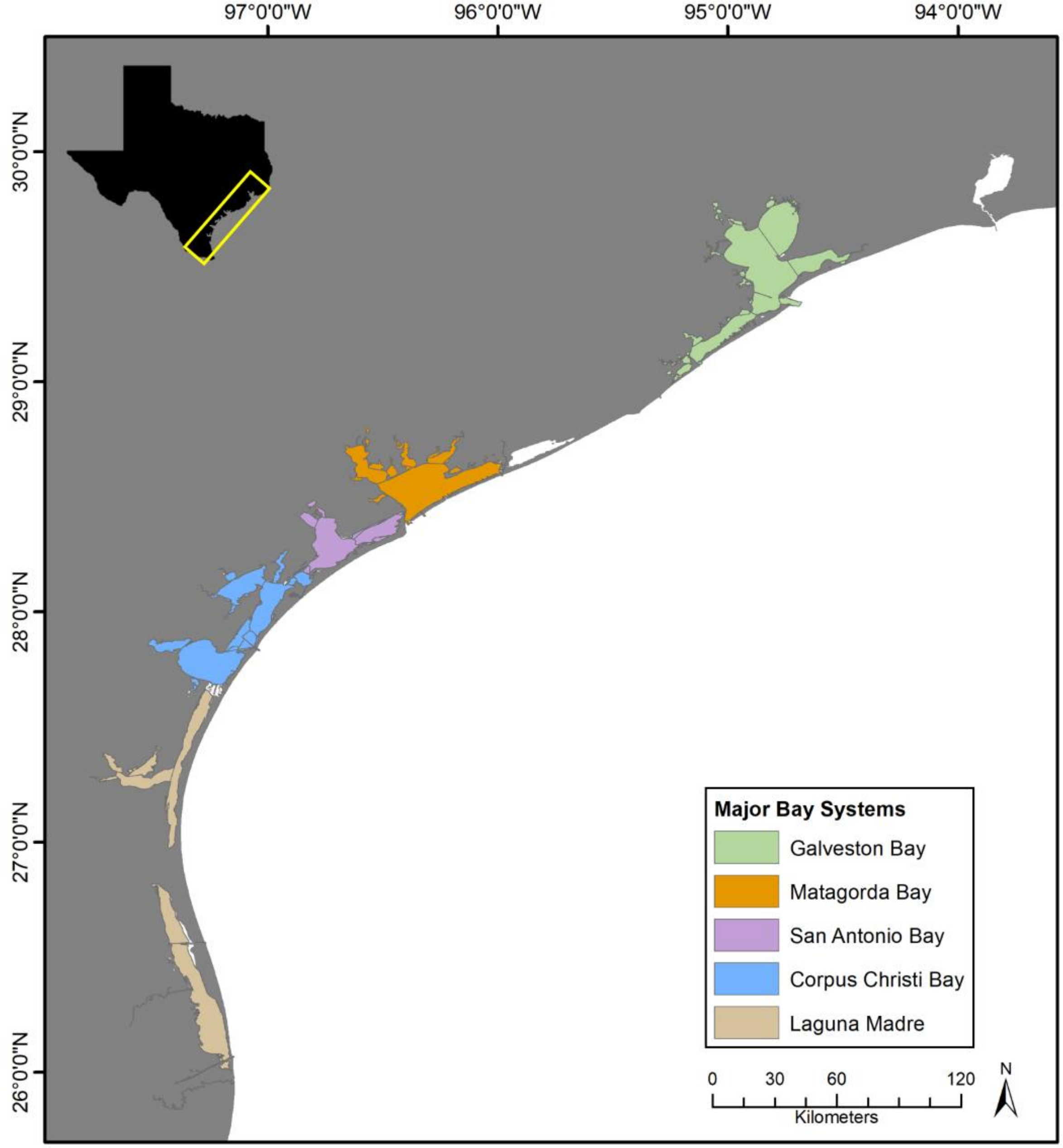

Figure 1. Map showing the five major bay systems along the Texas coast used in this study.

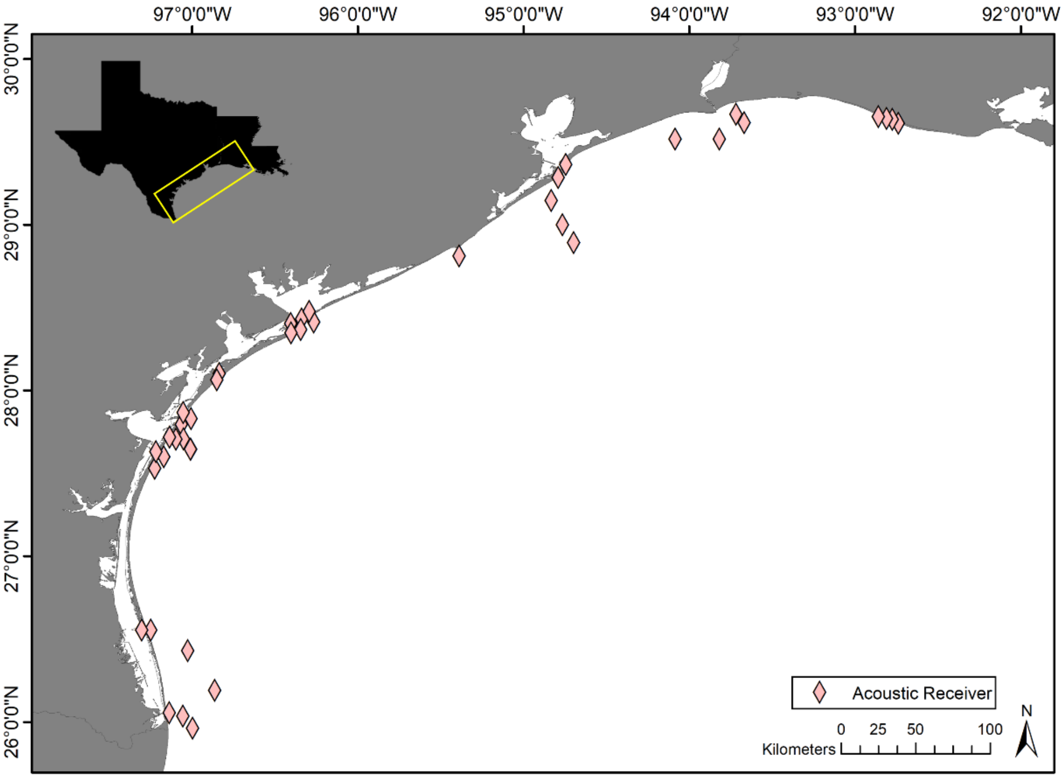

Figure 2. Map showing coastal array located in the western Gulf of Mexico comprised of Innovasea acoustic receivers along the Texas coast and western Louisiana.

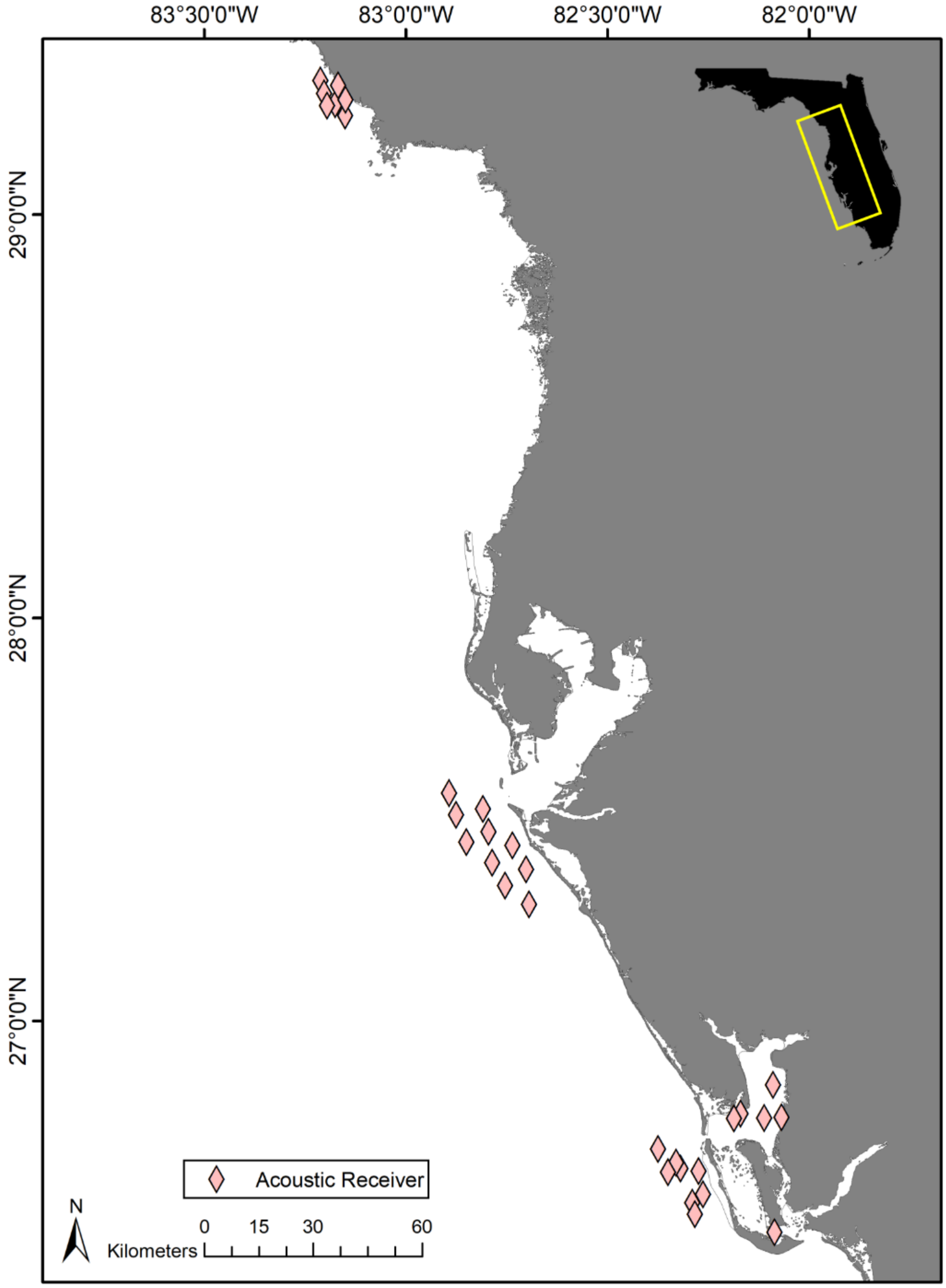

Figure 3. Map showing acoustic receivers along the western Florida coast that detected tarpon acoustically tagged in this study.

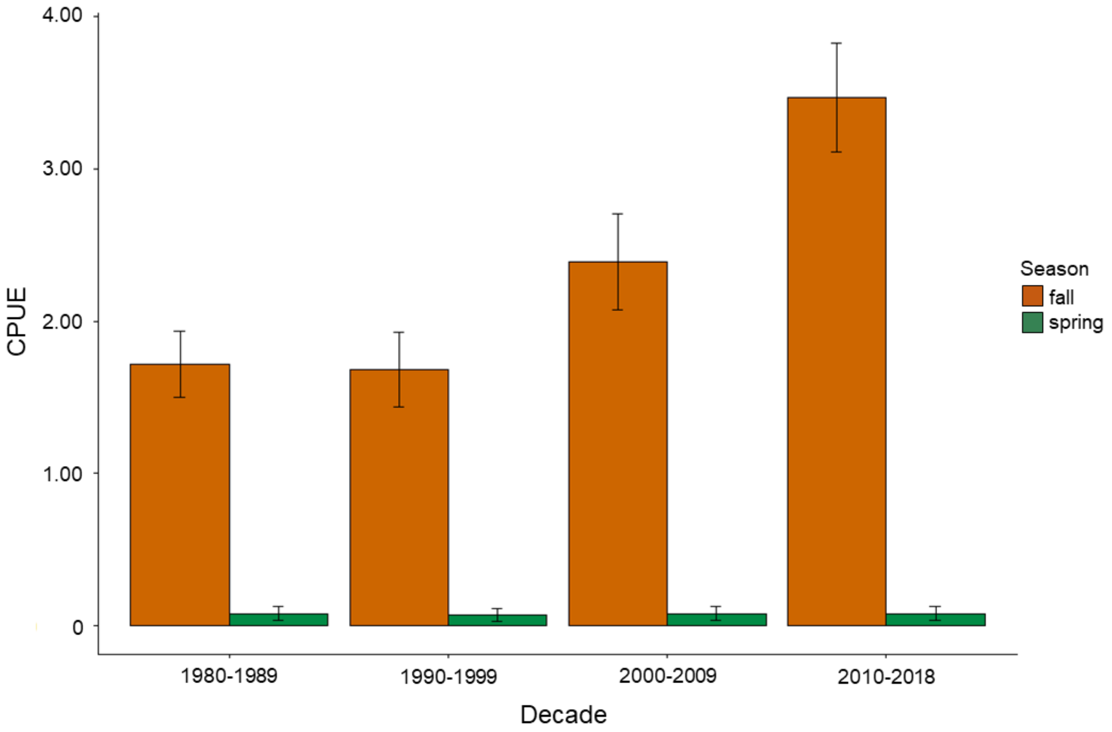

Figure 4. Seasonal variation (spring and fall) in mean decadal CPUE (catch per 1,000 hrs. soak time) of tarpon collected in TPWD gillnet surveys from all five bay systems surveyed (Galveston Bay, Matagorda Bay, San Antonio Bay, Corpus Christi Bay, and Laguna Madre) pooled.

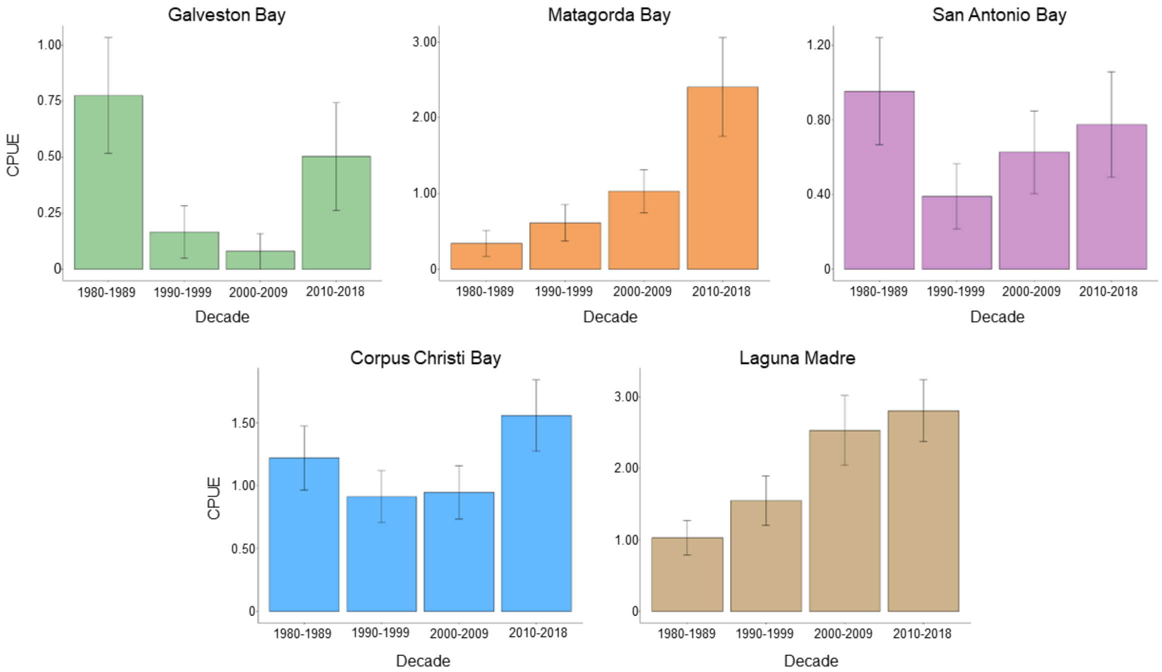

Figure 5. Mean decadal CPUE (catch per 1,000 hrs. soak time) of tarpon in gillnet surveys for each of the five bay systems (Galveston Bay, Matagorda Bay, San Antonio Bay, Corpus Christi Bay, and Laguna Madre) from 1980 to 2018.

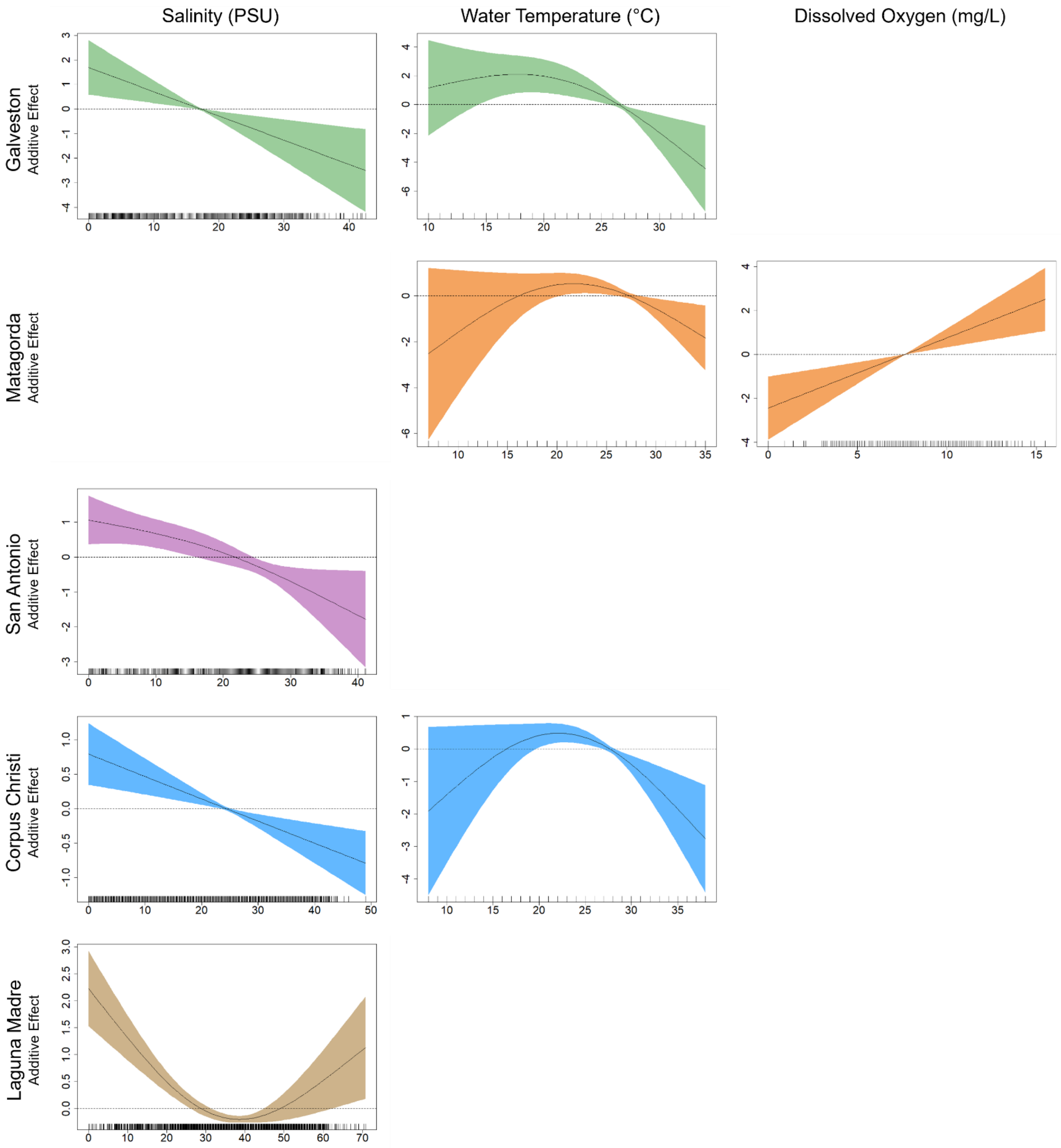

Figure 6. Response plots showing additive effect of significant abiotic variables having an effect on tarpon presence from the final generalized additive models (GAMs) for each of the five major bay system along the Texas Coast. Plot contains salinity (PSU) (left), temperature (°C) (middle), and dissolved oxygen (mg l^{-1}) (right). Solid line represents smoothed values while shaded areas indicate 95% confidence intervals.

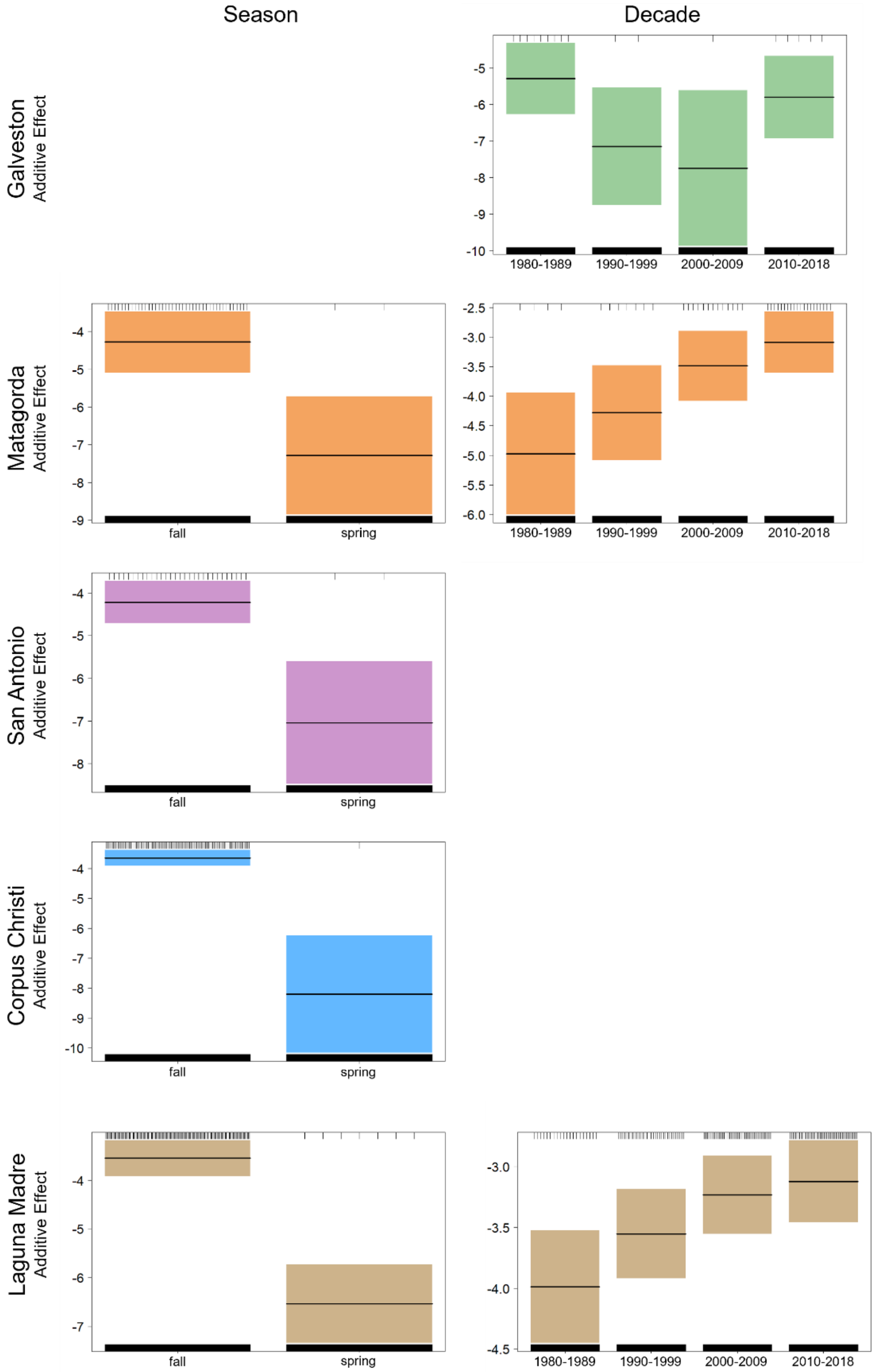

Figure 7. Response plots from the final generalized additive models (GAMs) for significant temporal variables having an effect on tarpon presence across each of the five major bay system on the Texas Coast. Plot depicts season (left) and decade (right). Shaded areas represent 95% confidence intervals.

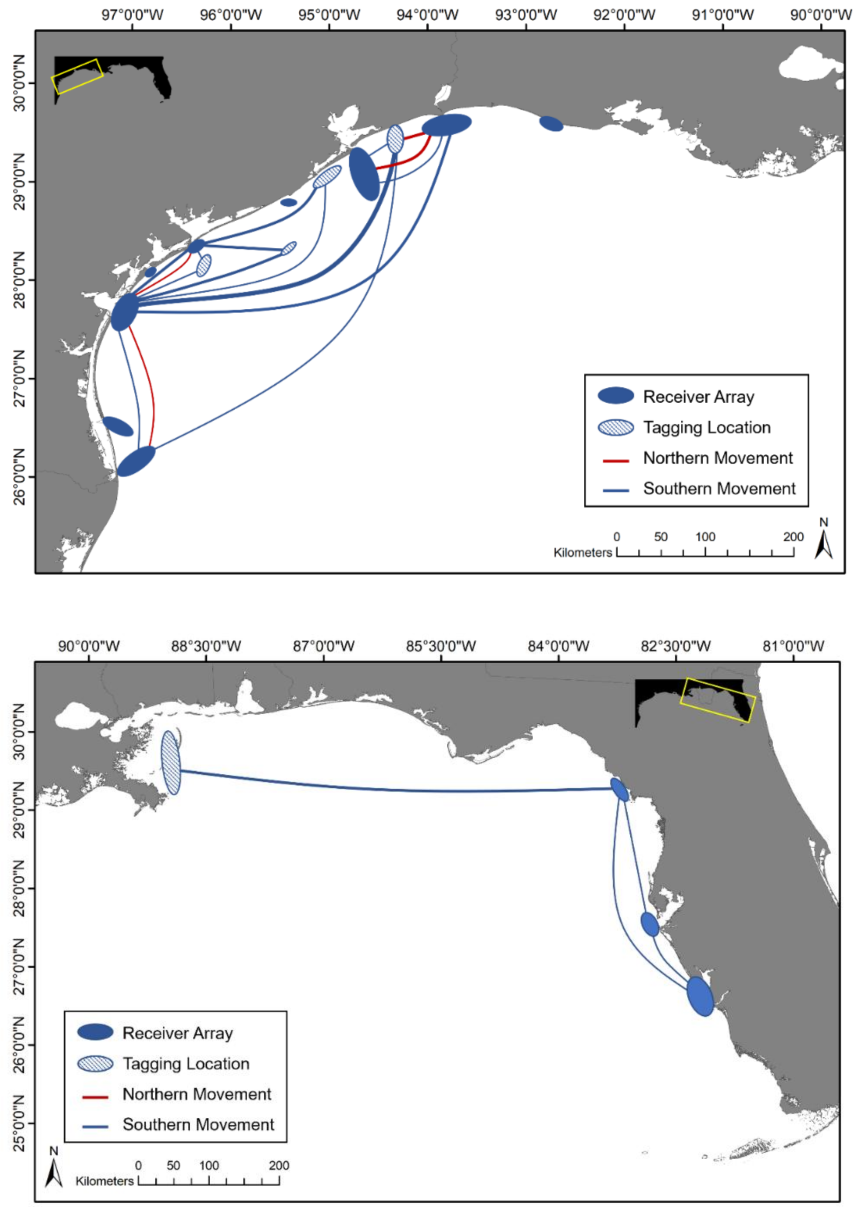

Figure 8. Tarpon movement between coastal acoustic arrays in the western Gulf of Mexico (top) and eastern Gulf of Mexico (bottom) derived from acoustic transmitter detections. Red lines represent northern movements whereas southern movements are shown with blue lines with line weight used to represent number of times the path of travel was utilized ranging from one (lightest) to three (heaviest). Solid blue areas on the map indicate sections of the coastal acoustic array. Dashed blue areas indicate locations that were used for tagging tarpon.

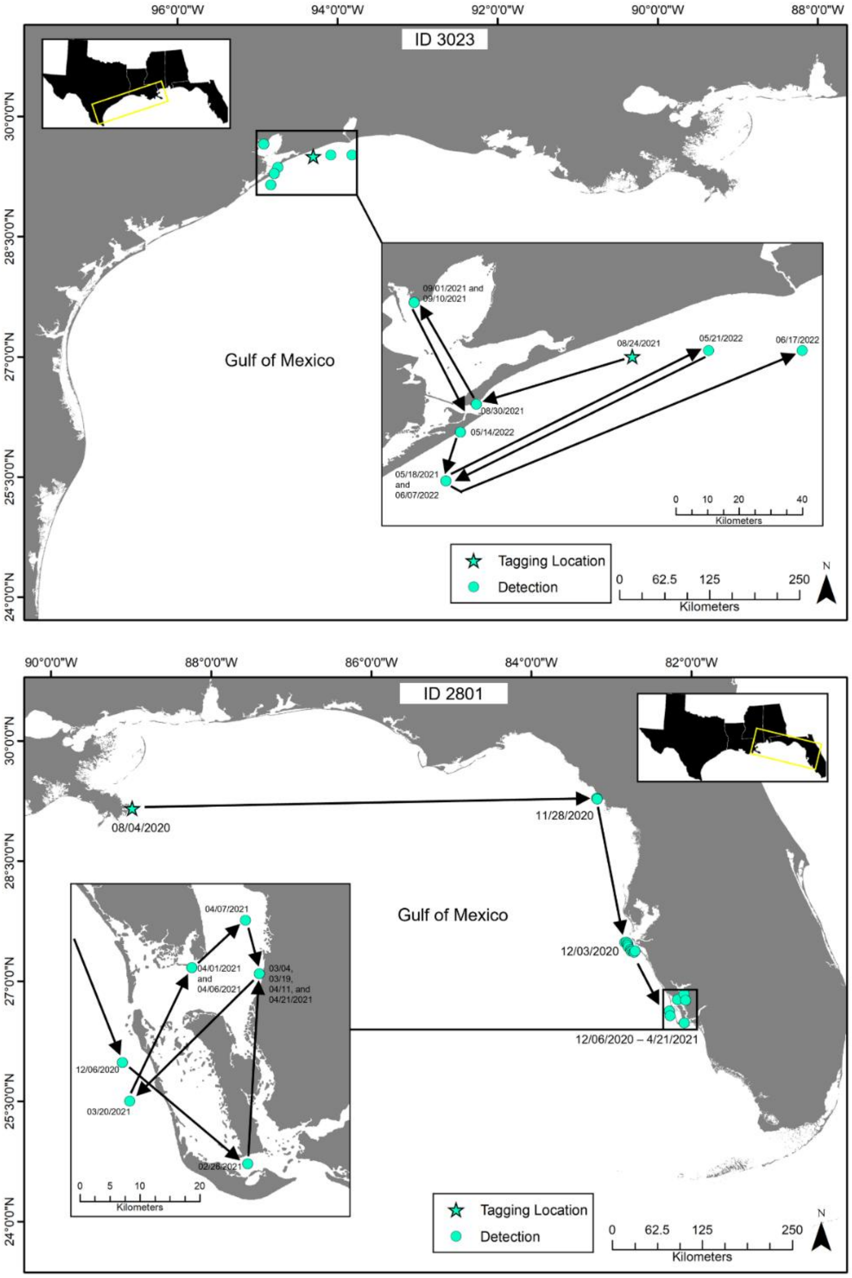

Figure 9. Estimated straight-line tracks, derived from acoustic detections, of tagged tarpon showing examples of coastal-bay connectivity. Star symbols indicates tagging location of the individual and dots represent acoustic receivers that detected the tagged tarpon. Tarpon (ID 3023) (top) and tarpon (ID 2801) (bottom) show movement into bay systems for varying lengths of time during their migrations.

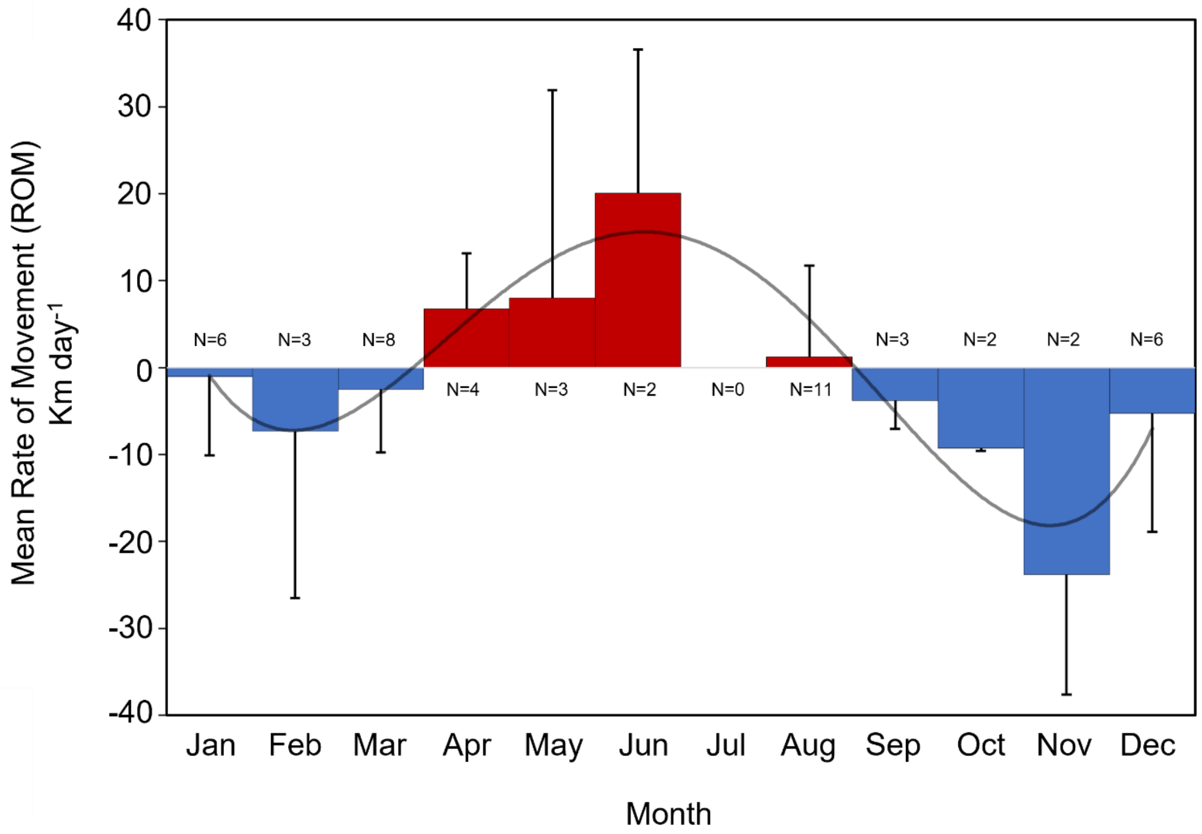

Figure 10. Plot showing mean monthly rate of movement (ROM) (km day-1) estimates of tarpon acoustically tagged in this study. Months with higher northern movements are shown with positive values and red columns, whereas months with southern movement trends are shown with negative values with blue columns. The number of movements used to calculate mean monthly ROM is listed for each month (N).