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Factors related to common bottlenose dolphin (*Tursiops truncatus*) seasonal migration along South Carolina and Georgia coasts, USA

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Abstract: Little is known about common bottlenose dolphin (*Tursiops truncatus*) seasonal migration along the United States southeastern Atlantic coast, or what factors influence migratory patterns. Therefore, our objectives were to: 1) document evidence for seasonal movement of dolphins in this region (that would indicate migratory behavior) and 2) determine if seasonal changes in abundance and temporary emigration (i.e., migration indicators) for dolphins along South Carolina and Georgia coasts are related to changes in water quality variables. Previously collected capture-recapture data (from visual sightings of individual dolphins) and water quality data from Charleston, South Carolina and St. Catherine's Island, Georgia were used to achieve our objective. Robust design models were used to estimate seasonal abundance and temporary emigration for the Charleston population, whereas closed population capture-recapture models were used to estimate seasonal abundances for the St. Catherine's Island population. The Charleston population showed seasonal abundance and temporary emigration patterns with low estimates in winter, which increased in spring, peaked in summer, and decreased in fall. Seasonal temporary emigration was best explained by water temperature, which followed the same general pattern. Seasonal abundance in the St. Catherine's population was best explained by salinity, but no consistent pattern in abundance was observed. Our results not only provide the first evidence of a clear seasonal migration of dolphins in this region, but can aid in conservation and

management efforts by increasing accuracy of abundance estimates.

Keywords: Common bottlenose dolphin, migration, temporary emigration, seasonal abundance, Robust design, closed capture, capture-mark-recapture, photo-identification

1 Introduction

Despite being the most commonly studied marine mammal, little is known about common bottlenose dolphin (*Tursiops truncatus*; Fig. 1) migration patterns along the southeastern United States Atlantic coast [1,2,3]. Migration, in this context, is defined as periodic two-way movement that usually involves the animals returning to the area originally vacated. Many odontocete (i.e., toothed whale) species have complex distributions; therefore, understanding their migration patterns is challenging [4,5]. The southeastern bottlenose dolphin population is comprised of geographically defined subpopulations, known as stocks, including estuarine, coastal, and offshore ecotypes [2]. The estuarine bottlenose dolphin stocks contain residents (i.e., individuals observed in every season throughout the year), while other stocks (e.g., coastal stocks) are generally thought to seasonally migrate through the same area [2-5]. The lack of information regarding seasonal migration in the Southeast may make abundance estimates unreliable because migratory dolphins artificially inflate resident abundance estimates [2,6]. Understanding environmental factors that initiate migrations may help explain seasonal fluctuations in abundance estimates.

Although two migrations, north in the spring and south in the fall, are thought to occur each year in the North Atlantic coastal dolphin population [7], factors related to timing of migrations are unknown [5]. Many environmental factors are believed to be related to

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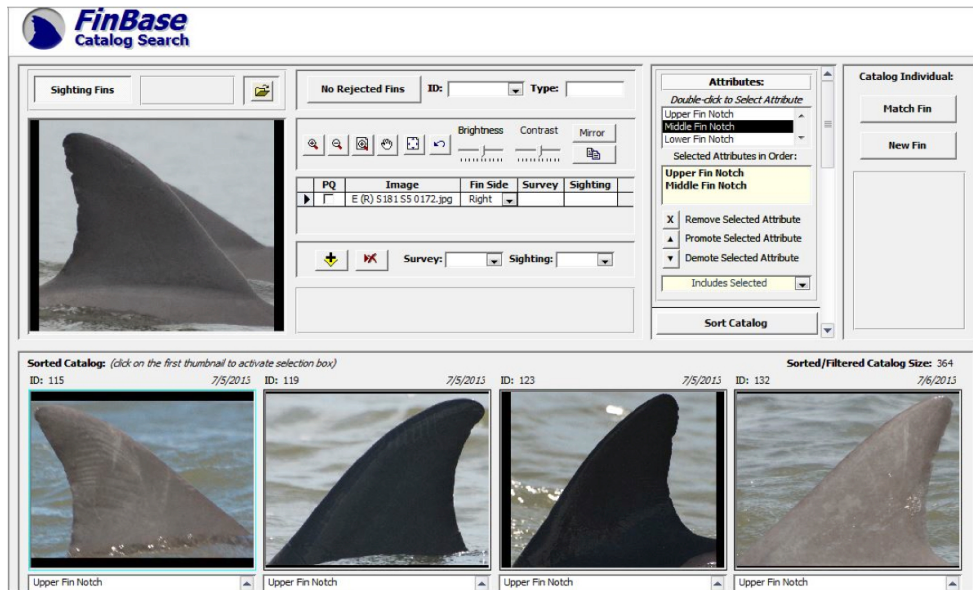


Fig. 1. An illustration of a common bottlenose dolphin (*Tursiops truncatus*) contributed by Garth Mix Designs (© Garth Mix) and an example of the photo-identification matching process using common bottlenose dolphin dorsal fins within FinBase to obtain individual sighting histories. Photographs taken by the Georgia Dolphin Ecology Program under National Oceanic and Atmospheric Administration research permit (Letter of Confirmation 17245).

seasonal dolphin migration patterns [4,8-11], however, few empirical data are available. For example, as water temperature and prey abundance decrease in northern areas, dolphins likely migrate south to warmer waters with higher prey availability [3,5,11]. However, prey availability data are difficult to obtain at a large scale, whereas environmental data are easier to obtain, making environmental factors more practical for managers to evaluate and use as predictors of migration. Examining environmental variables (e.g., water quality) possibly related to migration and seasonal abundance fluctuations may provide a better understanding of when a migration is likely to be observed in an area.

From a conservation perspective, accurate assessments of abundance and migration timing are needed for bottlenose dolphins in southeastern United States estuaries, as dolphins in this area are exposed to

multiple natural and anthropogenic mortality factors. In South Carolina, McFee et al. (2006) found 25% of strandings, in which the reason for stranding was evident (47% of total strandings), were caused by anthropogenic factors. Of these strandings, 44% were from crab pot rope entanglements [12]. Contaminants from agricultural runoff can concentrate in blubber tissue, likely effecting population health and reproduction [13,14,15]. Additionally, recreation and direct human contact (e.g., propellers and feeding dolphins) also can put dolphins at risk [2]. The effects of these factors are largely unknown because of insufficient abundance data [2,16].

Photo-identification (photo-ID) using natural markings is an established method in cetacean research to identify individuals and estimate population parameters [17]. For example, individual North Atlantic right whales are identified by their unique callosity patterns [18], and

individual Florida manatees are identified by their unique scar patterns [19]. In most dolphin species, individuals can be identified using natural markings found on the dorsal fin, which typically last the lifetime of the individual [20]. Photo-ID databases contain sighting histories for each individual, which can be extracted as capture-recapture data (Fig. 1 [3,20,21]). Capture-recapture models applied to photo-ID data can provide abundance and other population parameter estimates, as well as identification of resident and migratory individuals [3,17,21,22].

To better understand bottlenose dolphin migratory movement and seasonal abundance fluctuations along the southeastern Atlantic coast, we used capture-recapture data extracted from photo-ID databases to examine environmental factors potentially related to migration. Our specific objectives were to 1) determine the general pattern (i.e., timing) of migration in this region, and 2) determine if changes in water quality variables (i.e., water temperature, salinity, pH, dissolved oxygen, and turbidity) were related to seasonal changes in abundance estimates and temporary emigration probabilities along South Carolina and Georgia coasts. Temporary emigration, or γ , is the probability that an individual was not available for observation at a certain sampling period, which can provide insight into movement patterns and thus migration [23]. Previous studies have suggested that changes in water temperature can possibly trigger

dolphin movements [3,5,11], but have not evaluated other water quality variables. Knowledge of factors related to migration will provide a basis for obtaining a more accurate estimate of resident abundance, allowing for effective management decisions regarding natural and anthropogenic impacts on resident dolphins [6].

2 Methods

2.1 Study Area

The South Carolina study area included five estuarine rivers (Stono, Folly, Ashley, Cooper, and Wando), upper and lower portions of Charleston Harbor, and along the coast one km from shore stretching from Isle of Palms to Kiawah Island near Charleston, South Carolina (Fig. 2 [3]). The focal stock in South Carolina was the Charleston Estuarine System Stock (CES [2]). The Georgia study area included tidal waters and embayments around St. Catherine's Island, Georgia (e.g., North and South Newport Rivers, Johnson Creek, Walburg Creek, Sapelo Sound, and St. Catherine's Sound; Fig. 3). The focal stock in Georgia was an undefined stock between the Southern Georgia Estuarine System Stock and the Northern Georgia/Southern South Carolina Estuarine System Stock, which we refer to as the "St. Catherine's population" [2].

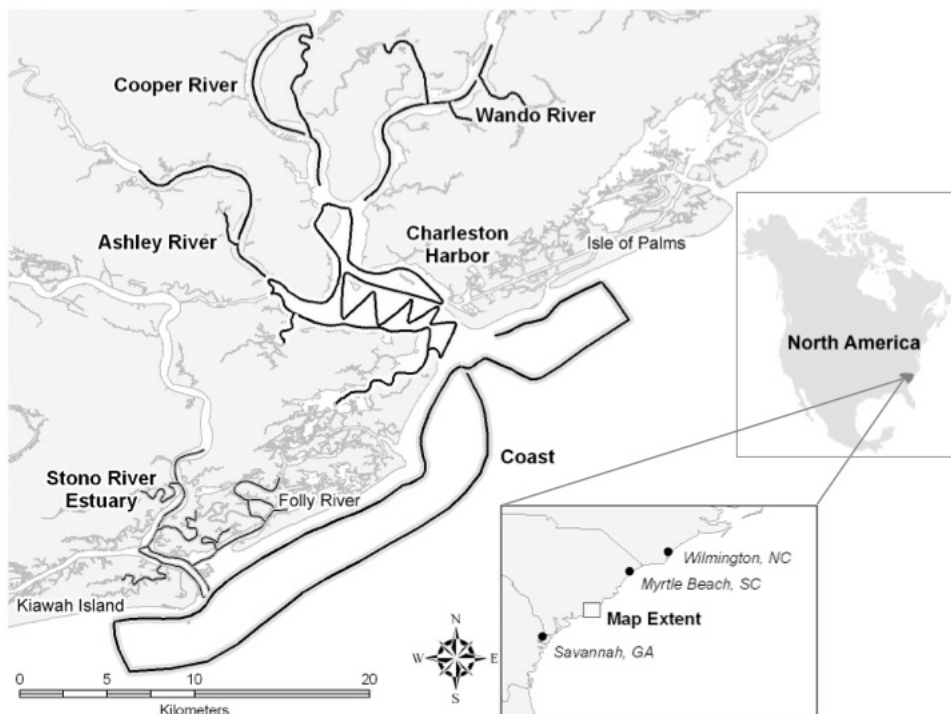


Fig. 2. Survey transects (black lines) conducted by the National Oceanic and Atmospheric Administration National Ocean Service lab in Charleston, South Carolina to obtain bottlenose dolphin photo-identification data near Charleston, South Carolina, 2004-2006 (Speakman *et al.* 2010).

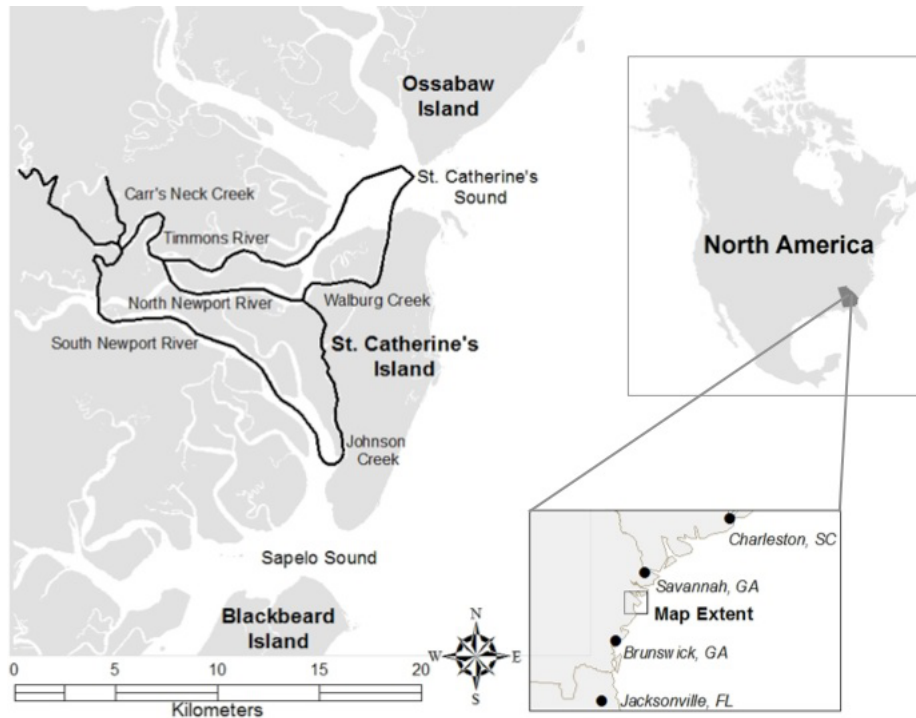


Fig. 3. Survey transects (black lines) conducted by the Georgia Dolphin Ecology Program to obtain bottlenose dolphin photo-identification data near St. Catherine's Island, Georgia, 2011-2013.

2.2 Field Data Collection

The capture-recapture data used in this study were collected by National Oceanic and Atmospheric Administration (NOAA) National Ocean Service lab in Charleston, South Carolina and the Georgia Dolphin Ecology Program (GDEP). NOAA conducted boat-based photo-ID surveys from 2004-2006 as part of a long-term study to monitor bottlenose dolphin abundance and distribution near Charleston, South Carolina [3]. Seasonal surveys were conducted in winter (January), spring (April), summer (July), and fall (October), which produced four primary sampling periods per year (total primaries = 12), each with two secondary periods (total secondaries = 24). Secondary periods (three-five days to sample all transects) were conducted within three weeks of each other, with two months separating each primary period. NOAA photo-ID survey protocols are detailed in Speakman et al. (2010).

GDEP conducted boat-based photo-ID surveys from 2011-2013 as part of a long-term study to assess the ecology and behavior of bottlenose dolphins near St. Catherine's Island, Georgia. Two-day surveys were conducted twice per month as weather permitted, resulting in 49 total surveys. Surveys were categorized by season (i.e., winter = December-February; spring = March-May; summer = June-August; fall = September-November).

GDEP surveys were similar to NOAA survey protocols. Surveys were conducted by two-four crew members aboard a 5.8 m skiff with a 70 horsepower engine. Survey speed was 24 km per hour until a dolphin sighting occurred. A Nikon D90 DSLR with a 75-300 mm NIKKOR telephoto zoom lens was used to photograph dorsal fins. Data collected at the time of sighting included date, time of day, spatial coordinates, total number of animals, number of calves, behavior, and environmental conditions.

2.3 Photo Analysis

Images were organized by survey date and sighting event. Images were graded for quality on a weighted scale based on five characteristics: focus, contrast, angle, fin visibility/obscurity, and the proportion of the frame filled by the fin [3]. Only photographs of average or excellent quality were retained to reduce fin-matching errors. Retained images were transferred to FinBase [21]. Matched fins were entered under the same catalog identification number, and those without a match were assigned a new catalog identification number (Fig. 1). At least two persons verified matches and new individuals in the cataloging process to avoid introduction of observer bias and to reduce the chances of missing matches or misidentifying fins that

have changed (i.e., gained markings over time). Fins with minimal or no markings were designated as ‘unmarked.’ Sighting histories of each ‘marked’ individual observed by NOAA and GDEP were contained within their respective photo catalogs, and capture-recapture files were extracted from each dataset.

2.4 Water Quality Data

Water quality data were obtained for the Ashepoo, Combahee, and Edisto (ACE) Basin, South Carolina (approximately 62 km from CES) and Sapelo Island, Georgia (approximately 20 km from St. Catherine’s) from the National Estuarine Research Reserve System Centralized Data Management Office (NERRS [24]). Water quality variables used for analysis included water temperature, pH, dissolved oxygen, salinity and turbidity. NERRS collected water quality data from at least four stations within ACE Basin and Sapelo Island at 15 minute intervals. Depth at which data were collected depended on tidal state at time of recording. Data for ACE Basin were collected at an average depth of 2.25 m, and data for Sapelo were collected at an average depth of 2.06 m. We extracted data from all stations within the ACE Basin data for NOAA sampling dates and all stations within the Sapelo Island data for GDEP sampling dates. We calculated means for each water quality variable per season. For standardization, we subtracted values for each primary by the mean of the respective variable, and divided by the standard deviation of the variable (i.e., mean = 0 and standard deviation = 1).

2.5 Data Analysis

Because our objective was to determine the general pattern of migration, we estimated abundances for only the marked portion of each population. We did not adjust the estimates to include the unmarked portion, as it cannot be determined if unmarked individuals remain in or leave the area. To estimate abundance and temporary emigration for CES, we used Robust Design (RD [23,25]) models in program RMark [26], which is an interface for program MARK [27] within program R [28]. We assumed *a priori* that survival probability was constant, as stranding records from the study area indicated there were no seasonal effects on the number of dolphin stranding events [3]. We also assumed that capture and recapture probabilities were equal, as the probability of resighting an individual should not have been affected by the initial

sighting. We estimated number of marked dolphins present in the study area (N), probability of a dolphin temporarily emigrating during the current sampling period given that it was observable in the previous sampling period (i.e., emigration, γ''), and probability of a dolphin temporarily emigrating during the current sampling period given that it was unobservable in the previous sampling period (i.e., immigration, γ' [23]). We evaluated whether the CES exhibited random or Markovian temporary emigration. In cases of random temporary emigration the probability of an individual temporarily emigrating between primary periods is independent of whether the individual was observable (γ'') or unobservable (γ') during the previous period (i.e., $\gamma'' = \gamma'$). With Markovian temporary emigration, the probability of an individual temporarily emigrating between primary periods is dependent on whether the individual was observable or unobservable during the previous period (i.e., $\gamma'' \neq \gamma'$ [23,29]).

We first created a constant Markovian emigration model in which capture probability and temporary emigration remained constant across sampling periods. We also created Markovian emigration models with temporary emigration containing a single water quality variable and constant capture probability to evaluate which water quality variable best explained temporary emigration probabilities. We used a step-wise Akaike’s Information Criterion corrected for small sample size (AIC_c [30]) approach to find the best combination of predictor variables [31]. We then created random emigration models using the same steps used to create Markovian models and assumed that if multiple variable models were not necessary for Markovian emigration models, they were not necessary for random emigration models.

We also created Markovian and random emigration models with time-varying capture probability to account for capture variability among seasons (i.e., primary periods) or secondary periods. We created a Markovian emigration model with capture probability varying by primary periods with constant temporary emigration, as well as models with temporary emigration containing uncorrelated water variables. We then created a random emigration model with capture probability varying by secondary periods with constant temporary emigration, then added models with temporary emigration containing uncorrelated water variables. We evaluated all models using AIC_c to determine which model best explained the data.

We were unable to estimate abundance and temporary emigration for the St. Catherine’s population using RD because four secondary surveys were not completed due to inclement weather. Therefore, we used full likelihood

closed population capture-recapture (closed-capture [32]) models using program RMark [26] to estimate abundance for marked dolphins within each season. We assumed *a priori* that the population was closed within each season and that capture and recapture probabilities were equal, as the probability of resighting an individual should not have been affected by the initial sighting. We also assumed that capture probability was constant, as each season represented one primary period and there were no secondary periods.

We separated sighting history data into seasons and created a full likelihood closed-capture model for each season, each with mark-recapture data for respective season and a constant capture probability. This model was used to estimate abundance for each season with more than two surveys ($n = 11$; winter 2011 and winter 2013 were excluded from analyses because only one-two surveys were conducted). After seasonal abundance estimates were obtained, we examined the relationship of seasonal abundance with uncorrelated water quality variables using simple linear regression models, via package stats [33] within program R [33], to determine which water quality variable best explained changes in seasonal abundance. We created one linear regression model for each water quality variable with abundance estimates as the response variable. Statistical significance was accepted at $P \leq 0.05$.

3 Results

3.1 General

NOAA completed 47 surveys from 2004-2006, with 1,423 hours on the water, 9,217 km surveyed on-effort, and 1,961 on-effort dolphin sightings [3]. The CES contained 694 individual dolphin capture histories after photographic quality constraints were applied to the data. GDEP completed 50 surveys from 2011-2013, with 600 hours on the water, 11,312 km surveyed on-effort, and 729 on-effort dolphin sightings. After the removal of poor quality images, the St. Catherine's population contained 297 individual marked dolphins during the three-year photo-ID study.

3.2 Water Quality

For the ACE Basin and Sapelo, mean water temperature was lowest in the winter, increased from spring to summer, and decreased in fall. Mean salinity decreased from winter

to spring and increased from summer through fall. Mean dissolved oxygen and pH decreased from winter through summer and increased in fall. Mean turbidity pattern was inconsistent. For the ACE Basin, mean turbidity was lowest in winter, increased in spring, decreased in summer, and increased in fall, whereas values increased from winter to summer and decreased in fall for Sapelo (Table 1).

Table 1. Mean values for water temperature (°C), salinity in parts per thousand (PPT), dissolved oxygen (DO) in mg/L, pH, and turbidity in nephelometric turbidity units (NTU) for each season from multiple water quality stations in Ashepoo, Combahee, and Edisto (ACE) Basin, South Carolina, 2004-2006, and Sapelo Island, Georgia, 2011-2013, collected by the National Estuarine Research Reserve System Centralized Data Management Office [23].

	Season	Water Temp	Salinity	DO	pH	Turbidity
ACE Basin	Winter	10.82	20.00	8.97	7.85	22.66
	Spring	20.32	17.64	6.55	7.56	85.81
	Summer	29.81	20.08	4.22	7.28	71.30
	Fall	22.39	22.96	5.21	7.52	147.02
Sapelo	Winter	13.75	33.80	7.20	7.99	27.88
	Spring	20.30	24.84	5.37	7.66	38.08
	Summer	29.55	29.49	3.98	7.41	76.94
	Fall	23.14	31.49	5.12	7.64	26.70

For both the CES and the St. Catherine's population, Pearson's correlation coefficient tests indicated that water temperature was negatively correlated with dissolved oxygen and pH ($r = -0.97$ and $r = -0.92$, respectively, for CES; $r = -0.97$ and $r = -0.93$, respectively, for St. Catherine's population), and dissolved oxygen and pH were positively correlated ($r = 0.89$ for CES and $r = 0.94$ for St. Catherine's population). We excluded dissolved oxygen and pH from further analyses to avoid collinearity [34], as water temperature influences the values of dissolved oxygen and pH [35]. Our step-wise AIC_c selection process indicated that no multiple variable models were needed. Therefore, each of our models only included water temperature, salinity, or turbidity.

3.3 Seasonal Trends

The model with the most support ($w_i = 0.999$) for the CES was Markovian temporary emigration containing water temperature (Fig. 4 & 5) and capture probability varying by primary period (Table 2). Abundance estimates for CES followed a general seasonal trend of lowest in winter,

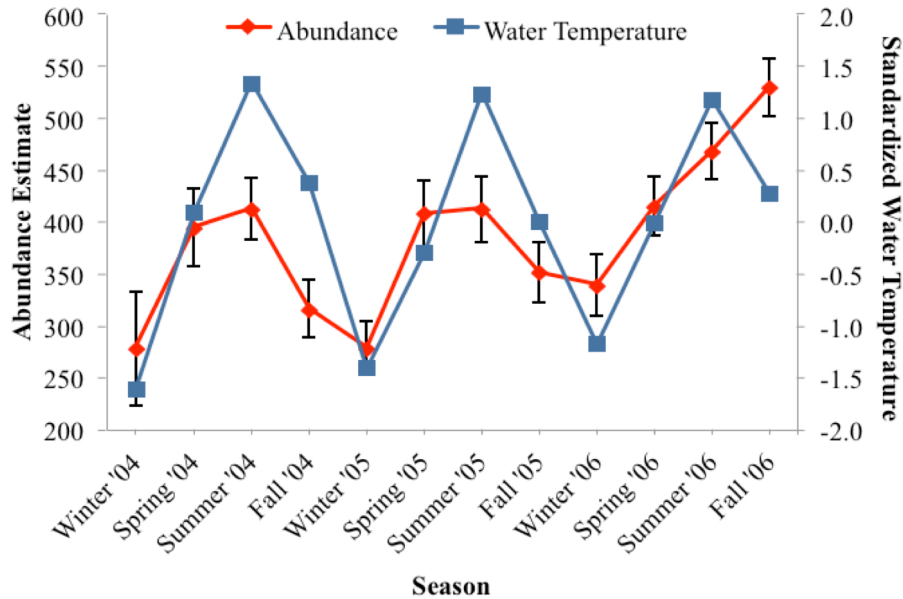


Fig. 4. Seasonal bottlenose dolphin abundance estimates with standard errors and water temperature near Charleston Harbor population, South Carolina, 2004-2006.

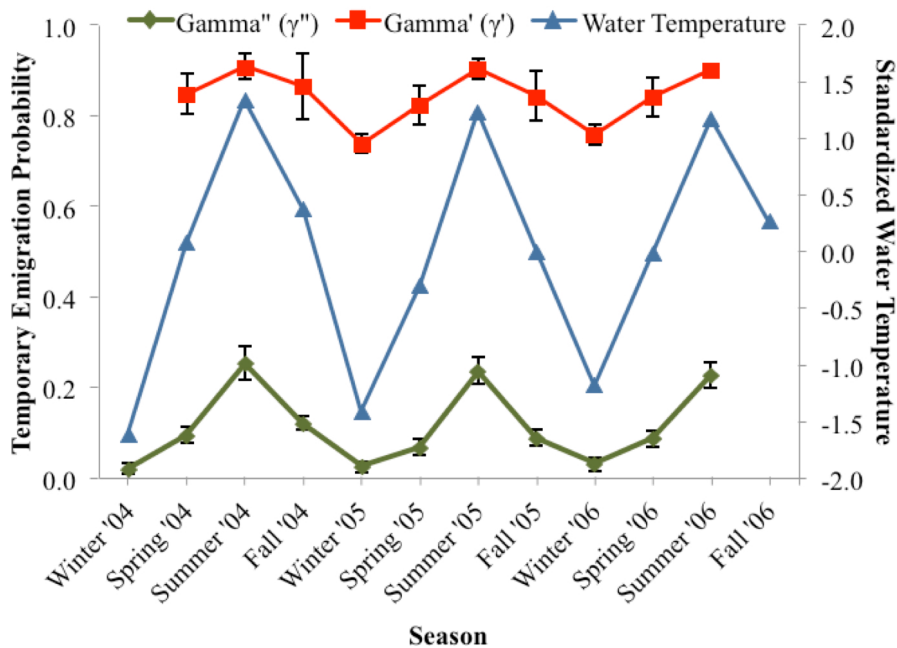


Fig. 5. Seasonal bottlenose dolphin temporary emigration probabilities with standard errors and water temperature for the Charleston population, South Carolina, 2004-2006.

which increased in spring, peaked in summer, and decreased in fall (Fig. 4). The lowest abundance estimate occurred in winter 2004 ($N = 277 \pm 54$, 95% CI = 200-424), which coincided with the lowest water temperature value (Fig. 4). Highest abundance estimates were in summer in 2004 ($N = 413 \pm 30$, 95% CI = 363-479) and 2005 ($N = 413 \pm 32$, 95% CI = 359-484) and in fall 2006 ($N = 529 \pm 27$,

95% CI = 483-592). High abundances in summer 2004 and 2005 coincided with the highest water temperature values (Fig. 4).

Temporary emigration probabilities for the CES followed the same seasonal pattern as abundance estimates, with lowest probabilities in the winter and highest in the summer (Fig. 5). The lowest γ'' was in winter

Table 2. Random ($\gamma'' = \gamma'$) and Markovian ($\gamma'' \neq \gamma'$) temporary emigration model selection results, including number of parameters (K), AIC_c values, ΔAIC_c values, model weights (w_i), and deviances, used to estimate abundance and temporary emigration probability for the Charleston population, South Carolina, 2004-2006. Survival (S), random temporary emigration ($\gamma'' = \gamma'$), Markovian temporary emigration ($\gamma'' \neq \gamma'$), capture (p) and recapture (c) probability, and number of dolphins (N) were modeled constant ($.$), by primary period (s), by secondary period (t), by water temperature ($temp$), by salinity (sal), and by turbidity ($turb$).

Model	K	AIC_c	ΔAIC_c	w_i	Deviance
$S(.) \gamma''(temp) \neq \gamma'(temp) p(s) = c(s) N(s)$	29	-9701.484	0.000	0.999	3241.007
$S(.) \gamma''(turb) \neq \gamma'(turb) p(s) = c(s) N(s)$	29	-9686.605	14.879	0.001	3255.886
$S(.) \gamma''(sal) \neq \gamma'(sal) p(s) = c(s) N(s)$	29	-9686.187	15.298	0	3256.305
$S(.) \gamma''(.) \neq \gamma'(.) p(s) = c(s) N(s)$	27	-9681.743	19.741	0	3264.830
$S(.) \gamma''(temp) \neq \gamma'(temp) p(t) = c(t) N(s)$	19	-9676.834	24.650	0	3286.010
$S(.) \gamma''(temp) \neq \gamma'(temp) p(.) = c(.) N(s)$	18	-9670.953	30.531	0	3293.918
$S(.) \gamma''(turb) \neq \gamma'(turb) p(t) = c(t) N(s)$	19	-9664.428	37.056	0	3298.416
$S(.) \gamma''(turb) \neq \gamma'(turb) p(.) = c(.) N(s)$	18	-9656.565	44.919	0	3308.306
$S(.) \gamma''(sal) \neq \gamma'(sal) p(t) = c(t) N(s)$	19	-9655.665	45.819	0	3307.179
$S(.) \gamma''(sal) \neq \gamma'(sal) p(.) = c(.) N(s)$	18	-9649.639	51.845	0	3315.232
$S(.) \gamma''(.) \neq \gamma'(.) p(t) = c(t) N(s)$	17	-9645.161	56.323	0	3321.736
$S(.) \gamma''(turb) = \gamma'(turb) p(s) = c(s) N(s)$	27	-9643.536	57.978	0	3303.037
$S(.) \gamma''(.) \neq \gamma'(.) p(.) = c(.) N(s)$	16	-9639.167	62.317	0	3329.755
$S(.) \gamma''(sal) = \gamma'(sal) p(s) = c(s) N(s)$	27	-9635.965	65.519	0	3310.608
$S(.) \gamma''(.) = \gamma'(.) p(s) = c(s) N(s)$	26	-9632.358	69.126	0	3316.255
$S(.) \gamma''(temp) = \gamma'(temp) p(s) = c(s) N(s)$	27	-9630.353	71.131	0	3316.221
$S(.) \gamma''(turb) = \gamma'(turb) p(t) = c(t) N(s)$	17	-9597.219	104.265	0	3369.678
$S(.) \gamma''(turb) = \gamma'(turb) p(.) = c(.) N(s)$	16	-9591.212	110.272	0	3377.710
$S(.) \gamma''(sal) = \gamma'(sal) p(t) = c(t) N(s)$	17	-9583.275	118.209	0	3383.622
$S(.) \gamma''(.) = \gamma'(.) p(t) = c(t) N(s)$	16	-9580.193	121.292	0	3388.729
$S(.) \gamma''(temp) = \gamma'(temp) p(t) = c(t) N(s)$	17	-9578.546	122.939	0	3388.352
$S(.) \gamma''(sal) = \gamma'(sal) p(.) = c(.) N(s)$	16	-977.275	124.209	0	3391.646
$S(.) \gamma''(.) = \gamma'(.) p(.) = c(.) N(s)$	15	-9574.191	127.293	0	3396.753
$S(.) \gamma''(temp) = \gamma'(temp) p(.) = c(.) N(s)$	16	-9572.546	128.938	0	3396.376

2004 (0.021 ± 0.011 , 95% CI = 0.007-0.061) and the lowest γ' was in winter 2005 (0.739 ± 0.072 , 95% CI = 0.576-0.864). Both of the lowest temporary emigration probabilities coincided with low water temperature values. The highest γ'' and γ' occurred in summer 2004 (0.255 ± 0.036 , 95% CI = 0.191-0.331 and 0.908 ± 0.044 , 95% CI = 0.779-0.965, respectively), coinciding with the high water temperature values (Fig. 5).

The St. Catherine's population abundance estimates varied annually (Fig. 6). Abundance decreased from spring 2011 to fall 2011 and increased slightly in winter 2011-2012, remaining relatively constant through fall 2012. Abundance began to increase in winter 2012-2013 and continued to increase through summer 2013, decreasing in fall 2013. Linear regression results indicated that salinity

was significantly related to abundance ($F_{1,9} = 9$, $p = 0.01$, $r^2 = 0.44$). The lowest abundance estimate was found in fall 2011 ($N = 20 \pm 11$, 95% CI = 12-64), which corresponded to the highest salinity value (Fig. 6). Although summer had low abundance estimates in 2011 ($N = 52 \pm 7$, 95% CI = 44-73) and 2012 ($N = 34 \pm 9$, 95% CI = 25-62), the highest abundance estimate occurred in summer 2013 ($N = 266 \pm 35$, 95% CI = 212-352).

4 Discussion

Our study provides evidence that dolphin migratory movements along South Carolina and Georgia coasts likely occur from spring through fall based on the seasonal

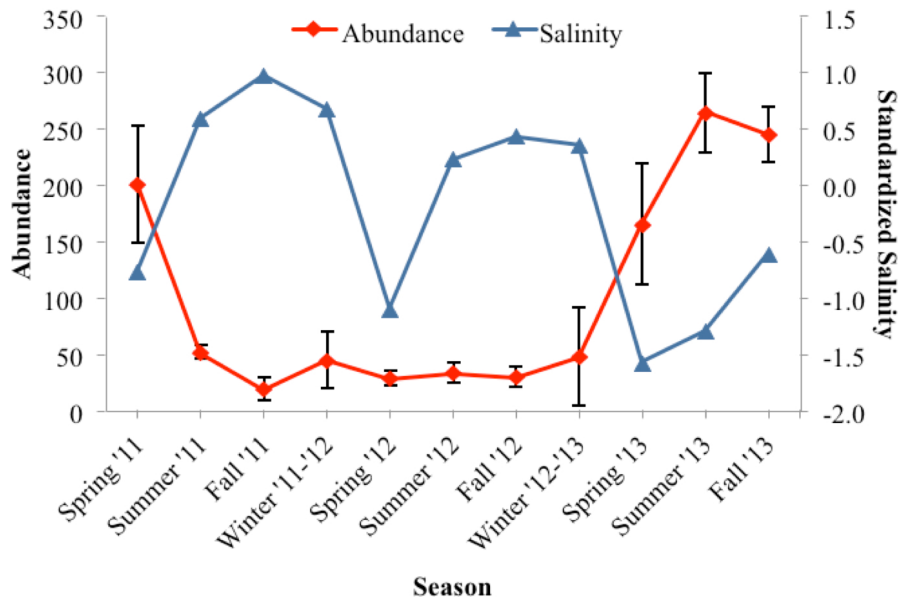


Fig. 6. Seasonal bottlenose dolphin abundance estimates with standard errors and salinity for the St. Catherine's population, Georgia, 2011-2013.

abundance estimates and temporary emigration patterns (i.e., indicators of seasonal migration). Abundance estimates for the CES showed a consistent seasonal trend; low abundance occurred in winter, increased in the spring, peaked in the summer, and decreased in the fall (excluding fall 2006). Seasonal patterns of localized dolphin abundance have also been documented in Florida [36,37], North Carolina [11], South Carolina [3,22], and Texas [7,8]. Consistent low abundance estimates in winter likely represent resident individuals, as there are dolphins present year-round, and only residents are likely to stay throughout the winter [3,7,22].

The CES abundance estimates also suggest the presence of seasonally resident dolphins (i.e., dolphins occurring in the area in the same season for multiple years, but not consecutive seasons). Seasonal residents likely move into the area during warmer seasons and emigrate before winter, resulting in an increase in abundance estimates from spring to summer [3,22,38]. Therefore, abundance estimates for the CES likely included dolphins that resided in the study area, as well as dolphins that moved within the study area and eventually emigrated. Evidence of seasonal residents was also noted in South Carolina [22] and in Texas [7]. The seasonal abundance trend for the CES supports the possibility of seasonal resident migration beginning in spring and ending in fall.

Temporary emigration probabilities for the CES followed the same seasonal pattern as abundance estimates. Based on the best fitting model, the CES exhibited

Markovian temporary emigration, meaning dolphins showed a seasonal emigration pattern [3,23,36,39]. Low temporary emigration probabilities in winter, along with low abundance estimates, provide evidence of resident dolphins present. In addition, more dolphins immigrated than emigrated, as γ' was consistently higher than γ'' [23]. In Australia, Smith et al. (2013) found that Indo-Pacific bottlenose dolphins (*T. aduncus*) also exhibit Markovian temporary emigration rather than random. The seasonal pattern of temporary emigration probabilities, coinciding with seasonal abundance estimates, provides evidence that seasonal residents likely overlap with the CES during spring, summer, and possibly fall.

Model results indicate that water temperature was related to CES temporary emigration probabilities. Water temperature has previously been proposed as a dolphin migration cue [11,22,40-43], but water temperature could be correlated with other factors. For example, water temperature could influence prey availability [3,4,5,10,11] and other environmental factors (e.g., dissolved oxygen, pH, and salinity [35]). Atlantic menhaden (*Brevoortia tyrannus*) are reported to have a water temperature threshold and are not found in estuaries below 3°C [44]. Therefore, as water temperature increases, it is likely the abundance of Atlantic menhaden increases within estuaries. Temporary emigration probability trends could indicate that dolphins immigrate to the Charleston Harbor because of increased prey, which are likely being influenced by warmer water temperature. Increased prey

availability also usually leads to increased commercial fishing efforts. Shrimp trawling increases within the Charleston Harbor in summer, which could attract migratory dolphins to the area to feed on discarded bycatch [3]. Therefore, temporary emigration could be indirectly related to other factors that are influenced by water temperature.

Abundance estimates from closed-capture models demonstrated considerable annual variation in the St. Catherine's population. Although abundance results do not show a consistent yearly trend as the CES, results confirm that seasonal abundance variability [7,8,11,22,36,37] exists for the St. Catherine's population. The data also suggest that the St. Catherine's population contains residents, as there are some individuals that remain in the area through all seasons [3,7,22]. Similar to the CES, increases in abundance estimates for the St. Catherine's population provide evidence that abundance estimates likely included dolphins that resided within the study area, as well as dolphins that moved within the study area and eventually emigrated.

Of the variables evaluated, salinity best explained variation in dolphin abundance estimates for the St. Catherine's population. Low salinity levels are likely to occur in spring when rainfall increases freshwater flow, and high salinity levels likely occur in summer when evaporation increases [10,35]. Higher abundance estimates occurred at unusually low salinity levels in spring through fall 2013, which indicates that migration is likely to occur at low salinity values. These results add salinity as a possible factor related to dolphin migration, which has not been evaluated as a migration cue in previous studies. However, possible dolphin prey, such as Atlantic menhaden and spot (*Leiostomus xanthurus*), are influenced by salinity [10,44]. For example, larvae and juvenile Atlantic menhaden tend to inhabit low-salinity areas [44]. An increased amount of juvenile menhaden or other prey near mouths of estuaries could attract migratory dolphins to the area; therefore, salinity could be indirectly related to seasonal fluctuations of the St. Catherine's population abundance estimates.

It is important to note that our results indicated water temperature and salinity were related to, not necessarily driving factors of, seasonal abundance fluctuations and seasonal temporary emigration probabilities related to migration. The highest abundance estimate for CES occurred in fall 2006, which did not correspond to the highest water temperature as expected. Therefore, there is evidence that other factors may be influencing movement of migratory dolphins. Other vertebrate species, such as birds [45,46] and fish [47,48], rely on photoperiod as

a migration cue. In fish, photoperiod can determine a range of dates in which a migration can occur, but other environmental factors (e.g., water temperature) act as releasing factors [49]. For example, photoperiod may trigger an increase in an animal's activity, or migratory restlessness. This increased activity can cause sensitivity to releasing factors, which initiate migration [50]. Zolman (2002) found a relationship between dolphin density and photoperiod in a South Carolina estuary. Therefore, it is likely that photoperiod is a primary dolphin migration cue, while water temperature and salinity are secondary migration cues for the CES and St. Catherine's population, respectively.

Both datasets showed evidence of transients (i.e., dolphins only sighted once throughout the study period [6]) during spring, summer, and fall. It is important to note that single-sighted dolphins classified as transients might be residents who by chance were only seen once [6,22] and should be considered "possible transients." Given NOAA's study design, it is likely that individuals classified as possible transients found within the Charleston Harbor were indeed transients. However, a possible transient individual found within St. Catherine's might have been sighted only once due to uncontrollable survey conditions (e.g., inclement weather) or poor photographic quality images. For the CES, 32% of individuals observed were possible transients. The number of possible transient encounters was low in winter, increasing the spring and summer, and decreasing in fall (excluding fall 2006). Speakman et al. (2010) observed an unusually high number of possible transients in fall 2006, resulting in an upward bias in abundance estimates [22]. Zolman (2002) proposed that transients encountered in a South Carolina estuary could be migratory dolphins, as they are only encountered within the study area once. Therefore, the presence of possible transients, along with increased abundance estimates and temporary emigration probability trends, further supports the idea that migratory dolphins overlap with the CES in spring through fall. The RD model assumption that the population is closed to immigration and emigration during all secondary sampling periods [23] could have been violated by the presence of possible transients in CES with would have increased abundance estimates and decreased capture probability. Although secondary periods were conducted within three-five days, it is possible that transients utilized the area and emigrated during secondary periods. Another assumption of RD models is that temporary emigration is either completely random, Markovian, or based on a temporary response to first capture [23]. Violation of this model assumption is unlikely, as we evaluated

temporary emigration as both random and Markovian. Under the RD, survival probability is assumed equal for all animals [23]. Because primary periods were conducted within a relatively short time interval (i.e., three months), a violation of this assumption is unlikely. However, RD models can only estimate temporary emigration [23] and cannot differentiate between temporary emigration, death, and permanent emigration, which would cause an inflated survival estimate [3].

For the St. Catherine's population, 56% of individuals were only sighted once. The high percentage of possible transients could be due, in part, to sampling effort. For example, missed surveys due to weather could have resulted in missed resighting opportunities, thus increasing the number of possible transients. The number of possible transient encounters was consistently low in winter seasons. The seasons with the highest number of possible transients corresponded to higher abundance estimates, indicating that the presence of transients does inflate abundance estimates. Similar to the CES, the seasonal pattern of possible transients overlapping with the St. Catherine's population, along with the increased abundance estimates, supports a migration pattern in spring through fall [3,5,22]. Abundance for the St. Catherine's population could also have been biased because of possible transient presence. Although seasonal surveys were conducted within relatively short time intervals (i.e., three months), it is possible that transients could have utilized the area and emigrated within these intervals, thereby violating the assumption of a closed population [32]. The assumption that all animals have the same likelihood to be captured [32] could have also been violated by transient dolphins, which have a lower capture probability than resident dolphins, as transients are only sighted once. In addition, seasonal residents that emigrate would also have a lower capture probability than residents because seasonal residents are only present in the area during certain seasons. The model assumption that marks are constant and not overlooked [32] was likely satisfied. Natural markings typically last an individual's lifetime [17]. However, it is possible for an individual to gain markings or become unrecognizable. To decrease the chances of misidentification and overlooking a match, surveys were conducted within short time intervals and at least two persons were involved in the fin matching process.

Our study is the first to identify environmental variables related to bottlenose dolphin migratory movements in South Carolina and Georgia. From our results, we infer that migration likely occurs from spring to fall in both populations based on seasonal abundance

estimates, seasonal temporary emigration trends for the CES, and evidence of seasonal residents and possible transients (i.e., possible migrants). For example, estimates for the CES showed that increases in abundance occurred when temporary emigration probability (γ') was high, which correlated with water temperature. High abundance estimates, which correlated with salinity for the St. Catherine's population, occurred when encounters of possible transients were high.

Knowing that water temperature and salinity are related to seasonal abundance and temporary emigration fluctuations for these two southeastern dolphin populations is an important step to understanding dolphin migration. Managers could monitor environmental data, such as water temperature and salinity, to predict when a migration is likely to occur. With migration information, managers could warn trawlers of increased possibility of dolphin by-catch. Predicting migrations can also lead to a better understanding of resident population parameters, which will be important in future population monitoring to accurately assess the impacts of natural and anthropogenic factors on resident dolphins.

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