

Does variation in movement tactics and trophic interactions among American alligators create habitat linkages?

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Summary

1. Highly mobile top predators are hypothesized to spatially and/or temporally link disparate habitats through the combination of their movement and feeding patterns, but recent studies suggest that individual specialization in habitat use and feeding could keep habitats compartmentalized.

2. We used passive acoustic telemetry and stable isotope analysis to investigate whether specialization in movement and feeding patterns of American alligators (*Alligator mississippiensis*) in an oligotrophic subtropical estuary created habitat linkages between marine and estuarine/freshwater food webs.

3. Individual alligators adopted one of the three relatively distinct movement tactics that were linked to variation in diets. Fifty-six per cent of alligators regularly travelled from the upstream (freshwater/mid-estuary) areas into the downstream (marine-influenced) areas where salinities exceed those typically tolerated by alligators. Thirty-one per cent of the alligators made regular trips from the mid-estuarine habitat into the upstream habitat; 13% remained in the mid-estuary zone year-round.

4. Stable isotopic analysis indicated that, unlike individuals remaining in the mid-estuary and upstream zones, alligators that used the downstream zone fed at least partially from marine food webs and likely moved to access higher prey abundance at the expense of salt stress. Therefore, 'commuting' alligators may link marine food webs with those of the estuary and marshes in the coastal Everglades and create an upstream vector for allochthonous nutrient inputs into the estuary.

5. This study lends further support to the hypothesis that large-bodied highly mobile predators faced with trade-offs are likely to exhibit individual specialization leading to habitat linkages, rather than compartmentalization. However, the conditions under which this scenario occurs require further investigation.

Key-words: community dynamics, connectivity, consumer-mediated nutrient transport, estuary, individual specialization, stable isotopes, top predators

Introduction

Top predators can play important roles in the dynamics of their communities and ecosystems by coupling spatially and/or temporally segregated food webs (Polis, Anderson & Holt 1997; McCann, Rasmussen & Umbanhowar 2005; Rooney *et al.* 2006). Coupling may occur because diet breadth increases at higher trophic levels and top predators

are more likely to feed from multiple resource pools (Pimm, Lawton & Cohen 1991). When top predators are highly mobile and capable of using a wide variety of distinct resource pools, then they act as a stabilizing force in community and ecosystem dynamics (McCann, Rasmussen & Umbanhowar 2005; Rooney *et al.* 2006; Rooney, McCann & Moore 2008). The majority of studies investigating trophic coupling by predators, however, assume that all of the individuals in a population exhibit similar behaviours (e.g. Helfield & Naiman 2006). Recent tracking and stable isotopic

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studies, however, have revealed that even individuals from the same population can display quite different behaviours (e.g. Eichhorn *et al.* 2009; Fossette *et al.* 2010). Assumptions of population homogeneity in trophic studies, therefore, may overlook important temporally stable variation among individuals in their movements, foraging tactics and diets ('individual specialization'; see Bolnick *et al.* 2003). For example, Eurasian perch (*Perca fluviatilis*) captured within the same lake were hypothesized to couple littoral and pelagic food webs, but in fact individuals displayed individual specialization in both diets and habitat use and therefore perch did not couple these food webs (Quevedo, Svanback & Eklov 2009). Whether specialization in highly mobile top predators outside of lake systems might lead to compartmentalization of food webs is poorly known and is perhaps less likely because the scale of their movements allows them to access food resources at a distance from locations that might be used for other behaviours. In such situations, individual variation in behaviours might actually enhance trophic coupling or lead to unexpected directions of predator-mediated nutrient flow (e.g. Matich, Heithaus & Layman 2011).

Estuaries are critical habitats for many species of recreational, commercial and ecological importance because they are characterized by high primary and secondary productivity and serve as 'nurseries' for many fish and invertebrate species (Beck *et al.* 2001). Species with broad salinity tolerances are generally thought to connect estuaries with other coastal ecosystems whereby they feed in productive estuaries and then move into coastal waters where they deposit nutrients. For example, female blue crabs (*Callinectes sapidus*) feed in estuaries and then move to the mouth of the estuary after mating to release their eggs during spawning (Kennedy & Cronin 2007). Despite the large amount of effort devoted to studying the dynamics of estuaries and their connections to the surrounding terrestrial and aquatic ecosystems, the role of large predators in these systems has largely been overlooked as has the possibility that they may exhibit specialization in their behaviours that could influence ecosystem dynamics.

American alligators (*Alligator mississippiensis* Daudin) are the most abundant large-bodied predators in the south-eastern United States (Mazzotti & Brandt 1994). Although they are generally thought of as a freshwater species, they are also found in brackish waters of estuaries (Mazzotti & Brandt 1994). Alligators require frequent access to low salinity waters throughout their lives because, unlike some crocodilians, they lack functioning salt glands that can excrete excess salt (Taplin 1988). Thus, although the American alligator may inhabit diverse habitats within a broad geographic range, the species is limited by its osmoregulatory capabilities in coastal areas (Dunson & Mazzotti 1989). Indeed, studies of juvenile alligators suggest that they cannot survive for long periods in salinities over 10 ppt (Lauren 1985). Alligators are opportunistic generalist predators (Wolfe, Bradshaw & Chabreck 1987) that are capable of long-range movements over short time periods (Joanen & McNease 1972), but are somewhat constrained in their habitat choices by physiological

limitations. Because of their large bodies, however, adult alligators could tolerate short-term exposure to salt stress and, therefore, have the capacity to be a vector of nutrient flow within and among estuaries and adjacent habitats.

Alligator-mediated nutrient flow may be particularly likely where marine waters are more productive than estuarine or freshwater habitats. One such ecosystem is the 'upside-down' (Childers *et al.* 2006) coastal estuaries of south-west Florida, including the Shark River Estuary (SRE). Alligators are present throughout the SRE from upstream marshes to its mouth. Alligators in this area are almost always detected alone and appear to primarily be engaged in foraging, traveling and resting behaviours (personal observation). Previous work in the SRE suggests that sex ratios are highly male biased (Rice, Hart & Mazzotti 2009), which is probably due to male alligators' preference for deeper open water habitats that typify the SRE, while females generally prefer shallower ponds in marsh landscapes (Joanen & McNease 1970, 1972; Goodwin & Marion 1979) that occur upstream of the estuary. Alligator mating occurs during April–June in south Florida (Mazzotti & Brandt 1994), but only a third of females tend to breed in any year (reviewed in Thorbjarnarson & Wang 2010). Therefore, the low number of females captured historically in the SRE likely is not because of seasonal breeding movements.

We used American alligators moving throughout the SRE as a model system for investigating whether top predators might link spatially disparate food webs and whether individual specialization in movements might be an important feature of estuarine top predator behaviour. Specifically, we used a combination of acoustic tracking and stable isotope analysis to quantify movement tactics of individual alligators and to determine whether variation in movement tactics was related to differences in trophic interactions (e.g. foraging locations) and their possible role in nutrient transport.

Materials and methods

STUDY SYSTEM

The study was conducted from November 2007 to December 2009 in the SRE of Everglades National Park (ENP), Florida, USA (c. 25°25'N, 81°00'W, Fig. 1). The waters that flow through the SRE originate in the Shark River Slough (SRS), the main source of freshwater flow through ENP (Dalrymple 1996). The SRE is a mangrove dominated tidal river with tidal mean amplitude of 0.5–1.0 m (Romigh *et al.* 2006) and depths that range from 0.5 to 4.0 m. In downstream areas, the mangrove forests are well developed with a dense canopy, while mid-estuary areas support smaller mangrove trees that form a thin buffer between the marsh and open waters (Simard *et al.* 2006). Upstream marshes are dominated by sawgrass (*Cladium jamaicense*). Salinity varies spatially and temporally throughout the estuary as the system alternates between high-precipitation 'wet' seasons and low-precipitation 'dry' seasons (Romigh *et al.* 2006). During the dry season (January–June), salinities measuring > 20 ppt may occur up to 17 km from the mouth of the estuary (A. E. Rosenblatt, unpublished data), while salinities at the mouth, where oceanic waters dominate, can fall in the wet season (July–December) to < 15 ppt (Childers *et al.* 2006).

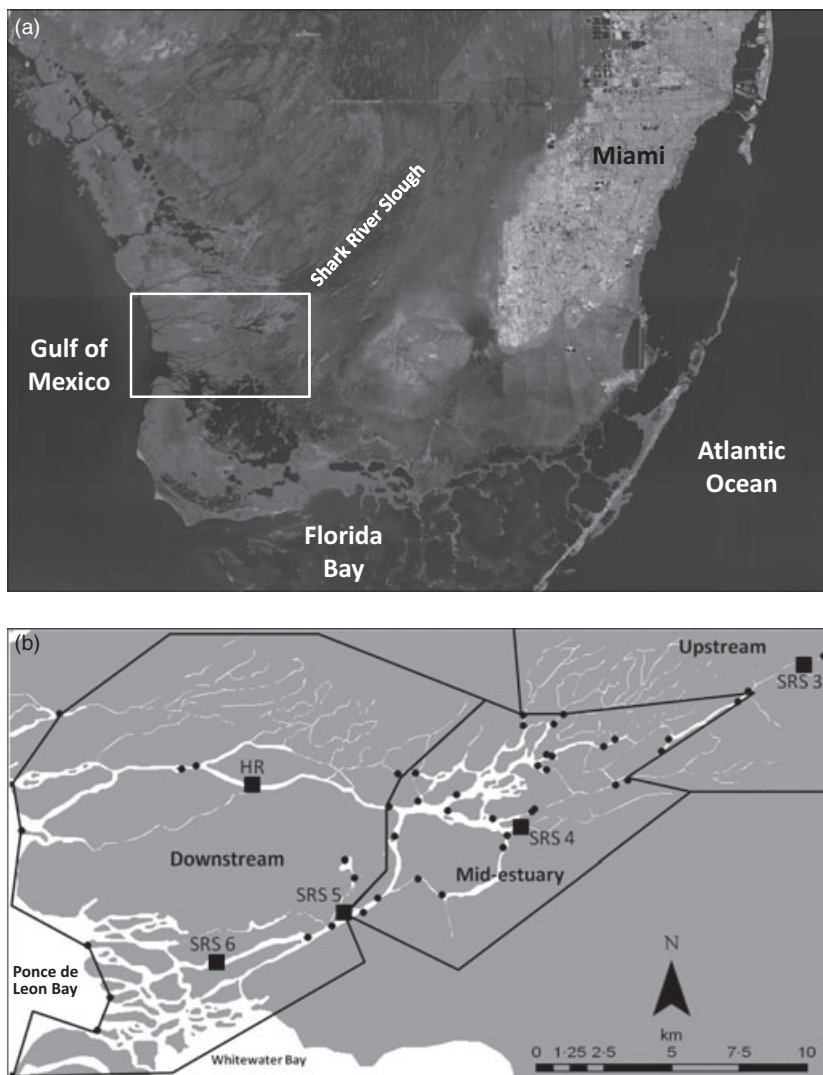


Fig. 1. (a) The study site (white box) is located in the Shark River Estuary of southwestern Florida. (b) Acoustic-monitoring stations (circles) and salinity-monitoring stations (squares) were located throughout the study site and were used to delineate sampling zones (delineated by black lines). Salinity monitors in the Shark River Slough ('SRS') are operated by FCE LTER, and the monitor in the Harney River ('HR') is operated by Everglades National Park.

We divided the SRE into three broad habitats for the purposes of understanding how alligator use of the estuary might vary in response to shifts in physical conditions and whether individuals might show consistent differences in their movement patterns: (i) the 'downstream' marine-influenced zone, (ii) the 'mid-estuary' mixing zone and (iii) the 'upstream' freshwater zone. The boundary lines for each zone were delineated by the placement of four permanent salinity-monitoring stations operated by the Florida Coastal Everglades Long Term Ecological Research (FCE LTER) program (SRS 3, 4, 5, and 6; data available at <http://fcelter.fiu.edu/>) and one by ENP (HR), and the movement-monitoring stations nearest to each of them (Fig. 1). While these zones do not represent distinct habitats, this division of the estuary is appropriate for investigating broadscale changes in space use of alligators, spatiotemporal variation in the environmental conditions that they may encounter and their potential access to marine-derived food webs.

FIELD METHODS

Alligators were captured in the downstream and mid-estuary zones of the SRE during both seasons using standard techniques (Chabreck 1963). Briefly, we searched for alligators at night from a 6-m boat using high-powered spotlights. Searches were made from near the

mouth of the river into the upper reaches of the mid-estuary zone. Narrow channels and/or shallow water depths made it impossible to capture alligators in the upstream zone. Search effort was not equal across the two zones (*c.* 75% mid-estuary, *c.* 25% downstream) because of higher encounter rates with alligators' mid-estuary, but the spatial distribution of effort was similar across seasons. Potential biases introduced by capture distributions were further minimized by deploying relatively few transmitters on a particular night and searching widely every night. When an individual was located, we approached and slipped a metal snare around the neck using a long pole and tightened the snare. Before bringing an alligator onboard, we secured the mouth with a second snare and then with electrical tape. We measured total length, snout-vent length, head length and tail girth to the nearest 0.2 cm. Sex was determined by cloacal examination (Chabreck 1963). All captured individuals were over 1.8 m total length and, therefore, adults (size at maturity in south Florida is 1.5–1.8 m for both sexes; Abercrombie 1989; Dalrymple 1996). For stable isotope analysis, we collected small skin samples (*c.* 1 cm²) from the terminal tail scutes of each captured alligator using sterile surgical scissors. The samples were placed on ice and transported to the laboratory where they were stored at –20 °C.

Alligator movement patterns were quantified with passive acoustic telemetry. Passive acoustic telemetry provides a relatively low-cost

means to determine movements of aquatic organisms within restricted areas or across broad spatial scales and has been used previously for crocodylians (e.g. Franklin *et al.* 2009, Campbell *et al.* 2010). Individually coded V16-4H (Vemco, Halifax, NS, Canada) acoustic transmitters (6.8 cm long \times 1.6 cm diameter, 24 g in air, random transmission interval every 60–120 s, lifespan *c.* 1250 days) were attached using stainless steel wire (encased in nylon tubing to prevent abrasion) threaded through holes made in four tail scutes. The transmitter and wire were then encased in a cool-setting marine-grade epoxy (West Marine, Watsonville, CA, USA) to streamline the attachment and eliminate tangling.

To determine the position of tagged alligators, we deployed an array of 46 Vemco VR2W monitors, each recording the time and identity of tags detected, from downstream exits of the SRE to upstream marshes (Fig. 1). On the basis of range testing in the array, transmitters were detectable at up to 1149 m (Table S1). To determine the general location of alligators when they were not within detection range of a monitor and to assess the direction of travel, most monitors were set in pairs – on opposite sides of the bank and displaced *c.* 400 m along the channel – to form ‘gates.’ Because of the large detection ranges of the monitors relative to channel width (Table S1) and the density of mangroves along the shore making over-land movement difficult, alligators rarely escaped detection. During this study, there were no cases in which an alligator was detected by one set of monitors and then was detected on a second set without being detected on monitors between them (i.e. a gate was never ‘missed’ owing to moving around it overland or missed detections during transit). Monitors were partially housed in PVC pipes embedded in 15-kg concrete blocks attached by chain to a Danforth anchor on one end and a subsurface float on the other. Data were downloaded from the monitors every 2–3 months during the course of the study.

Permanent water monitoring sites collected composite water samples consisting of four 250 mL subsamples drawn every 18 h over 3 days using ISCO autosamplers (Teledyne ISCO Inc., Lincoln, NE, USA), thereby averaging daily salinities across dawn, noon, dusk and midnight. Water temperature was measured at the five monitors closest to each of the five salinity sampling stations using HOBO Pro v2 data loggers (Onset, Cape Cod, MA, USA). Water temperature (accuracy \pm 0.2 °C) was automatically recorded every 10 min throughout the study, and daily means were used for all analyses.

We used salinity variation among sites as an indicator of the physiological stress that would be experienced by alligators residing in each zone. Experimental studies show that salinities above 10 ppt have negative effects on juvenile alligators (Lauren 1985). Although the animals tracked in this study were all adults and may have higher salinity tolerances than juveniles, there are no data on salinity tolerances for adults. We therefore used the proportion of days that salinity at the most seaward salinity-monitoring station in each zone (SRS 6 for downstream, SRS 5 for mid-estuary, and SRS 3 for upstream) exceeded 10 ppt as an estimate of the relative physiological stress alligators would experience there. We also used the 10 ppt threshold for our definitions of the wet and dry seasons: the wet season started when salinity at SRS 5 (the boundary between the downstream and mid-estuary zones) first dropped below 10 ppt (July), and the dry season began when salinity first went above 10 ppt at this site (January).

LABORATORY METHODS

Stable isotopes provide a time-integrated view of the diet of an individual and can be used to track the ultimate source(s) of the consumer’s assimilated nutrients, relative trophic position in food webs

(Fry 2006) and patterns of individual specialization (e.g. Hatase *et al.* 2002; Vander Zanden *et al.* 2010). Nutrient sources are tracked using the $^{13}\text{C} : ^{12}\text{C}$ ratio ($\delta^{13}\text{C}$), and relative trophic position is tracked using the ratio of $^{15}\text{N} : ^{14}\text{N}$ ($\delta^{15}\text{N}$). We used $\delta^{13}\text{C}$ to differentiate the relative importance of marine-based and freshwater/estuary-based food webs. Within the SRE, primary producers and low mobility consumers resident in the freshwater/estuarine food web exhibit $\delta^{13}\text{C}$ values always $< -25\text{‰}$ and usually $< -28\text{‰}$, while residents in the marine food web exhibit $\delta^{13}\text{C}$ values between -11‰ and -19‰ (Chasar *et al.* 2005; Williams & Trexler 2006; Matich, Heithaus & Layman 2011). We used the combination of stable carbon isotope values of individuals and their patterns of movements to estimate the relative degree of habitat coupling.

Tissue samples from the field were washed with deionized water and then dried at 60 °C for at least 72 h before being powdered using a mortar and pestle. Between 0.4 and 0.7 mg of sample was placed in a 5 \times 3 mm tin cup for analysis. We did not extract lipids or make mathematical lipid corrections because C : N ratios (max. = 3.2) were all below the recommended threshold for extraction or correction (3.5; Post *et al.* 2007). Isotopic analyses were performed at Florida International University’s Stable Isotope Laboratory using standard elemental analyzer isotope ratio mass spectrometer procedures. One fifth of the samples were analysed in duplicate, and the mean error attributable to the equipment was 0.25‰ (\pm 0.11‰ SE) for $\delta^{15}\text{N}$ and 0.15‰ (\pm 0.06‰ SE) for $\delta^{13}\text{C}$. The standard deviations of an internal standard (glycine) used by the isotope laboratory were 0.18‰ for $\delta^{15}\text{N}$ and 0.17‰ for $\delta^{13}\text{C}$.

DATA ANALYSIS

Because of the large number of individual detections (up to 180 000 for one individual), we used a custom computer program (Gated Acoustic Telemetry Optimization Routine; Andrew Fritz, FritzTech, Houston, TX, USA) that used the last known location and direction of travel for each alligator (determined from the order of detection and disappearance from monitors) to collapse raw data into dates and times of entry into and exit out of specific ‘zones’ of the study area. We considered any individual alligator that was detected by the same monitor at least twice in one hour as being in the vicinity for the entire hour. When an alligator travelled from one zone (zone A) to another (zone B), we calculated the maximum displacement as the Euclidean distance between the monitor marking the boundary between the two zones and the furthest monitor in zone B that detected the alligator on that trip. Our estimates of distance travelled per trip are conservative because the density of monitoring stations was relatively low and distances between gates were long, especially in the downstream zone (Fig. 1).

To determine the factors that influenced the probability of alligator movement between zones, we used multiple logistic regressions (MLR). Multiple logistic regressions can be used to identify the factors which contribute to the probability of occurrence of a binary response variable (Hosmer & Lemeshow 1989), in this case whether an alligator occupies a certain zone or not. We used MLR to determine the effects of body length, salinity, temperature (daily mean) and length \times salinity on alligator use of zones. Independent MLRs were used for different groups of alligators depending on their zone-use characteristics and were run in the program R 2.1 (R Development Core Team 2009) as generalized linear models with binomial distributions and logit link functions. The model’s goodness-of-fit was determined using the Pearson’s chi-square test.

We calculated Layman *et al.*’s (2007) total area (TA) metric in isotope bi-plot ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$) space for groups of alligators with similar

movement tactics. The TA metric is a quantitative measure of the isotopic niche space occupied by each group, and by measuring the amount of overlap between the different polygons, we could elucidate possible differences in trophic interactions of the groups. Because isotopic signatures of alligator skin turns over relatively slowly (likely hundreds of days on the basis of laboratory studies of other reptiles; e.g. Seminoff, Bjorndal & Bolten 2007), differentiation of isotopic niche spaces reflect long-term differences in average trophic interactions of individuals. We used a jackknife randomization protocol to test whether observed overlaps of TAs of groups of alligators that varied in movement patterns were less than expected by chance. For each iteration, we randomly reassigned observed isotopic values to individuals with known movement tactics and calculated the resulting overlap in convex hulls of the isotope space occupied by each group of alligators. We completed 1000 iterations of the protocol and considered groups to show significant differentiation if more than 95% of iterations produced greater overlap of convex hulls than were observed (i.e. $P < 0.05$ for a one-tailed test). We used a one-tailed test because our *a priori* expectation was for there to be differentiation (rather than significant overlap) on the basis of movement tactics. We further explored the relationships between stable isotopes and body length, capture season, capture location, distance travelled, average trip duration and 'pause time' using multiple linear regression. We were unable to assess the influence of alligator body condition on stable isotope values because mass measurements were not collected for all individuals.

Results

INTERZONE VARIATION IN ABIOTIC CONDITIONS

There was significant variation in daily average salinities among sites (Kruskal–Wallis test, $H_4 = 780.9$, $P < 0.001$) and between seasons (Mann–Whitney rank sum test, $T = 885475.5$, $P \leq 0.001$) with salinity decreasing as distance from the Gulf of Mexico increased and remaining higher in the dry season than in the wet (Fig. 2). *Post hoc* pairwise Dunn's tests revealed significant variation (all $P \leq 0.01$) in salinities among all the sites. During the wet season, salinities were never above 10 ppt in the upstream zone, above 10 ppt 40% of the time in the mid-estuary zone and 94% of the time

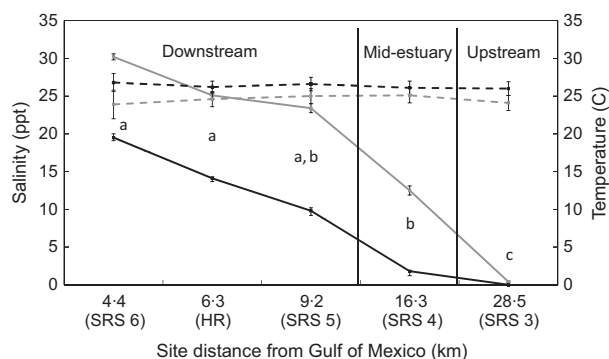


Fig. 2. Spatial variation in temperature (dashed lines) and salinity (solid lines) during the wet (black lines) and dry (grey lines) seasons. Vertical black lines indicate boundaries between zones. Sites with different letters exhibited significant differences in average monthly salinity within a season. Error bars are \pm SE.

in the downstream zone. During the dry season, salinities were > 10 ppt 0% of the time in the upstream zone, 92% of the time in the mid-estuary zone and 100% of the time in the downstream zone. Daily mean water temperature was significantly higher in the wet season (26.2 °C \pm 0.08 SE) than the dry season (24.6 °C \pm 0.09 SE; $T = 2579521.0$, $P \leq 0.001$) across all sites, and water temperature varied across sites ($H_4 = 22.2$, $P \leq 0.001$; Fig. 2) with water temperature increasing slightly (*c.* 0.7 ° between upstream monitors and the mouth of the Shark River) as distance from the Gulf of Mexico decreased. *Post hoc* pairwise Dunn's tests showed that water temperatures varied significantly only between SRS 6 and SRS 3 and between SRS 5 and SRS 3. Therefore, spatial variation in water temperatures existed within the tracking array and alligators could access slightly higher water temperatures in the downstream zone. Daily average salinity and temperature were not temporally correlated at any site (linear regression, all $R^2 \leq 0.01$, $P \geq 0.6$ for all sites).

MOVEMENT TACTICS

From November 2007 to December 2009, we captured and tracked 35 alligators ranging from 184.0 to 280.6 cm total length (mean = 229.3 cm \pm 3.2 SE). The sex ratio was heavily skewed towards males (32 : 3). Interestingly, the three females were captured at different times of the year (January and July). Seven individuals were captured downstream and 28 mid-estuary, and 20 were captured during the dry season and 15 during the wet. Four of the alligators were never detected within our monitoring array.

Sixteen alligators (all males) were detected within the tracking array for at least six continuous months that included part of one wet and one dry season (Table 1). These 16 individuals had average times between first and last detection on our array of 418.6 days (\pm 56.6 SE). Because the other 19 individuals spent much shorter amounts of time on our array (mean = 41.7 days \pm 8.8 SE) and were only present during a single season, they were not included in further analyses. During the wet season, the 16 alligators collectively spent 48% of their time in the downstream zone, 44% in the mid-estuarine zone and 8% in the upstream zone. During the dry season, they spent 16% of their time in the downstream zone, 73% in the mid-estuary zone and 11% in the upstream zone. These trends in zone use were generally consistent throughout the study except for the 2009 wet season when downstream zone use was almost triple that of mid-estuary zone use (Fig. 3); though, this result was most likely caused by small sample size near the end of the study.

Despite the appearance of general population habitat-use patterns, three different broad classes of alligator movements were identified among these 16 individuals (Table 1). The first group ('residents,' $n = 2$) remained within the mid-estuary zone for the entire detection period. The second group ('downstream commuters (DCs),' $n = 9$) regularly moved between the mid-estuary and downstream zones and occasionally entered the upstream zone. The third group ('upstream commuters,' $n = 5$) regularly moved between the

Table 1. Summary of acoustic-monitoring data for the 16 American alligators (all male) tracked in the Shark River Estuary that yielded sufficient data for comparisons of movements among seasons

Date deployed	Xmitter code	Movement tactic	Capture zone	Total length (cm)	Total detection period (days)	Total number of trips	Mean trip duration days (\pm SE)	Min./max. trip duration (days)	Min./max. displacement downstream (km)
4 October 2007	6825	UC	Mid-estuary	221.8	193	4	13.2 (\pm 9.8)	0.1/42.3	NA
4 October 2007	6827	DC	Downstream	254.6	483	43	5.5 (\pm 1.5)	0.1/64.3	1.0/13.4
19 October 2007	6822	DC	Mid-estuary	255.4	796	28	6.0 (\pm 3.1)	0.02/81.5	1.0/1.0
19 October 2007	6824	DC	Mid-estuary	218.6	750	52	2.9 (\pm 0.4)	0.1/11.2	1.0/2.4
19 October 2007	6826	DC	Mid-estuary	243.6	598	24	6.2 (\pm 1.8)	0.5/39.2	1.0/11.6
19 October 2007	6828	DC	Mid-estuary	249.0	288	17	0.7 (\pm 0.3)	0.1/4.2	1.0/2.2
20 November 2007	6821	DC	Mid-estuary	234.0	771	20	15.6 (\pm 3.6)	0.6/60.8	2.4/2.4
20 November 2007	6823	DC	Downstream	213.8	261	25	5.1 (\pm 3.0)	0.3/74.1	1.0/2.4
20 November 2007	6829	Resident	Mid-estuary	234.0	268	0	NA	NA	NA
31 January 2008	9636	DC	Mid-estuary	230.2	697	13	22.2 (\pm 20.1)	0.5/263.6	1.0/11.6
20 February 2008	9635	Resident	Mid-estuary	244.2	169	0	NA	NA	NA
9 April 2008	2162	UC	Mid-estuary	280.6	314	526	0.4 (\pm 0.02)	0.04/3.0	NA
9 April 2008	2169	UC	Mid-estuary	239.2	298	12	8.4 (\pm 1.7)	0.05/21.6	NA
28 April 2008	2165	UC	Mid-estuary	252.4	346	247	0.3 (\pm 0.02)	0.01/2.0	NA
18 July 2008	2167	UC	Mid-estuary	226.4	241	6	15.8 (\pm 6.2)	0.2/36.4	NA
25 July 2008	2163	DC	Downstream	261.2	224	22	7.2 (\pm 2.0)	0.1/31.2	1.0/11.6

A 'trip' is defined as the period of time after an alligator moves from the mid-estuary zone into the downstream zone or from the mid-estuary zone into the upstream zone.

UC, upstream commuter; DC, downstream commuter.

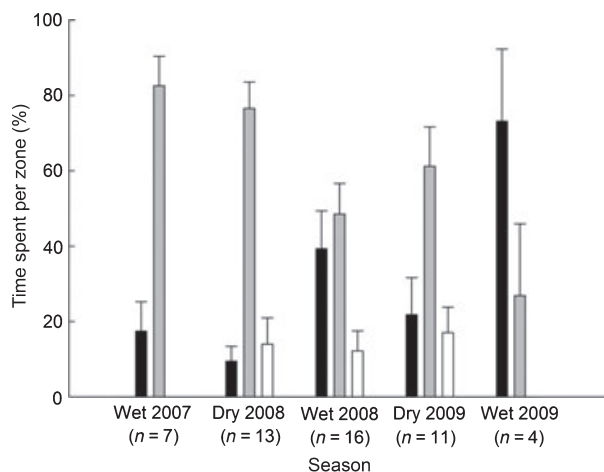


Fig. 3. Mean variation in the use of the downstream (black bars), mid-estuary (grey bars) and upstream (white bars) zones during wet and dry seasons by 16 American alligators. Not all 16 alligators produced data during every season. Error bars are \pm SE.

mid-estuary and upstream zones and never used the downstream zone. No alligators remained resident in the downstream zone and the spatial pattern of our captures and array layout made it impossible to document upstream residents. We did not detect any difference in body length between alligators that used downstream zones and those that did not (t -test, $t_{14} = -0.3$, $P = 0.8$).

Commuting alligators made frequent trips between multiple zones and varied widely in the amount of time spent in the downstream or upstream zones (Table 1). Downstream commuters travelled between the mid-estuary and downstream

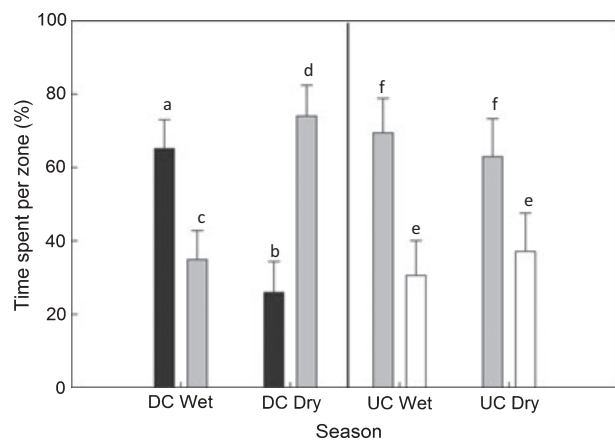


Fig. 4. Seasonal variation in mean zone use among downstream commuters (DC, $n = 9$) and upstream commuters (UC, $n = 5$). Downstream = black bars, mid-estuary = grey bars and upstream = white bars. Bars of the same colour with different letters above them are significantly different. Error bars are \pm SE.

zones between 13 and 52 times each during the course of the study (mean = 27.1 ± 4.2 SE) and spent significantly more time downstream during the wet season than during the dry (paired t -test, $t_8 = 4.4$, $P = 0.002$; Fig. 4), although one individual displayed the opposite trend. Downstream commuters generally did not spend much time downstream per trip, averaging 6.6 days (± 1.3 SE). However, four of the DCs remained within the downstream zone for more than 60 consecutive days, indicating a high degree of variation in trip duration. 'Pause' times between downstream trips were consistent, averaging 3.0 days (± 0.4 SE) in the mid-estuary

zone. Only two individuals paused for more than 40 days at a time. Interestingly, trip duration and pause time were not correlated ($R^2 = 0.002$, $P = 0.5$). Distance travelled per trip was relatively short for the DCs, averaging 2.6 km (± 0.2 SE), but because of the spacing of monitors in this zone DCs may have actually moved considerably further. Indeed, four alligators travelled to the coastal waters of the Gulf of Mexico (22–26 km roundtrip) during some trips (Table 1). Movements into the downstream zone occurred mostly during the wet season ($74\% \pm 10$ SE). Eight of the nine DCs were tracked during portions of two wet seasons, and all of these individuals displayed downstream commuting behaviour in both seasons. Therefore, movement tactics appear to be stable across years. Indeed, for the six individuals that were tracked for two consecutive full-length wet seasons (none were detected in the array for more than two), there was no evidence of interannual variation in the number of trips made per wet season ($t_5 = -0.1$, $P = 0.9$). Three DCs made trips into the upstream zone; all of these trips ($n = 5$) occurred during the dry season.

Upstream commuters (UCs) did not differ significantly in the amount of time spent upstream or in the mid-estuarine zone across seasons ($t_4 = -0.9$, $P = 0.4$; Fig. 4). Also, UCs did not vary seasonally in the number of trips made per individual (Wilcoxon signed rank test, $z = -0.7$, $P = 0.6$) or average trip duration ($t_4 = -0.2$, $P = 0.9$). There were two distinct patterns of alligator movements into upstream habitats. Two individuals (2162 and 2165) made hundreds of short trips, with each trip averaging only 8.5 h (± 0.3 SE) spent upstream. In contrast, the other three UCs (2167, 2169, and 6825) made infrequent, but longer, trips that averaged 10.2 days (± 2.8 SE) per trip. The distribution of trips between wet and dry seasons followed the opposite pattern as that for DCs, with 44% (± 13 SE) of trips occurring during the wet season and 56% (± 13 SE) during the dry. We were unable to gather data on distance travelled per trip into the upstream zone because it lacked distinct channels, and therefore, we only placed one monitoring station 2.6 km upstream

from our furthest upstream 'gate.' This monitor detected two alligators [one UC (2165) and one DC (6822)] over 4 days and 1 day, respectively, during the 2009 dry season.

Salinity, temperature, body length and length \times salinity were significant predictors of downstream habitat use for DCs (Table 2). The DCs were more likely to be present in the downstream zone when salinity was low and water temperature was high, and smaller DCs were more likely to be found downstream than larger DCs, with the smallest DCs reducing their use of the downstream zone during higher salinities less than larger DCs (Fig. 5). Body length and temperature were significant predictors of upstream habitat use by UCs but salinity was not (Table 2). The UCs were more likely to be found upstream when temperatures were higher and larger UCs were more likely to be found upstream than smaller UCs.

TROPHIC INTERACTIONS

The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all 35 alligators were -24.8‰ (± 0.3 SE) and 8.1‰ (± 0.2 SE), respectively. Values of $\delta^{13}\text{C}$ ranged from -27.61‰ to -21.41‰ and $\delta^{15}\text{N}$ ranged from 6.3‰ to 10.3‰ . Although there was no significant difference in $\delta^{15}\text{N}$ values between DC alligators and individuals that did not use downstream areas ($t_{14} = -1.7$, $P = 0.1$), the average $\delta^{13}\text{C}$ of DC alligators ($-24.1\text{‰} \pm 0.5$ SE) was significantly greater than that of mid-estuary residents and UC alligators combined ($-26.7\text{‰} \pm 0.3$ SE, $t_{14} = 3.9$, $P = 0.002$). Furthermore, only 1.9% of the TA of alligators that used downstream areas overlapped with that of individuals that never used downstream areas, and this overlap was driven by a single alligator (Fig. 6). The amount of overlap was significantly less than expected by chance. Only three of the 1000 jackknife randomizations of isotopic values of alligators resulted in equal or less overlap than was observed ($P = 0.003$). The isotopic values of the 19 alligators for which movement tactic was unknown fell largely within the TAs of those with known movement tactics (Fig. 6).

Table 2. Multiple logistic regression analysis of the effects of salinity, temperature and body length on the presence/absence of downstream commuter alligators in downstream zone and upstream commuter alligators in upstream zone. Bold P values indicate significant results at $\alpha = 0.05$

Movement type	Ind. Variable	Estimate	Standard error	z value	P value	
Downstream commuter use of downstream zone	Intercept	-3.97	1.41	-2.81	0.005	
	Length	0.01	0.006	2.24	0.025	
	Salinity	0.24	0.07	3.21	0.001	
	Temperature	0.12	0.01	12.15	< 0.001	
	Length \times salinity	-0.002	0.0003	-5.04	< 0.001	
	Residual deviance = 4004.3 on 3956 d.f.					
	Pearson chi-square P value = 0.71					
Upstream commuter use of upstream zone	Intercept	-15.19	0.95	-15.99	< 0.001	
	Length	0.06	0.004	15.83	< 0.001	
	Salinity	14.70	8.81	1.67	0.10	
	Temperature	0.05	0.01	3.05	0.002	
	Length \times salinity	-0.06	0.04	-1.60	0.11	
	Residual deviance = 1497.0 on 1340 d.f.					
	Pearson chi-square P value = 0.99					

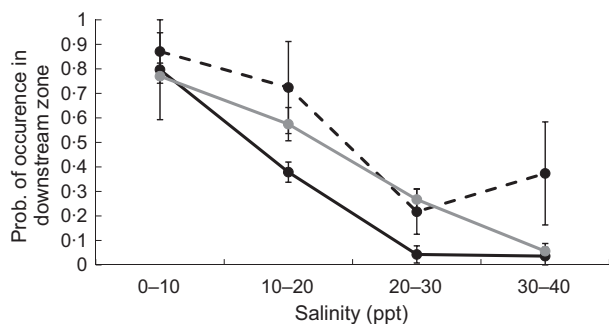


Fig. 5. Probability of occurrence in the downstream zone for the largest third of the downstream commuters alligators (grey line), medium third (black line) and smallest third (dashed black line) at varying levels of salinity. Error bars are \pm SE.

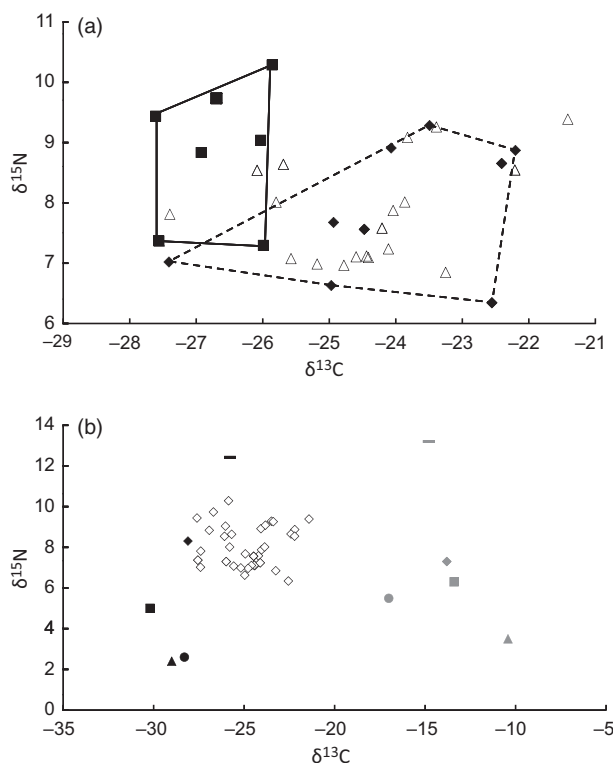


Fig. 6. (a) Stable isotopic values of skin from residents/upstream commuters (UC) (black squares) and downstream commuters (DCs) (black diamonds). White triangles represent alligators for which movement tactic is unknown. Boundaries representing convex hull polygons are shown for residents/UC (solid line) and DCs (dashed line). (b) Mean isotope values of representative primary producers and consumers in the Shark River Estuary relative to the signatures of all alligators captured during this study (white diamonds). Black shapes represent species that reside in the freshwater/estuarine food web, and grey shapes represent species that reside in the marine food web. The freshwater/estuarine food web consists of floc (▲), periphyton (●), ramshorn snail (■, Planorbidae), blue crab (◆, *Callinectes sapidus*) and Florida gar (–, *Lepisosteus platyrhincus*). The marine food web consists of turtle grass (▲, *Thalassia testudinum*), seston (●), bay scallop (■, *Argopecten irradians*), shrimp (◆, Penaeidae) and tarpon (–, *Megalops atlanticus*). Error bars are omitted for simplicity. Data from species other than alligators are from Chasar *et al.* (2005), Williams & Trexler (2006) and M. R. Heithaus (unpublished data).

We used multiple linear regression to test for the effects of body length, maximum distance travelled downstream, total time in the downstream zone, total pause time between trips downstream, average trip duration and average pause duration on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for DCs and body length, total time upstream and average trip duration on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for UCs (Table 3). The only significant relationship was between $\delta^{15}\text{N}$ and maximum distance travelled downstream for DCs, with $\delta^{15}\text{N}$ increasing as distance travelled increased. When all of the alligators were grouped together, there was a significant increase in $\delta^{15}\text{N}$ ($R^2 = 0.4$, $P = 0.03$) with body size, but there was no relationship with $\delta^{13}\text{C}$ ($R^2 = 0.001$, $P = 0.9$). Lastly, there was no significant difference in $\delta^{13}\text{C}$ between individuals with known movement tactics captured in the dry (mean = -26.1‰ , ± 0.6 SE) or wet (mean = -24.8‰ , ± 0.6 SE) seasons ($t_{14} = -1.7$, $P = 0.1$) or between individuals captured in the downstream (mean = -23.6‰ , ± 0.7 SE) or mid-estuary (-25.6‰ , ± 0.5 SE) zones ($t_{14} = 1.3$, $P = 0.2$).

Discussion

Highly mobile predators faced with spatial and temporal heterogeneity in resource availability or abiotic stresses often adopt flexible behaviours (e.g. Estes *et al.* 1998). In some cases, however, individuals specialize on consuming a particular suite of resources, foraging in particular habitats or using different feeding tactics (e.g. Hatase *et al.* 2002; Urton & Hobson 2005; Caut *et al.* 2008; Woo *et al.* 2008; Darimont, Paquet & Reimchen 2009). Although the majority of food web studies tend to ignore consistent differences among individuals in their trophic interactions, a growing literature suggests that individual specialization is widespread (Bolnick *et al.* 2003) and can have important implications for evolutionary (Baird, Abrams & Dill 1992; Bolnick *et al.* 2003) and ecological (e.g. Quevedo, Svanback & Eklov 2009) dynamics. We found that American alligators in the SRE exhibit individual specialization in movement tactics that is linked to long-term variation in trophic interactions and the coupling of habitats in the coastal Everglades. We identified three broad classes of alligator movements that were linked to differences in trophic interactions. The first two movement tactics – individuals that remained in the mid-estuarine brackish zone year-round (residents) and individuals that made periodic trips from the brackish zone into the upstream freshwater zone (UCs) – were associated with feeding primarily in estuarine and freshwater food webs, while individuals using the third tactic – making frequent trips into the downstream zone of the estuary (DCs), including coastal waters – exhibited increased foraging in marine food webs despite spending a large proportion of time in mid-estuary habitats.

For this study, we used passive acoustic telemetry to determine broadscale movements by alligators. One obvious limitation of this approach in a system as large and complex as the SRE is the relatively low spatial resolution of movements. This is especially evident for alligators moving into the

Table 3. Results of multiple linear regression analysis of the effects of multiple variables on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of downstream commuter alligators (top) and upstream commuter alligators (bottom). For the definition of 'trip' see Table 1. 'Pause time' is the amount of time spent in the mid-estuary zone between trips into the downstream zone. Bold *P* values indicate significant results at $\alpha = 0.05$

Ind. Variable	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	Estimate	Standard error	<i>t</i> value	<i>P</i> value	Estimate	Standard error	<i>t</i> value	<i>P</i> value
Intercept	-12.8	10.2	-1.3	0.3	2.4	1.8	1.4	0.3
Avg. pause time	-0.01	0.3	-0.05	0.9	0.09	0.05	1.7	0.2
Avg. trip duration	-0.2	0.3	-0.6	0.6	0.03	0.05	0.7	0.6
Body length	-0.5	0.04	-1.2	0.3	0.02	0.007	2.6	0.1
Max. distance travelled downstream	0.3	0.2	2.0	0.2	0.2	0.03	5.6	0.03
Total pause time	0.0005	0.01	0.04	0.9	-0.004	0.002	-1.6	0.2
Total time downstream	0.003	0.02	0.2	0.9	-0.001	0.003	-0.4	0.7
	Residual SE = 1.64 on 2 d.f. <i>F</i> -statistic = 1.02 on 6 and 2 d.f., <i>P</i> = 0.6				Residual SE = 0.28 on 2 d.f. <i>F</i> -statistic = 19.38 on 6 and 2 d.f., <i>P</i> = 0.05			
Intercept	-18.6	28.9	-0.6	0.6	-19.2	23.7	-0.8	0.6
Total time upstream	0.005	0.02	0.2	0.9	-0.02	0.02	-1.3	0.4
Avg. trip duration	-0.1	0.3	-0.5	0.7	0.1	0.2	0.6	0.6
Body length	-0.03	0.1	-0.3	0.8	0.1	0.1	1.2	0.4
	Residual SE = 1.03 on 1 d.f. <i>F</i> -statistic = 0.31 on 3 and 1 d.f., <i>P</i> = 0.8				Residual SE = 0.85 on 1 d.f. <i>F</i> -statistic = 1.97 on 3 and 1 d.f., <i>P</i> = 0.5			

upstream or marsh habitats, which cannot be tracked within this zone using our methods, and those moving downstream where the nature of the habitat makes it impossible to accurately determine how far downstream alligators have moved in many cases. For the latter, isotopic data helped to resolve movements somewhat. The greater contribution of marine-based food webs to the diets of DCs suggests they move reasonable distances downstream where prey from marine-based food webs are available. Global Positioning System (GPS) tracking, especially Fastloc technology, could provide much more accurate descriptions of movements (Rutz & Hays 2009). Indeed, an alligator equipped with a GPS tag moved into coastal waters and hauled out on islands at the mouth of the SRE (A. E. Rosenblatt, unpublished data). The drawback to GPS technology, however, is its high cost that can limit sample sizes. For example, in our system, where recapturing alligators to remove tags is likely to be unsuccessful in many cases (personal observation), our sample sizes using GPS transmitters would have been limited to only a few individuals, and therefore, we would have been unable to answer questions about tactical variation in movements and its links to variation in alligator trophic interactions. Despite its high cost, GPS technology would be useful in gaining further insights into alligator movements both within our study area and across broader spatial scales.

Although we attached acoustic transmitters to 35 alligators, we only obtained sufficient data to elucidate movements of 16 across both wet and dry seasons. Some of the transmitters on the 'lost' alligators may have failed (four tags released within the array never produced data), which is a common aspect of tracking studies (Hays *et al.* 2007). Other individuals ($n = 2$) had transmitters attached relatively late in the study and had not been active in the system for a long enough time to be included in analyses. Based on their movement patterns before disappearing, we suspect that the majority of

'lost' individuals ($n = 13$) left the study area by permanently relocating to marsh habitats or adjacent estuarine waters outside of our tracking array. Another possibility is that some of these individuals took up residence in areas between monitors that were not within detection range of any monitors. Although three transmitters were deployed on females, none of them produced enough data to be included in our analyses. One exited the system at the mouth of the estuary (Ponce de Leon Bay), one exited into the marsh and one transmitter was never detected. Interestingly, even though a large number of alligators left the system, isotopic values of these alligators mostly fell within the isotopic niches of the well-defined movement tactics. In fact, 14 (74%) of the individuals with unresolved feeding tactics fell within the TA of DCs and two (13%) within the TA of alligators remaining mid-estuary and upstream. Therefore, individuals for which we could not identify movement tactics likely do not represent a distinct group with different movement tactics and trophic interactions.

It is apparent that alligators that used different movement tactics were exposed to different degrees of physiological stresses on a broad scale and likely also experienced different abundances of potential prey. Seasonal changes in movement patterns of alligators suggest that the relative costs and benefits of particular movement tactics vary seasonally. Indeed, DCs made the large majority of their trips into the downstream zone during the wet season when salinities were low (i.e. lower physiological costs) and spent almost triple the amount of time in the downstream zone during the wet season vs. the dry, indicating that this zone may be too stressful physiologically during the dry season for most alligators or potential foraging benefits do not outweigh physiological costs. Two individuals, however, used this zone during the dry season. Although changes in salinity likely are the primary physical driver of alligator use of the downstream zone,

we also found that DCs were more likely to be found downstream when temperatures were higher (generally during the wet season). High temperatures in the Everglades have been hypothesized to negatively affect alligators through increased metabolic costs associated with thermoregulatory behaviours (Jacobsen & Kushlan 1989). Therefore, it is likely that the temperature effect is driven by alligators responding to the generally lower salinities in the downstream zone during the warmest times of the year rather than selecting warmer habitats.

Alligators likely use downstream areas in spite of salt stress to access greater prey resources. The SRE is an 'upside-down' phosphorus-limited estuary (Childers *et al.* 2006). It receives the majority of its phosphorus from the Gulf of Mexico and exhibits decreasing P and productivity as distance from the river mouth increases (Childers *et al.* 2006; Simard *et al.* 2006). Unlike most estuaries, there is no productivity peak where marine and freshwaters meet (Childers 2006). As a result of increased precipitation during the wet season, P inputs from the ocean are compressed towards the downstream portion of the estuary (Childers *et al.* 2006). These trends in P supply and productivity, combined with relatively lower prey availability in mangrove-lined channels of the mid-estuary and upstream zone (Rehage & Loftus 2007), suggest that downstream and coastal areas likely have higher prey availability for alligators during the wet season when most downstream commuting is occurring. In the dry season, patterns of prey availability may be more complicated than during the wet season. Freshwater fishes move into mangrove channels of the upstream and mid-estuary zones in response to marsh dry-down (Rehage & Loftus 2007), and DC alligators may reduce movements downstream because of greater prey availability in mid-estuary areas as well as increased salt stress downstream. Because most mating and nesting activities occur in freshwater marsh habitats (Mazzotti & Brandt 1994) and adult alligators are not subject to predation, reproductive and anti-predator explanations for movements downstream are unlikely. Furthermore, movements downstream would not be expected if similar or greater prey resources were available in the mid-estuary and upstream areas, and carbon isotopic values of DC alligators suggest that they forage at least partially in downstream areas. Finally, alligators using the DC tactic were not smaller than those in upstream and mid-estuary zones suggesting that dominance interactions are not likely forcing DCs to adopt a 'best of a bad job' tactic whereby individuals must move into high-stress and low-prey habitats.

The UCs did not change their habitat-use patterns seasonally in the same ways as the DCs. Although the UCs made more trips into the upstream zone during the dry season than during the wet, the overall amount of time they spent upstream was consistent across seasons. Salinity in the upstream zone was at or near 0 ppt for the duration of the study, and use of the upstream zone was not affected by salinity. Larger individuals were more likely to be found upstream, and individuals were more likely to move upstream when water temperatures were high. It is likely that

these movement patterns are associated with the onset of the mating season, which occurs in freshwater habitats of the Everglades in April–June (Mazzotti & Brandt 1994).

Stable isotope analyses revealed that alligators with different movement tactics were feeding partially in different food webs. The freshwater/estuarine areas that the residents and UCs occupied support consumers with relatively low $\delta^{13}\text{C}$ values ($< -25\text{‰}$), while the coastal waters of the downstream zone support a food web characterized by higher $\delta^{13}\text{C}$ values ($> -19\text{‰}$; Matich, Heithaus & Layman 2011). Upstream commuter and resident alligators had $\delta^{13}\text{C}$ values similar to those of the freshwater/estuarine food webs, while the $\delta^{13}\text{C}$ values of most DC alligators, and many individuals for which movement tactic was unknown, fell above this range and suggest that they feed at least partially from marine food webs (Fig. 6). None of the $\delta^{13}\text{C}$ values for DC alligators suggested feeding exclusively from marine food webs and were below the most extreme values found for other highly mobile upper trophic level predators in the SRE that may commute to marine waters to feed (e.g. juvenile bull sharks; Matich, Heithaus & Layman 2011). Isotopic values between marine and freshwater/estuarine food webs are not unexpected even if DC alligators feed largely in marine food webs during the wet season. Although there are no published studies on isotopic turnover rates in crocodylians, skin of other reptiles turns over relatively slowly compared to mammals and birds (reviewed in Dalerum & Angerbjorn 2005). For example, skin tissue in slider turtles (*Trachemys scripta*) was found to fully turnover its isotopic values in > 192 days (Seminoff, Bjorndal & Bolten 2007). Adult alligators are much larger than pond sliders, and their isotope turnover times are most likely longer (Tieszen *et al.* 1983; Martinez del Rio *et al.* 2009) so isotopic values of skin likely reflect diets over multiple seasons. Therefore, because DC individuals spend at least half of each year in the mid-estuarine/freshwater zones, a large portion of their diets reflected in the isotopic values of skin will be from the freshwater and mid-estuarine zones.

Although stable isotope data in this study represent feeding that occurred before we quantified individual movements, they still are useful in understanding links between movement and trophic interactions and patterns of individual specialization. First, there was remarkable temporal consistency in individual movement tactics across years. No alligator that was tracked across multiple years switched movement tactics, suggesting that movement tactics that were used during the time period that isotopic values developed were similar to those recorded during our study. If this was not the case, we would not have expected isotopic niches of the movement tactic groups to be as highly differentiated as we found, especially for a tissue that turns over slowly. Incorporating data on stomach contents and isotopic values of tissues with shorter turnover rates (e.g. blood plasma) would provide greater resolution on temporal variation in the relative contributions of marine and freshwater/estuarine prey to alligator diets.

Although the average diets or behaviours of predators often leads to the appearance that they couple food webs,

recent studies have suggested that individual specialization may result in the separation of food webs through niche partitioning. For example, Eurasian perch separate into littoral and pelagic specialists that do not move between habitats, thereby keeping these food webs separate (Quevedo, Svanback & Eklov 2009). However, when individuals can easily traverse habitats that contain separate food webs, individual specialists may actually enhance connectivity (e.g. Matich, Heithaus & Layman 2011). Our results suggest that, like juvenile bull sharks (Matich, Heithaus & Layman 2011), alligators inhabiting an oligotrophic estuary likely link separate habitats, but only some individuals fulfil this ecological role. In the case of alligators, different suites of individuals appear to link different portions of the Everglades landscape. UC alligators may link marsh and estuarine areas, while a different subset of the population, DCs, link coastal marine food webs with estuaries and even the marsh.

Long-distance, potentially habitat-coupling, movements are not unique to American alligators within the crocodylian family. Using acoustic tracking, Campbell *et al.* (2010) documented estuarine crocodiles (*Crocodylus porosus*) in northern Australia using river tidal currents to sometimes travel more than 50 km between freshwater rivers and coastal marine waters where they may remain for up to 64 days at a time, possibly to feed. Although the movements of alligators in the SRE are also likely for foraging, the duration of their trips is more constrained than those of estuarine crocodiles because of their lack of functional salt glands and resulting susceptibility to salt-induced physiological stress (Taplin 1988).

The presence of trade-offs appears to be an important driver of individual specialization (e.g. orcas, *Orcinus orca*, Baird, Abrams & Dill 1992; black-tailed deer, *Odocoileus hemionus*, Darimont, Paquet & Reimchen 2007), which may be enhanced by resource scarcity (e.g. Svanback & Bolnick 2007; Tinker, Bental & Estes 2008; Darimont, Paquet & Reimchen 2009). Trade-offs appear to be important both in driving individual specialization in alligators and bull sharks in the SRE as well as their coupling of marine and estuarine/freshwater systems. Juvenile bull sharks experience enhanced foraging opportunities downstream where the risk of predation from larger sharks is higher (Matich, Heithaus & Layman 2011), while alligators appear to face the trade-off between foraging opportunities and increased salt stress. Like bull sharks, only some alligators accept higher costs to access marine-based food webs and do so primarily during the least stressful times of year. It might be expected that larger individuals that would be less susceptible to salt stress would be more likely to use downstream areas. However, this was not the case, and in fact within the DC group, smaller individuals had higher probabilities of using the downstream zone during the highest salinity periods. This counterintuitive result could have been caused by smaller individuals seeking out areas with higher prey abundances necessary for growth (though even the small alligators had already reached sexual maturity), smaller individuals actively avoiding the territories of larger males, or larger males preferring to stay closer to upstream areas so that they would not have to travel as far

during the mating season to find mates. Clearly, further studies are needed to understand the factors driving the use of particular movement and feeding tactics by alligators within the SRE.

In addition to linking the population dynamics of predators and prey across habitat boundaries (e.g. Polis, Anderson & Holt 1997), movements by alligators into downstream areas could play a role in nutrient dynamics of the oligotrophic estuary, specifically by transporting P derived from prey inhabiting the marine-dominated parts of the estuary to the freshwater-dominated areas of the SRE. Unfortunately, data on feeding and gastric evacuation rates are lacking for alligators in the SRE, making it impossible to estimate the potential role of alligators in nutrient dynamics at this time. However, alligators are large-bodied and relatively abundant in the system and the downstream commuting tactic, which involves short-duration trips into downstream waters, appears to be somewhat common. Therefore, it is possible that if DCs consistently haul out or bask at particular locations, they could create nutrient 'hotspots' in the mid-estuary zone derived from marine resources that are somewhat akin to the nutrient hotspots created by fish movements and habitat use in tropical rivers (e.g. McIntyre *et al.* 2008). A similar role has been suggested for other species of crocodylians. Fittkau (1973) hypothesized that caiman populations (*Melanosuchus niger* and *Caiman crocodylus*) in the Amazon were key nutrient recyclers and thereby contributed to increasing primary production and the size of fish populations. Further studies will be needed to assess whether alligators could likewise play an important role in nutrient dynamics in the coastal Everglades.

Our study suggests that highly mobile predators could play an important role in linking coastal habitats including marine, estuarine and freshwater zones. Unlike species with lower mobility or smaller body sizes, individual specialization by mobile large-bodied species that are buffered against short-term abiotic stress may lead to habitat connections that are maintained only by a subset of the population. While trade-offs appear to be an important driver of specialization and habitat linkages in the SRE, further studies investigating the generality of these results within other estuaries, the factors that lead to the adoption of particular movement tactics and the overall importance of nutrient translocation by highly mobile predators, like alligators, to the dynamics of the coastal Everglades ecosystem are still required.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Summary of detection ranges of 39 monitors in relation to the width of the channels containing those monitors.

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