Ecological niche partitioning within a large predator guild in a nutrient-limited estuary

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Abstract

Within oligotrophic ecosystems, resource limitations coupled with interspecific variation in morphology, physiology, and life history traits may lead to niche partitioning among species. How generalist predators partition resources and their mechanisms, however, remain unclear across many ecosystems. We quantified niche partitioning among upper trophic level coastal and estuarine species: American alligators (*Alligator mississippiensis*), bull sharks (*Carcharhinus leucas*), common bottlenose dolphins (*Tursiops truncatus*), common snook (*Centropomus undecimalis*), and Atlantic tarpon (*Megalops atlanticus*) in the Shark River Estuary of the Florida Coastal Everglades, USA using acoustic telemetry, stable isotope analysis, and visual surveys, combined with published diet and life history demographic information. Spatial and isotopic niche overlap occurred among most species, with variability in partitioning among interspecific interactions. However, seasonal variability in habitat use, movements patterns, and trophic interactions may promote coexistence within this resource-limited estuary. Beyond guild-level niche partitioning, predators within the Shark River Estuary also exhibit partitioning within species through individual specializations and divergent phenotypes, which may lead to intraspecific variability in niche overlap with other predators. Niche differentiation expressed across multiple organizational levels (i.e., populations and communities) coupled with behavioral plasticity among predators in oligotrophic ecosystems may promote high species diversity despite resource limitations, which may be important when species respond to natural and human-driven environmental change.

Predators fill an important and diverse set of roles within their ecosystems, and can exert top–down effects through consumptive and non-consumptive interactions, and stimulate bottom-up processes through nutrient translocation across ecosystem boundaries (Helfield and Naiman 2006; Schmitz et al. 2010). Changes in predator population dynamics, abundance, and distribution, therefore, may influence food web stability, especially in coastal marine ecosystems (Heithaus et al. 2008; Estes et al. 2011). Of particular importance for understanding the potential impacts of changes in predator abundance is the extent of trophic redundancy within predator guilds (i.e., whether the role of

a particular species might be filled by another), which is thought to dictate ecosystem resilience (e.g., Peterson et al. 1998; Mouillot et al. 2013). Recent research suggests that predator guilds often thought to be ecologically similar actually show some degree of niche partitioning, which also occurs within populations through ontogenetic niche shifts and individual specializations (e.g., Rosenfeld 2002; Bolnick et al. 2003; Elbroch et al. 2015). Elucidation of niche partitioning within coastal estuarine communities can thus facilitate improved understanding of both food web dynamics and community responses to environmental perturbations and anthropogenic impacts.

The ecological niche of species is multi-dimensional, with three axes of particular importance—trophic interactions, habitat use, and their temporal variability—because they explicitly impact diets, and spatial and temporal patterns of abundance (Chase and Leibold 2003). Within ecological

communities, sympatric species should have distinct resource use patterns and different niches to coexist in resource-limited contexts (Pianka 1974; Schluter and McPhail 1992), however extrinsic factors may lead to substantial variability in behavior by altering both the ecological niches species fill, and their overlap in resource use with other species (e.g., Hjelm et al. 2000; White et al. 2015). In ecosystems where resource availability is limited (e.g., oligotrophic systems), changes leading to niche contraction can have substantial effects on the role(s) species play, and lead to increased susceptibility to environmental change in species with more small niches, like those with specialized behaviors (e.g., Colles et al. 2009; Clutton-Brock and Sheldon 2010). For example, increased habitat specialization among temperate bat species in North America and Europe increases the risk of extinction (Safi and Kerth 2004), and declines among coral gobies (*Gobiodon* spp.) in Papua New Guinea in response to coral loss are more pronounced among specialists than generalists (Munday 2005). As such, studying niche partitioning and redundancy within ecosystems where productivity is limited is especially important in light of chronic and ephemeral changes in the environment.

The Florida Coastal Everglades supports a diverse assemblage of species that coexist through seasonal pulses of freshwater, habitat availability, and food resources (Brown et al. 2006; Childers 2006). The ebb and flow of water across the landscape affects species distributions and abundances, and in turn likely affects competitive interactions and resource availability that shape ecosystem dynamics (Ruetz et al. 2005; Rehage and Trexler 2006). At the population level, resource availability and intraspecific competition appear to be important drivers of behavior among some species in coastal ecosystems of the Everglades. For instance, both American alligators (hereafter alligators; *Alligator mississippiensis*) and juvenile bull sharks (*Carcharhinus leucas*) appear to partition resources within species through individual specialization in movement patterns and foraging locations (e.g., Rosenblatt and Heithaus 2011; Rosenblatt et al. 2013*a*; Matich and Heithaus 2015). However, it is unclear how predators that occupy similar trophic levels within the coastal Everglades partition resources at the guild level, and if relatively low productivity throughout much of the ecosystem leads to niche width contraction (Pianka 1973; Holt 2009).

Here we investigate if the most abundant large-bodied species representing different groups of aquatic predators (aquatic reptiles, elasmobranch fishes, marine mammals, teleost fishes) partition resources and habitat in low productivity environments of the Florida Coastal Everglades using acoustic telemetry, stable isotope analysis (δ^{13}C, δ^{15}N), and habitat occupancy data on alligators, Atlantic tarpon (*Megalops atlanticus*), bull sharks, common bottlenose dolphins (*Tursiops truncatus*), and common snook (hereafter snook; *Centropomus undecimalis*). All five species co-occur within the Florida Coastal Everglades, suggesting there is minimal overlap in resource use or variation in foraging in time and/or space to promote coexistence (Pianka 1974; Schluter and McPhail 1992), or populations are not food limited. Thus, we predicted that predators would exhibit niche partitioning in space, time, and/or trophic interactions.

Methods

Study site

The Shark River Estuary (Fig. 1) consists of a series of shallow bays and deeper channels lined by mangroves, which provide habitat for a variety of freshwater, estuarine, and marine taxa. Many predators, including crocodilians, elasmobranchs, teleost fishes, and marine mammals use the extent of the estuary seasonally or throughout the year for at least part of their life history, with some seasonal shifts in distribution attributed to temporal fluctuations in water temperature and salinity (e.g., Sarabia 2012; Boucek and Rehage 2013; Rosenblatt et al. 2013b; Fujisaki et al. 2016). Productivity varies spatially and temporally throughout the estuary, with outwelling and nutrient limitations upstream leading to higher levels of productivity in marine habitats (Childers 2006; Simard et al. 2006). There is, however, a pulse of freshwater prey that enters upstream portions of the estuary that may result in more even or bimodal patterns of food available to large predators during certain times of the year (Rehage and Loftus 2007).

Field methods
Spatial tracking

To quantify predator distribution, we divided the estuary into 10 regions that were delineated by the placement of 37 Vemco VR2W acoustic receivers (Vemco, Halifax, NS; Fig. 1) that tracked the long-term movements of predators with either attached or implanted transmitters. Regions were defined based on spatial variability in salinity with major boundaries of the ecotone occurring between 8 and 18 km from the Gulf of Mexico, broad-scale geomorphology of the estuary including river and bay boundaries (see Rosenblatt and Heithaus 2011; Matich and Heithaus 2012), and analysis of previous tracking data from alligators (Rosenblatt et al. 2013b) and bull sharks (Matich and Heithaus 2015). Throughout the receiver array, acoustic "gates" (paired receivers) were used to determine when individuals moved into or out of regions. Each receiver had a detection range of ~500 m (greater than the distance across each channel or bay receivers were deployed in), ensuring animals were unable to move among regions undetected (see Rosenblatt and Heithaus 2011 for further details of the sampling array). Data from receivers were downloaded every 2–4 months, with batteries replaced as needed.

Stable isotope analysis

Stable isotope analysis has become a commonly used tool in ecological studies to investigate trophic interactions and habitat use (reviewed by Martinez del Rio et al. 2009; Wolf
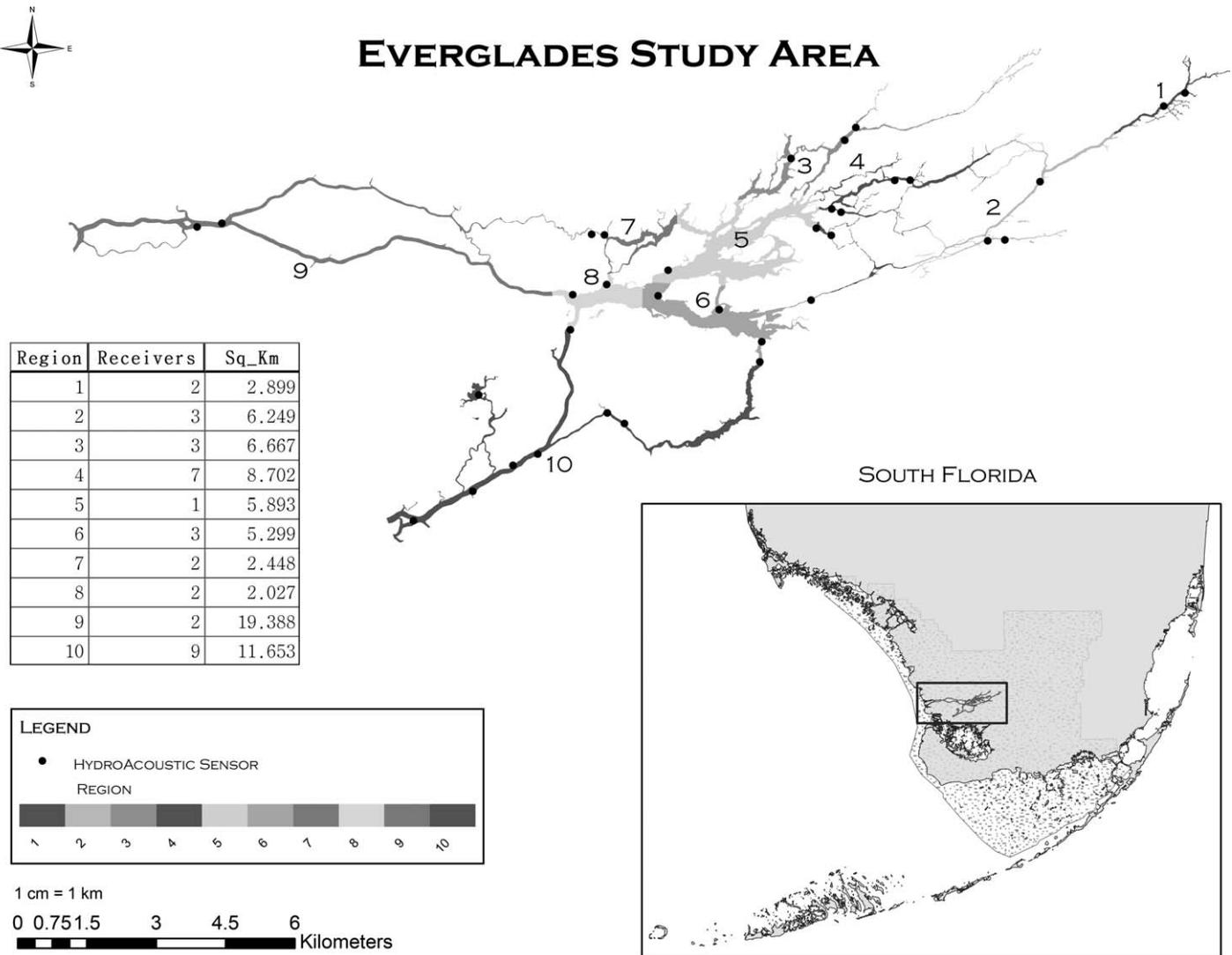
Fig. 1. Shark River Estuary, with location of acoustic receivers (black dots) and sampling regions.

et al. 2009). Stable isotope values do not provide the taxonomic resolution of stomach content analysis, but instead provide time-integrated views of trophic interactions over predictable time periods that vary among species and tissue types (reviewed by Layman et al. 2012). In addition to species-specific differences in turnover rates, isotopic discrimination values (i.e., enrichment or depletion between trophic steps) also vary across species and tissues, necessitating adjustments to stable isotope values prior to comparisons across taxa (reviewed by McCutchan et al. 2003; Vanderklift and Ponsard 2003). In light of these challenges, the tissues collected from each species for stable isotope analysis (see sampling descriptions for each predator below) were chosen based on their similarities in turnover rates to compare $\delta^{13}C$ and $\delta^{15}N$ values across similar time periods (1–2 month isotopic half-lives), and values were adjusted for differences in discrimination values prior to statistical analyses (see below; Table 1).

Alligator sampling

Alligator abundance in the Shark River Estuary varies in space and time because of their sensitivity to saltwater (Lauren 1985; Taplin 1988; Fujisaki et al. 2016). During the wet season, when salinities throughout the ecosystem are relatively low (<10 ppt through the study area; Rosenblatt and Heithaus 2011), alligators can be found in all habitats. As salinities rise during the dry season, alligators reduce their use of downstream waters and become concentrated in freshwater marshes, although some continue to make rare forays into saltier marine habitats (Rosenblatt and Heithaus 2011; Rosenblatt et al. 2013b).

From 2007 to 2011, alligators were captured in the Shark River Estuary using standard pole-snare methods and were sexed and measured to assess maturity (Rosenblatt and Heithaus 2011). To quantify alligator movements and habitat use, acoustic transmitters (model V16-4H; Vemco, Halifax,

Table 1. Trophic discrimination values (Δ^{13}C and Δ^{15}N in ‰) and turnover rates of study species based on controlled feeding studies.

Species	Tissue	Δ^{13}C	Δ^{15}N	δ^{13}C half-life	δ^{15}N half-life
American alligator	Blood plasma	−0.04[*]	+0.35[*]	63 d[*]	62 d[*]
Bottlenose dolphin	Blubber	+2.54[†]	+3.15[†]	*ca.* months[‡]	*ca.* months[‡]
Bull shark	Whole blood	+2.90[§]	+2.60[§]	45 d[§]	51 d[‖]
Snook	Fin	+1.530[¶,#,**]	+3.74[#,**]	31 d[**]	15 d[**,††]

[*] Rosenblatt and Heithaus (2013).
[†] Caut et al. (2011).
[‡] Abend and Smith (1995).
[§] Malpica-Cruz et al. (2012).
[‖] MacNeil et al. (2006).
[¶] Rounick and Hicks (1985).
[#] Peterson and Howarth (1987), Hesslein et al. (1993), Herzka and Holt (2000).
[**] Suzuki et al. (2005), German and Miles (2010).
[††] McIntyre and Flecker (2006), Heady and Moore (2013).

NS, Canada) were attached to the tails of 52 adult alligators (> 1.8 m total length) using stainless steel wire and marine-grade epoxy (see Rosenblatt and Heithaus 2011 for details). Transmitters were set to emit a unique series of pulses for each alligator at a random interval between 60 and 120 s. Here we include movement data from 23 individuals that were tracked for at least three months each within our array of acoustic receivers.

To quantify trophic interactions, a 21-gauge needle was used to collect 5 mL of blood from the cervical sinus of 85 alligators from 2008 to 2011 (Heithaus et al. 2016). Blood samples were placed into blood collection vials (Becton, Dickinson and Company, Franklin Lakes, NJ) with neither additives nor interior coating, and immediately separated into plasma and red blood cell components using a centrifuge spun for 20 s at 3000 rpm. Blood plasma in alligators has a δ^{13}C half-life of *ca.* 63 d and a δ^{15}N half-life of *ca.* 62 d (Rosenblatt and Heithaus 2013). Plasma samples were put on ice and frozen before laboratory preparations. All samples were dried and homogenized prior to stable isotopic analysis. Mean C : N was 3.80 ± 0.22, however lipids were not removed because lipid extraction does not significantly affect alligator plasma δ values (Rosenblatt and Heithaus 2013), likely due to the high protein content of alligator blood plasma (Coulson and Hernandez 1964).

Atlantic tarpon sampling

Tarpon use estuarine environments throughout their lifecycle as a nursery, foraging habitat, and refuge from predation (Ault et al. 2008). Their osmoregulatory capability coupled with their ability to breath air (Graham 1997) allow them to access remote anoxic habitats of both fresh and salt water, where they primarily feed on crustaceans and teleosts (Luo et al. 2018b). Juvenile tarpon are found in the shallow protected waters of the Everglades year round, while some large mature tarpon undertake extensive migrations along the eastern Gulf of Mexico, others remain resident in the estuary year-round (Luo et al. 2018b). Migratory tarpon use the Shark River Estuary seasonally for food and predator avoidance prior to offshore spawning (Crabtree et al. 1992). To gain a preliminary understanding of tarpon habitat use in relation to other predators within the ecosystem, three adult tarpon were captured with hook and line fishing and externally outfitted with a V9 acoustic transmitter with a single titanium anchor tag inserted directly above the lateral line 2/3 distance between head and dorsal fin in March 2013. Fork length and girth measurements were recorded.

Bull shark sampling

Juvenile bull sharks reside within the entirety of the Shark River Estuary year-round, and use the estuary as nursery habitat for their first 3–5 yr of life before emigrating to marine waters (Wiley and Simpfendorfer 2007; Heithaus et al. 2009). Bull sharks were captured from 2006 to 2013 on *ca.* 500 m longlines fitted with 40–55 14/0 or 15/0 Mustad tuna circle hooks baited with mullet (*Mugil* spp.) and attached to *ca.* 2 m of 400 kg monofilament line (see Heithaus et al. 2009 for further details on sampling equipment; Heithaus and Matich 2016). Shark total length was measured and sharks were externally tagged using a numbered roto tag affixed through the first dorsal fin to identify recaptured individuals.

To quantify shark distribution, 59 sharks caught in excellent condition (swimming strongly on capture) from October 2008 to September 2013 were surgically fitted with a Vemco V16-4H transmitter and tracked for at least 4 months within our array of acoustic receivers. Transmitters were set to emit a unique series of pulses for each shark at a random interval between 30 and 90 s. To quantify trophic interactions, an 18-gauge needle was used to collect 4 mL of blood from the caudal vein of 108 bull sharks from February 2006 to September 2013 (Heithaus et al. 2016). Whole blood in elasmobranchs has a δ^{13}C half-life of *ca.* 45 d and a δ^{15}N half-life of *ca.* 51 d (MacNeil et al. 2006; Malpica-Cruz et al. 2012). Blood samples were put on ice and frozen before laboratory

preparations. All samples were dried and homogenized prior to stable isotopic analysis. Mean C : N was 2.68 ± 0.14 SD, suggesting lipid extraction was not necessary (Post et al. 2007).

Common bottlenose dolphin sampling

Common bottlenose dolphins are abundant predators throughout the coastal Everglades, with higher densities found in coastal waters and inland bays than in river systems, including the Shark River (Sarabia 2012). However, use of rivers increases during the dry season (typically January to June), while densities in other habitats remain similar across seasons (Sarabia 2012). Sixteen bottlenose dolphin sighting and biopsy surveys were conducted within the Shark River Estuary across all study areas from August 2010 to September 2013 at 15 km/h in Beaufort wind conditions three or less. Sighting data during dry and wet seasons was used to estimate dolphin distribution within the greater estuarine area of the southern Shark River Slough (including Joe River, Ponce de Leon Bay, and Whitewater Bay; see Sarabia 2012), and within the spatial scope of the array of acoustic receivers. When dolphins were encountered, standard group data were recorded, including geographic position and group characteristics (e.g., group size, presence, and number of neonates and calves).

When dolphins could be approached closely (3–10 m), biopsy attempts were made. Biopsies were collected by using a crossbow (BARNETT Panzer V Veloci-Speed® Class, 68-kg draw weight) with Finn Larsen (Ceta-Dart, Copenhagen, Denmark) modified Easton® bolts and custom tips. Dolphins were sampled below the dorsal fin. Blubber and skin biopsy samples were put on ice and frozen before subsequent analysis. Blubber and skin were separated for each sample, and blubber was dried and homogenized. Although half-life estimates for isotopic values are not available for bottlenose dolphins, the half-life for skin is estimated at *ca.* < 1 month (Hicks et al. 1985, Giménez et al. 2016), with a long half-life for blubber, integrating diet over several months (Abend and Smith 1995). Following homogenization, lipids were extracted by agitating blubber samples in a chloroform : methanol mixture (2 : 1) for one minute with a solvent volume five times greater than the sample, and left undisturbed for 1 h at room temperature with subsequent centrifugation and removal of supernatant. The process of lipid removal was carried out three times prior to samples being rinsed in deionized water, re-dried, and weighed for stable isotope analyses (Kiszka et al. 2014). Mean C : N values were 2.81 ± 0.06 SD after extraction, suggesting no further lipid extraction was needed (Post et al. 2007).

Snook sampling

Snook are a tropical, euryhaline, estuarine-dependent piscivorous fish. In the Shark River Estuary and in other river floodplain systems, snook occupy freshwater rivers during the falling water season to capitalize on availability of allochthonous prey forced off of drying floodplains into rivers (Boucek and Rehage 2013). Following the dry season and during the re-flood and high water season, snook migrate to coastal environments to spawn (Andrade et al. 2013; Lowerre-Barbieri et al. 2014). It is important to note, however, that in Florida and likely in other regions, snook exhibit partial migration (Trotter et al. 2012; Lowerre-Barbieri et al. 2014).

Snook were captured using a boat-mounted, generator-powered electrofisher (two-anode, one cathode Smith-Root 9.0 unit; Boucek and Rehage 2014; Rehage 2017). On capture, snook were measured, weighed, and internally marked with a passive integrated transponder tag to identify recaptures. To quantify distribution patterns, 28 snook caught in good condition (based on swimming performance and visual inspection) from February 2012 to November 2013 were anesthetized in an ambient water and Alka-Seltzer solution (1–1.5 tablets per four liters of water) prior to surgery (Rehage 2016). Once a fish was anesthetized, a 30 mm incision was cut in the lower abdomen of each snook, and each individual was surgically fitted with a Vemco V16 transmitter following protocols in Adams et al. (2009). Transmitters were set to emit a unique series of pulses for each snook at a random interval between 60 and 180 s. Following the insertion of the transmitter, the incision was closed with three stitches, and snook were released once they regained full equilibrium.

To quantify trophic interactions, a small fin clip was taken from the caudal fin of 37 snook. Fin tissue in teleost fishes has a $\delta^{13}C$ half-life of *ca.* 31 d and a $\delta^{15}N$ half-life of *ca.* 17 d (Suzuki et al. 2005; McIntyre and Flecker 2006; German and Miles 2010; Heady and Moore 2013). Fin samples were put on ice and frozen before laboratory preparations. All samples were dried and homogenized prior to stable isotopic analysis. Mean C : N was 3.28 ± 0.09 SD, suggesting lipid extraction was not necessary (Post et al. 2007).

Data analysis
Spatial interactions

To quantify spatial overlap between species, mean monthly percent occurrence within sampling regions was calculated for each acoustically tagged animal tracked for the duration of the study (alligators, bull sharks, snook, and tarpon)—the proportion of time each species spent in each sampling region was quantified based on the mean for all individuals of that species with active acoustic transmitters detected by at least one receiver within the array for each month of the study period. Individuals not detected within the array during a month were not included in analyses for that month. Annual mean percent occurrence by species was calculated by taking the evenly weighted mean of monthly averages to reduce the influence of individuals that had been tracked for multiple years on species averages, and to reduce the influence of months with higher numbers of tracked

species on annual means. Kruskal-Wallis tests were used to test for annual differences in distribution patterns for alligators and for annual differences in distribution patterns for bull sharks to ensure data could be pooled for each species. A Mann-Whitney test was used to quantify annual differences in snook movements over 2012 and 2013 to ensure data could be pooled. Morisita index of similarity (Morisita 1959) was used to measure spatial overlap between the four species:

$$C = \frac{2\sum_i^n p_{ij}\, p_{ik}}{\sum_i^n p_{ij}\left[\frac{(n_{ij}-1)}{(N_j-1)}\right] + \sum_i^n p_{ik}\left[\frac{(n_{ik}-1)}{(N_k-1)}\right]}$$

C = Morisita index of spatial overlap between species j and k

P_{ij} = percent occurrence of species j in region i by month

P_{ik} = percent occurrence of species k in region i by month

n_{ij} = number of individuals of species j that were present in region i by month n_{ik} = number of individuals of species k that were present in region i by month

N_j, N_k = total number of individuals of each species tracked

The Morisita index provided a minimally biased means of quantifying spatial overlap of species encompassing small and large sample sizes (Smith and Zaret 1982), and its formulation, which includes the total number of organisms tracked along with the number observed in each resource state (month/region, (i)), was appropriate for our mismatched sample sizes. To quantify significant differences in spatial use and overlap among species, a single index value was calculated for each species pair, and a null model was created following the ra3 randomization algorithm described by Lawlor (1980) and Winemiller and Pianka (1990) using EcoSimR (Gotelli et al. 2015). In this randomization procedure, the number of animals tracked (N and n), resource states, and niche breadths were constant, but percent occurrence was randomly reassigned. One thousand simulations were run to evaluate whether the observed index values where significantly less (lower overlap) or greater (higher overlap) than random values. Morisita index values and null models for spatial overlap with tarpon were run only on data from the month of April. Additional monthly Morisita index values were generated to investigate seasonal changes in spatial overlap. Analyses were conducted in R v.3.1.2 (R Development Core Team 2013).

To provide an additional line of evidence from Morisita index of similarity, Analysis of Similarity (ANOSIM) was used based on Bray-Curtis similarity matrices to test for differences in habitat use among species (Field et al. 1982). Dissimilarity matrices were constructed based on square root transformed estimates of average monthly habitat use for each individual tracked. We constructed non-metric multi-dimensional scaling (NMDS) plots to illustrate dissimilarity among species. In these plots, the distance between data points is proportional to the degree of similarity between individuals. Analyses were conducted in Primer-E v.6 (Clarke 1993).

Qualitative assessments of dolphin distribution were conducted based on the proportion of dolphin groups that were sighted within the array compared to time sighted in nearby estuarine waters (Joe River, Ponce de Leon Bay, and Whitewater Bay), and the proportion of sightings in each sampling region within the acoustic array.

Trophic interactions

Stable isotope values (δ^{13}C and δ^{15}N) from alligators (blood plasma), dolphins (blubber), snook (fin), and bull sharks (whole blood) were plotted on an isotope biplot to compare trophic interactions among predators. Prior to interspecific comparisons, δ^{13}C and δ^{15}N values were adjusted to account for species-specific differences in isotope discrimination factors based on Δ^{13}C and Δ^{15}N values from captive studies (Table 1). Species-specific discrimination values were not available for all predators, and where such data were lacking we used estimates from captive studies of species most closely related to our focal taxa.

Differences in mean stable isotope values were quantified using Kruskal-Wallis tests, with post hoc Mann-Whitney tests. Adjusted stable isotope data were plotted, and minimum convex polygons (MCPs) (Layman et al. 2007) and standard ellipses corrected for small sample sizes (SEA$_c$; Jackson et al. 2011) were generated to quantify isotopic niche space occupied by each species using the R package SIAR (Parnell et al. 2008, 2010; R Development Core Team 2013). Total area of polygons and ellipses, and overlap of polygons and ellipses were quantified using SIAR. Although all species are found outside of the estuary in marine and/or freshwater habitats, the home range of many individuals is predominantly or exclusively comprised within the study area (e.g., Rosenblatt et al. 2013a,b; Matich and Heithaus 2015). Data were only analyzed for animals sampled within the confines of the acoustic receiver array to investigate niche partitioning at and adjacent to the ecotone where productivity is lowest and competition for resources may be highest (Childers 2006). Kruskal-Wallis tests were used to test for annual differences in stable isotope values for each species.

Monthly stable isotope values were quantified among alligators and sharks (sample sizes were too small for dolphins and snook) to investigate temporal variability in trophic overlap between the two species. A 1000-iteration randomization of stable isotope values for alligators and sharks was conducted to determine if niche widths were significantly different across months. Power analyses were run for each species to ensure sample sizes were adequate.

Results

Spatial interactions

From 2008 to 2013, over 1000 months of combined tracking data were collected from alligators, bull sharks, snook,

and tarpon (Table 2). There were no annual differences in distribution patterns within species, and therefore data were pooled for analyses (alligators: $H_3 = 1.73$, $p = 0.42$; bull sharks: $H_3 = 0.44$, $p = 0.80$; snook: $z = 1.60$, $p = 0.11$). Tracked alligators, bull sharks, and snook on average, each spent more than 70% of their time tracked within the acoustic array, while tarpon were only detected within the study area during April 2013 (Table 2). However, bull shark longline sampling resulted in six tarpon captures from 2007 to 2010 in April ($n = 3$), August ($n = 1$), October ($n = 1$), and November ($n = 1$). During 16 survey days across all sampling areas from 2010 to 2013 (816 km surveyed), 24 groups of bottlenose dolphins (mean group size ± SD = 2.0 ± 1.6 individuals) were sighted within the extent of the acoustic array, amounting to 15% of sightings within the southern Shark River Slough area during surveys (Table 3).

Species distributions varied spatially and temporally. Alligators spent most of their time upstream in Region 1 and downstream in Region 10, with the peak of detections downstream from June to December (41% increase in frequency of occurrence), and a subsequent decrease in detections upstream (35% decrease in frequency of occurrence) (Fig. 2; Supporting Information Tables 1 and 2). Bull sharks predominantly used midstream waters in Regions 5, 6, and 8, with moderate use of microhabitats downstream in Regions 9 and 10 (Fig. 2; Supporting Information Table 1). Bull sharks rarely used freshwater habitats, with 57% of time spent upstream in Regions 1–4 occurring in March to June (Supporting Information Table 2). Snook were most frequently detected upstream in Region 1, with less than 15% occurrence in any other region (Fig. 2; Supporting Information Table 1), but a notable increase in occurrence midstream in Region 6 from May to August (1.7-fold increase from September to April; Supporting Information Table 2). During April 2013, tarpon were most frequently detected midstream in Regions 5 and 7 (Fig. 2; Supporting Information Table 1). Large tarpon (> 1 m) caught as bycatch during longline surveys were captured in Region 1 ($n = 1$; April 2009), Region 5 ($n = 2$; October 2009 and April 2010), Region 6 ($n = 2$; August 2007 and November 2008), and Region 8 ($n = 1$; April 2010). Common bottlenose dolphins were predominantly sighted downstream in Regions 9 and 10 (83% of sightings), with 67% of sightings within the array occurring between February and May (Table 3).

Morisita index of similarity suggested weak spatial overlap between tracked species (Table 4; Fig. 2). Results from the null model indicated that the observed overlap between alligators and bull sharks, bull sharks and snook, and snook and tarpon were significantly lower than expected, suggesting very limited overlap. Spatial overlap between snook and alligators, which was driven by their high occurrence upstream in Region 1, was not significantly higher than expected when compared to the null model. Bull sharks and tarpon also exhibited considerable overlap attributed to their use of

Table 2. Sample sizes, size ranges (in centimeters total length), acoustic tracking period, and percent of time spent within the acoustic array for animals tracked during this study. Note, tarpon were only detected within the acoustic array in April 2013 during the study. Satellite telemetry indicated tarpon used other areas within the Shark River Slough and coastal waters, and migrated from south Florida during the study period (Ault et al. unpubl.).

	N	Size range (cm TL)	Years tracked	% Time in array (±SD)
Alligators	23	177–281	2008–2011	73 (26)
Bull sharks	59	71–136	2008–2013	76 (35)
Snook	28	53–90	2012–2013	85 (27)
Tarpon	3	127–183	2013	Only April 2013

Table 3. Number of dolphin groups sighted within each region of the study area, and in nearby estuarine areas (Joe River: 25°12′ N, 80°58′W; Ponce de Leon Bay: 25°21′ N, 80°08′W; and White Water Bay: 25°17′ N, 81°01′W) during 16 surveys.

Sampling area	Groups sighted
Region 1	0
Region 2	0
Region 3	0
Region 4	0
Region 5	1
Region 6	1
Region 7	0
Region 8	2
Region 9	2
Region 10	18
Joe River	35
Ponce de Leon Bay	13
White Water Bay	90

Region 5, however it was not significantly greater than expected based on chance ($p = 0.20$), suggesting mild overlap in April 2013. NMDS plots reinforced findings from Morisita index, and suggested significant differences in space use between alligators and bull sharks, bull sharks and snook, and snook and tarpon (Fig. 3; Supporting Information Table 3). Temporal analysis suggested limited seasonal shifts in habitat use overlap outside of a decrease in overlap in March and April among all species (Fig. 4). Bull sharks and alligators had slightly greater spatial overlap from August to November when alligator occurrence downstream was highest.

Trophic interactions

As a guild, the predators of the Shark River Estuary exhibited a wide range of $\delta^{13}C$ (−30.26 to −17.89‰) and $\delta^{15}N$ values (+4.65 to +11.51‰; Table 5; Fig. 5). Kruskal-Wallis tests
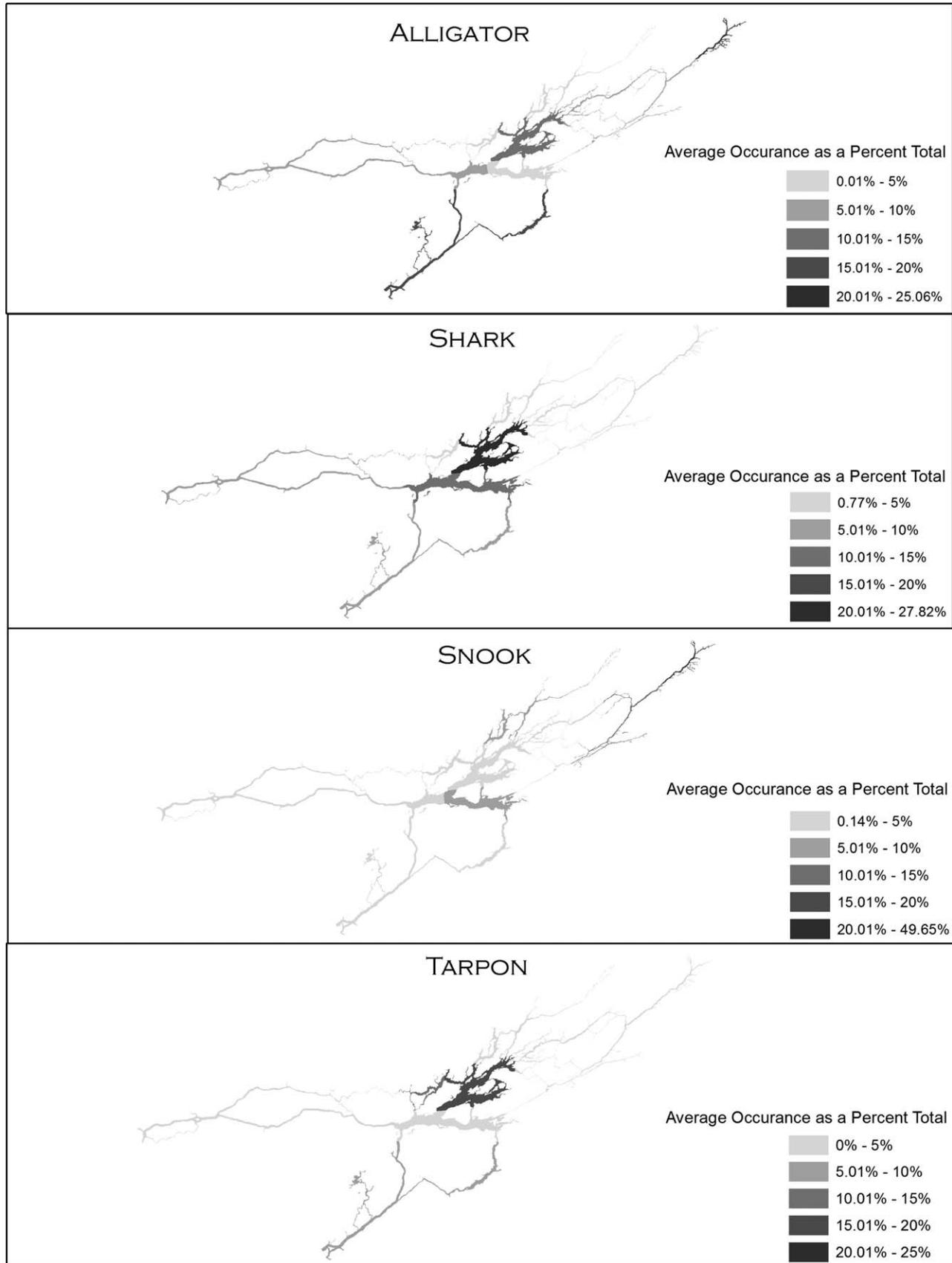
Fig. 2. Frequency of occurrence of alligators, bull sharks, snook, and tarpon based on acoustic tracking.

indicated significant differences in $\delta^{13}C$ and $\delta^{15}N$ values across taxa ($H_3 = 28.99$, $p < 0.01$, $H_3 = 145.73$, $p < 0.01$ for $\delta^{13}C$ and $\delta^{15}N$, respectively), excluding alligator and snook $\delta^{15}N$ values ($z = 1.66$, $p = 0.10$). Pairwise comparisons could not be made between dolphins and other species because sample sizes were too small. Power analyses with $1 - \beta = 0.80$ and $\alpha = 0.05$ suggested that bull shark and snook sample sizes were adequate for comparison of guild $\delta^{13}C$ (power = 0.98 and 0.99) and $\delta^{15}N$ values (power = 0.99 and 0.99), and alligators and dolphin sample sizes were adequate for comparison of guild $\delta^{15}N$ values (power = 0.99 and 0.99),

with larger sample sizes advised for alligators ($n = 232$) and dolphins ($n = 34$) for $\delta^{13}C$. Sample size for dolphins was too small to test for annual differences (suggested $n = 33$), and dolphin and snook sample sizes were too small to investigate monthly variability in isotopic values (minimum suggested $n > 100$ and 82, for dolphins and snook, respectively).

MCP areas and standard ellipse areas (SEA_c) suggested that alligators and bull sharks exhibited wider isotopic niche widths than dolphins and snook (Table 5, Fig. 5). Bull sharks and dolphins were more enriched in ^{15}N than alligators and snook, while alligators and bull sharks exhibited a much wider range of $\delta^{13}C$ values than snook, which predominantly fed on taxa that were more depleted in ^{13}C (Fig. 5, Table 5). Standard ellipse overlap among species suggested similarities in trophic interactions (i.e., similar trophic levels and carbon sources) among alligators and snook (20% and 57% overlap, respectively), and similarities in trophic interactions among bottlenose dolphins and bull sharks (90% and 44% overlap, respectively; Fig. 5). The snook MCP exhibited nearly complete overlap (99% of isotopic niche space) with alligators (Fig. 5, Table 6). Only sharks (41%) and alligators (45%) had unique isotopic niche space among the study species based on MCPs. Comparatively, SEA_c's showed that alligators and sharks had a greater proportion of unique core isotopic niche space (80% and 56%, respectively) than snook and dolphins (43% and 10%, respectively).

Alligators and bull sharks exhibited temporal variability in $\delta^{13}C$ and $\delta^{15}N$ values, with isotopic niche widths greatest in January for alligators ($SEA_c = 9.68\%_{oo}^2$, respectively;

Table 4. Morisita index of similarity scores for spatial overlap between alligators, bull sharks, snook, and tarpon (1 = complete overlap, 0 = no overlap). *p*-values from null model representing low overlap (observed < expected) or high overlap (observed > expected) indicate significant spatial separation between alligator/bull shark, bull shark/snook, and snook/tarpon ($p < 0.001$).

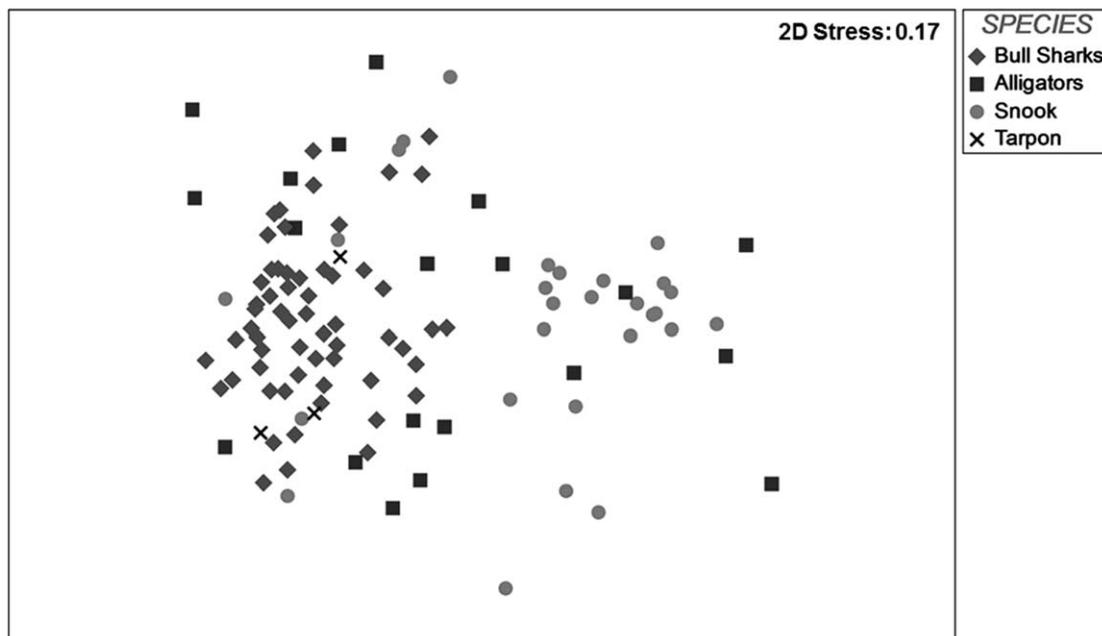|	Morisita index	*p*-value (observed < expected)	*p*-value (observed > expected)
Alligator/bull shark	0.197	<0.01	>0.99
Alligator/snook	0.431	0.19	0.81
Alligator/tarpon	0.086	0.08	0.92
Bull shark/snook	0.063	<0.01	>0.99
Bull shark/tarpon	0.175	0.79	0.21
Snook/tarpon	0.012	<0.01	>0.99

Fig. 3. Non-metric multi-dimensional scaling (NMDS) plot of monthly distribution patterns illustrates similarity/dissimilarity among species—proximity of data points is proportional to the degree of similarity between individuals (i.e., data points that are closer together are more similar, indicating more similar patterns in habitat use).
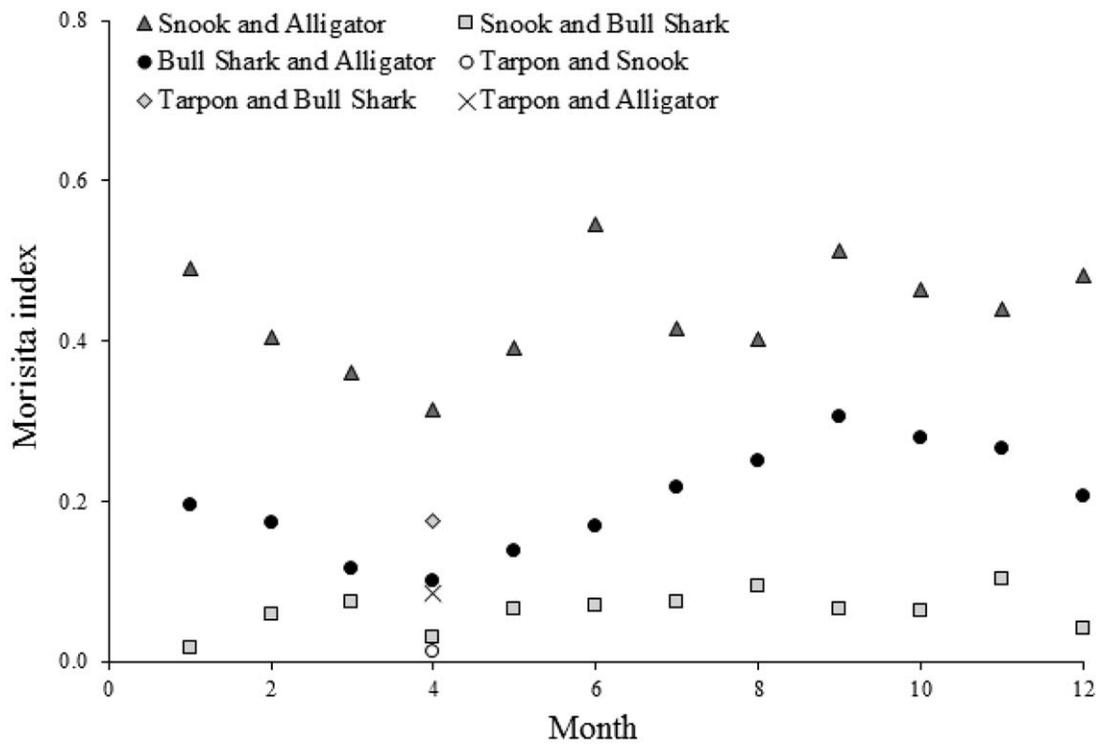
Fig. 4. Monthly variation (January to December) in spatial overlap of predators based on Morista's Index (1 = complete overlap, 0 = no overlap).

Table 5. Stable isotope minimums (in ‰), maximums (in ‰), minimum convex polygon (MCP) areas (in ‰^{2}), standard ellipse areas (SEA$_c$; in ‰^{2}), and unique isotopic niche space (in %) for alligators (blood plasma), bull sharks (whole blood), dolphins (blubber), and snook (fin).

	N	δ^{13}C min	δ^{13}C max	δ^{15}N min	δ^{15}N max	MCP area	P (unique MCP space)	SEA$_c$	P (unique SEA$_c$ space)
Alligators	85	−30.26	−19.16	+4.65	+9.24	26.99	0.45	6.94	0.80
Bull sharks	108	−29.43	−17.89	+7.92	+11.51	27.33	0.41	4.90	0.56
Dolphins	6	−28.09	−22.59	+8.98	+10.26	3.03	0.00	2.42	0.10
Snook	34	−29.04	−25.04	+5.51	+9.29	8.80	0.00	2.48	0.43

$p = 0.05$) and March for bull sharks (SEA$_c$ = 17.88‰^{2}; $p = 0.09$). Overlap of core isotopic niche space between alligators and bull sharks was highest in April to May (Supporting Information Figure 1). Alligators and snook did not exhibit annual differences in δ^{13}C (alligators: H$_3$ = 5.20, $p = 0.07$; snook: H$_2$ = 5.14, $p = 0.08$) or δ^{15}N values (alligators: H$_3$ = 2.51, $p = 0.29$; snook: H$_2$ = 4.74, $p = 0.09$). Bull sharks did exhibit significant differences in δ^{13}C (H = 9.88, $p = 0.01$) and δ^{15}N values (H = 20.17, $p < 0.01$) across years, however mean annual differences were small (δ^{13}C = 0.84‰ and δ^{15}N = 0.41‰).

Discussion

Many ecosystems, including open oceans (billfish, tuna, sharks), coastal ecosystems (sharks, dolphins, large teleosts), and African savannahs (canids and felids), feature the coexistence of large predator guilds (e.g., Belgrano et al. 2005; Owen-Smith and Mills 2008). There remain, however, questions about whether these predators are functionally redundant, as has been suggested for sharks, tuna, and billfish in open oceans (Kitchell et al. 2002), or if species partition resources through dietary divergence in space and time to reduce interspecific competition as exhibited by cetaceans in coastal ecosystems (e.g., Pierce et al. 2010; Pinela et al. 2010; Browning et al. 2014).

Within the Florida Coastal Everglades, large-bodied predator diversity is relatively high with elasmobranch, mammalian, reptilian, and teleost predators all vying for resources that are likely predictable in space and time within oligotrophic estuarine habitats (Brown et al. 2006; Childers 2006;
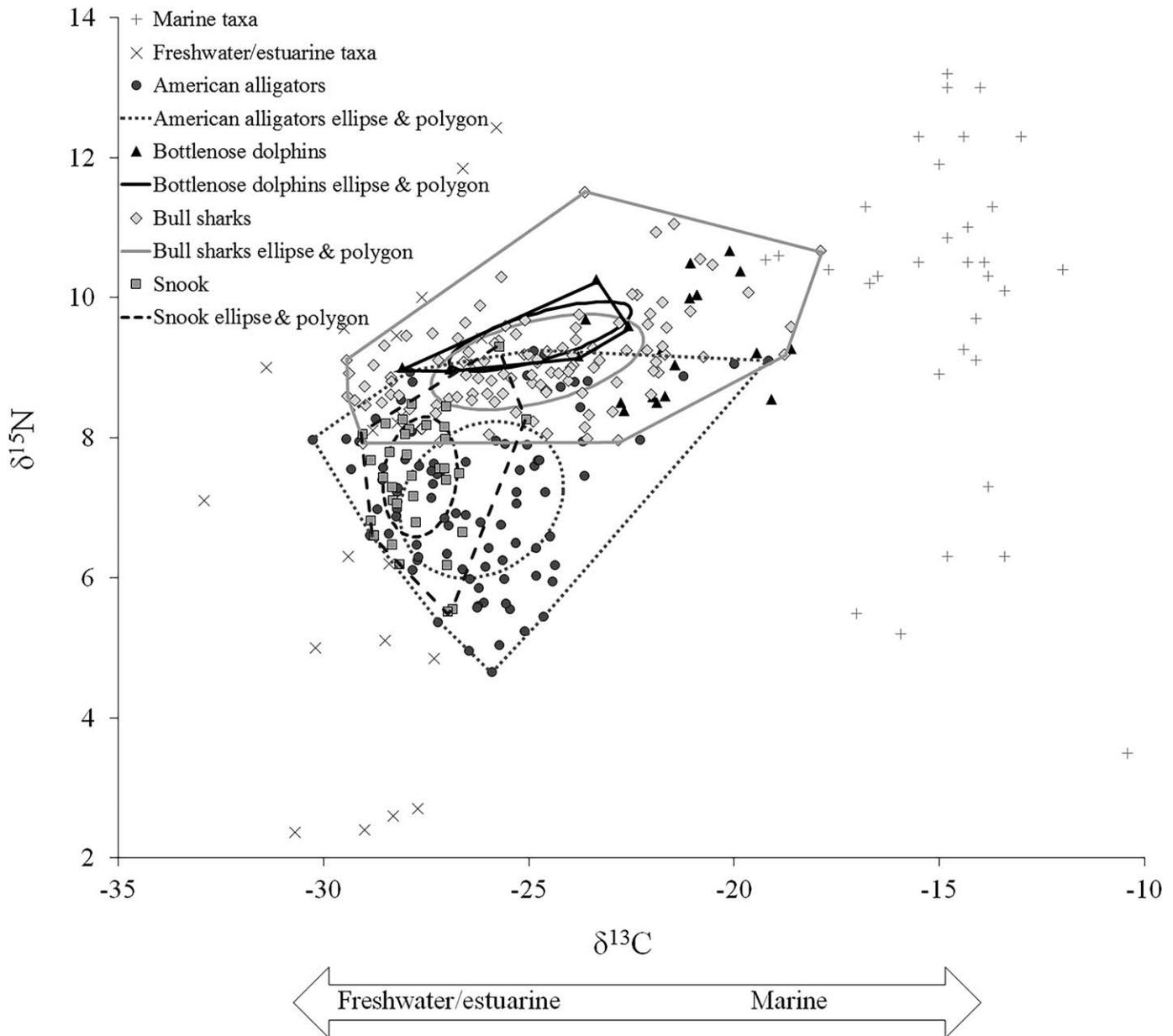
Fig. 5. Community perspective of discrimination-corrected stable isotope values (in ‰) of alligators (blood plasma), dolphins (blubber), bull sharks (whole blood), and snook (fin), and standard ellipses (SEA$_c$), including data from Fry and Smith (2002), Chasar et al. (2005), and Williams and Trexler (2006). Species with depleted ^{13}C values are typically found in freshwater and estuarine habitats, and species with enriched ^{13}C values are typically found in marine habitats. Note that the minimum convex polygon and standard ellipse for bottlenose dolphins only encompasses individuals sampled within the acoustic array despite individuals from adjacent regions also represented in the biplot.

Williams and Trexler 2006). Resource partitioning occurs within at least some of these predator populations through individual specialization in movements and foraging locations (e.g., alligators: Rosenblatt and Heithaus 2011; bull sharks: Matich et al. 2011). Our study suggests that partitioning also occurs among the most abundant species of large aquatic predators in the ecosystem.

Within the Shark River Estuary, spatial and isotopic niche overlap was low among some predators (e.g., snook and

dolphins), and apparently greater among others (e.g., alligators and snook; Table 7). Snook were predominantly detected in freshwater microhabitats and fed on prey depleted in ^{13}C and ^{15}N (i.e., prey in lower trophic levels within the freshwater/estuarine food web), while bottlenose dolphins were primarily sighted in areas downstream and fed on prey enriched in ^{15}N (i.e., prey in higher trophic levels, likely more mobile and energetically rewarding; Barros and Wells 1998). Tarpon used midstream areas most frequently

Table 6. Proportion of overlap in isotopic niche space of species on top row with species in first column based on minimum convex polygons.

	Alligator	Dolphin	Shark	Snook
Alligator		0.10	0.32	0.99
Dolphin	0.01		0.11	0.01
Shark	0.32	1.00		0.30
Snook	0.32	0.04	0.10	

where bull shark occurrence was highest, and the bull shark isotopic niche width suggested feeding on ^{15}N enriched taxa with a wide range of δ^{13}C values (i.e., prey in higher trophic levels in both marine and freshwater/estuarine food webs). Alligators had a wide-ranging isotopic niche width with a bimodal distribution, spending the most time in upstream and downstream microhabitats, and a bimodal trophic niche during the wet season, when some individuals access downstream waters and marine food webs adjacent to the Gulf of Mexico (Rosenblatt and Heithaus 2011). While the independent nature of the research conducted on each predator (i.e., study methods for space use, study periods [range of 1 month–6 yr of data], and sample sizes [*n* = 3–108]) was not originally designed for cross-species comparisons, data do suggest that niche partitioning occurs within the predator guild of the estuary despite these caveats.

Spatial overlap

Across space, each species overlapped with other predators: alligators and snook overlapped in their use of upstream microhabitats, bull sharks and tarpon overlapped in their use of midstream microhabitats, and alligators and dolphins overlapped in their use of downstream microhabitats. However, seasonal shifts in habitat use likely reduce spatial overlap and promote niche partitioning within the estuary. Indeed, dolphins were most frequently sighted downstream during the dry season (January to June), while alligators predominantly used downstream waters during the wet season (July to December). Tarpon overlapped in habitat use with bull sharks while they used the estuary, however tracking data and previous work (Luo et al. 2008b; J. Ault) suggest their use of the estuary and the study site is seasonally limited because of their migratory nature, reducing niche overlap among bull sharks and tarpon. Snook and alligators overlapped in their use of upstream waters. However, male alligators (all alligators tracked for this study were males) often migrate to adjacent marsh habitat during the dry season, potentially to mate (Rosenblatt and Heithaus 2011; Fujisaki et al. 2016), vacating upstream waters and reducing niche overlap with snook during the dry season when bull sharks increase their use of upstream waters (Matich and Heithaus 2014).

Predator guilds in other ecosystems also exhibit seasonal variability in habitat use, which can reduce interspecific competition for resources and promote coexistence (e.g., Frey and Conover 2006; Garneau et al. 2008; Cozzi et al. 2013). For example, wolves (*Canis lupus*) and coyotes (*Canis latrans*) overlap spatially in Yellowstone National Park. During winter months, when more energetically rewarding kills are made by wolves, spatial overlap of wolf and coyote home ranges increases (Metz et al. 2012), which is mitigated through different daily activity patterns between these predators (Arjo and Pletscher 1999). Life history and physiological constraints can be important factors in facilitating such seasonal shifts (e.g., Shine 1986; Humphries et al. 2002; Jessop et al. 2002). Indeed, habitat use and activity rates are often driven by environmental conditions. Within the Shark River Estuary, seasonal movements of alligators and snook attributed at least partly to reproduction (Rosenblatt and Heithaus 2011; Andrade et al. 2013; Lowerre-Barbieri et al. 2014), salinity tolerance of alligators (Rosenblatt and Heithaus 2011; Rosenblatt et al. 2013b), and apparent seasonal movement patterns of dolphins and tarpon (Luo et al. 2008b; Sarabia 2012) appear to reduce overlap, which may promote coexistence among predators (e.g., Rosenblatt and Heithaus 2011; Trotter et al. 2012; Matich and Heithaus 2014).

Passive acoustic tracking provided data on individual movements, which we used to estimated species distributions within our study area and quantify spatial overlap, providing insight into habitat partitioning. However, these data alone do not provide information on specific behaviors. Greater spatial overlap among species within a given region does not always indicate that competition for food resources is high, only that predators frequently use similar microhabitats. Similarly, reduced spatial overlap does not indicate that competition for food resources is low if species forage in areas they use infrequently. By combining acoustic tracking with stable isotope analysis our ability to elucidate patterns of niche partitioning among predators was enhanced, as we discuss below. Interspecific differences in seasonal distribution patterns also suggests relatively low overlap in distribution among most predators throughout the year.

The sampling design also limited our abilities to definitively quantify spatial overlap among all predators. Snook are found throughout estuarine waters, and must use marine regions for reproduction (e.g., Andrade et al. 2013; Lowerre-Barbieri et al. 2014). However, snook were not sampled downstream (i.e., Regions 9 and 10) due to limitations of electrofishing, which may have influenced our interpretation of movement data. If snook exhibit localized movement patterns, we would expect snook sampled downstream to predominantly use downstream waters, increasing overlap in habitat use with alligators and dolphins. Similarly, dolphin transects were not conducted in upstream microhabitats (i.e., Regions 1–4), and thus a wider sampling effort may

Table 7. Summary of spatial and trophic niches over time. Dry season was considered January to June, and wet season was considered July to December (Rosenblatt and Heithaus 2011).

	Spatial use	Temporal variation	Trophic interactions	Temporal variation
Alligators	Predominantly used upstream waters (Region 1), which overlapped with snook; and downstream waters (Region 10), which overlapped with dolphins	Used upstream waters more frequently in the dry season, and downstream waters more frequently in the wet season	Wide $\delta^{13}C$ and $\delta^{15}N$ ranges spanning freshwater/estuarine and marine prey taxa in lower trophic levels; overlapped considerably with snook and moderately with bull sharks	Wider $\delta^{15}N$ range and niche width during the dry season
Bottlenose dolphins	Predominantly spotted in downstream waters (Region 10), which overlapped with alligators	Predominantly sighted during the dry season	Moderate $\delta^{13}C$ range and minimal $\delta^{15}N$ range spanning freshwater/estuarine and marine prey taxa in upper trophic levels; overlapped completely with bull sharks	NA
Bull sharks	Predominantly used midstream waters (Regions 5, 6, & 8), which overlapped with tarpon	Increased use of upstream waters (Zones 1–4) during the dry season	Wide $\delta^{13}C$ and $\delta^{15}N$ ranges spanning freshwater/estuarine and marine prey taxa in upper trophic levels; overlapped moderately with alligators and dolphins, and minimally with snook	Wider $\delta^{13}C$ and $\delta^{15}N$ ranges and niche width during the wet season
Snook	Predominantly used upstream waters (Region 1), which overlapped with alligators	Increased use of midstream and downstream waters during the wet season	Moderate $\delta^{13}C$ range and wide $\delta^{15}N$ range spanning freshwater/estuarine taxa in lower trophic levels; overlapped almost completely with alligators and moderately with bull sharks	NA
Tarpon	Predominantly used midstream waters (Regions 5 & 7), which overlapped with bull sharks	Only detected during April, but also caught in midstream waters during the wet season	NA	NA

have revealed greater overlap among alligators, dolphins, and snook. Although rare, dolphins are known to use these upstream regions (Boucek, Matich, Rehage, and Rosenblatt *personal observations*). However, temporal variability in distribution patterns and life-history characteristics (e.g., seasonal patterns in abundance of dolphins, and seasonal spawning movements of snook) likely reduces spatial overlap among these predators, even in microhabitats where sampling was limited or absent. Tarpon were only sampled in 2013, and seasonal movement patterns (Luo et al. 2008*b*) and satellite telemetry data collected during the study (Ault et al. unpubl.) suggest tarpon use a wide variety of habitats within the Shark River Slough and make seasonal movements into and out of the study area, reducing the likelihood of spatial overlap with other predators within the study area during most months.

Trophic overlap

Similar to spatial overlap, each predator exhibited some overlap in isotopic niches with other predators: dolphins overlapped considerably with bull sharks (90% of core isotopic niche space), and snook core isotopic niche overlapped 43% with alligators, with seasonal variability in core isotopic niche overlap between alligators and bull sharks. However, isotope data paired with tracking data and previous research within the study system suggest that trophic overlap among predators is minimal among these species.

While dolphins completely overlapped in stable isotope values with bull sharks, interspecific differences in habitat use patterns suggest minimal overlap in access to food resources. Among bull sharks, some individuals (11%) make nocturnal foraging trips into downstream waters where dolphins were most frequently sighted (Matich and Heithaus 2015), however temporal variability in the distribution and foraging behavior of dolphins and bull sharks likely minimizes overlap: dolphins were predominantly found within the estuary during the dry season (January to June), during which water temperatures reach their minima ($< 15°C$ during typical years; Heithaus et al. 2009; Matich and Heithaus 2012). As an ectotherm, bull shark metabolism and energetic needs decrease in response to low temperatures during winter months (January to March), and many bull sharks increase their use of upstream waters in the late dry season (April to May) to forage on marsh prey subsidies (Matich and Heithaus 2014). As such, some bull sharks and dolphins overlap in space in downstream waters and may feed within the same food web(s), however competition is likely minimal. Similar interactions may occur between alligators and bull sharks—core isotopic niche overlap was greatest in April to May, however isotopic lag time (Layman et al. 2012) suggests this may reflect overlap in isotopic niche space at the end of the wet season in October to November (see turnover rates in Table 1) when alligators are more likely to use downstream habitats due to environmental conditions (i.e.,

salinities; Rosenblatt and Heithaus 2011; Fujisaki et al. 2014), and overlap in isotopic niche space is relatively low during this time period (7–16%).

Stable isotope data also suggest trophic overlap was moderate among snook and alligators, which overlapped in use of upstream microhabitats and exhibited similar $\delta^{15}N$ values, which may be indicative of trophic level (Layman et al. 2012). However, diet data from other studies suggest that trophic overlap among snook and alligators with depleted ^{13}C values may be over-estimated using stable isotope values: stomach content analysis shows that alligators predominantly feed on adult blue crabs (*Callinectes sapidus*) throughout the estuary, with opportunistic feeding on other species (A. Rosenblatt unpubl.), while snook predominantly feed on smaller-bodied invertebrates and fishes in upstream microhabitats (e.g., Boucek and Rehage 2013). Snook also meet a large proportion of their annual energetic needs from marsh prey subsidies during the dry season when male alligators may leave the estuary for freshwater marshes (Rosenblatt and Heithaus 2011; Fujisaki et al. 2016).

For species with different stable isotope values such as dolphins and snook, differences in $\delta^{13}C$ and $\delta^{15}N$ are informative of niche partitioning, however similarities in stable isotope values can be ambiguous, with different foraging behaviors and trophic interactions leading to similar $\delta^{13}C$ and $\delta^{15}N$ values (Martinez del Rio et al. 2009; Kiszka et al. 2010). Using complementary methods like telemetry and stomach content information with stable isotopes aids in understanding trophic ecologies of study species, and here suggests niche overlap among alligators and snook may be lower than predicted when relying on stable isotope values alone. Another important consideration when using stable isotopes to infer trophic interactions are species- and context-specific turnover rates and discrimination factors, which can affect data interpretation (McCutchan et al. 2003; Vanderklift & Ponsard 2003), as well as the effects of the chemical composition of tissues collected from different taxa that may affect $\delta^{13}C$ and $\delta^{15}N$ values. Analysis suggests minimal variation in $\delta^{13}C$ and $\delta^{15}N$ of study species across time, and relatively low C : N values, except for alligators for which lipid extraction does not affect plasma $\delta^{13}C$ and $\delta^{15}N$ values because of high protein content (Coulson and Hernandez 1964; Rosenblatt and Heithaus 2013), suggesting limited interpretation bias. Our relatively large sample sizes across multiple years also should have reduced the potential effects of context-specific differences on $\delta^{13}C$ and $\delta^{15}N$ values.

Consequences of niche partitioning

The oligotrophic nature of the Shark River Estuary limits productivity within much of the ecosystem, especially the ecotone region where the acoustic array was located (Childers 2006). As such, nutrient and resource limitations likely are important drivers of population-, community-, and

ecosystem-level processes within the ecosystem, including interspecific interactions and resource use by large-bodied predators. Results support our hypotheses that niche partitioning occurs among the most abundant species within the aquatic predator guild, which is likely facilitated by a variety of factors including character displacement and interspecific differences in life-histories (e.g., Schluter and McPhail 1992; Fedriani et al. 2000; Elbroch et al. 2015).

While the proximate and ultimate causes of niche partitioning within the estuary may be apparent, the time frame over which character displacement developed, as well as the impact changes in resource availability and environmental conditions attributed to human disturbance and climate change will have on predator interactions is unclear. The Florida Everglades formed more than 5000 yr ago, however beginning in the early 20th century, water diversion by humans lead to a "re-plumbing" of the ecosystem, with changes in the length of hydroperiods, salinities, and water quality and quantity, significantly affecting terrestrial and aquatic communities (Davis and Ogden 1994). As such, the anthropogenically-managed Everglades is quite young on an evolutionary time-scale, and community structure and behavioral adjustments to water management among predators in coastal estuaries may be relatively new.

Despite the potential novelty of present conditions, the predators within the estuary are likely well adapted to contend with predicted changes attributed to sea-level rise, variability in precipitation, and Everglades restoration efforts (National Research Council 2014; Koch et al. 2015). The most abundant predators within the ecosystem are all considered generalists based on physiologies, habitat use, and diets, and previous research within the estuary suggests predators are not only generalized, but also plastic in their behaviors. Indeed, the predators studied are capable of taking advantage of allochthonous resources (Boucek and Rehage 2013; Matich and Heithaus 2014), adjusting to changes in abiotic conditions (Rosenblatt and Heithaus 2011; Rosenblatt et al. 2013*b*), and potentially filling vacant niche space, which is likely important in an ecosystem where changes in environmental conditions can be quite rapid and unpredictable (e.g., Hazlett 1988; Foster 1999; Matich and Heithaus 2012). This hypothesis, however, needs refinement with future studies, and niche partitioning based on stable isotope and movement data do not preclude these predators from exhibiting some functional redundancy.

Niche width partitioning, however, does not occur exclusively at the community/guild level within the Shark River Estuary. Intraspecific variation in movements and foraging behaviors is prominent among at least some of these predators: alligators vary in their tendencies to commute between marine, brackish, and freshwater microhabitats for access to food resources (Rosenblatt and Heithaus 2011), bull sharks vary in their degrees of trophic specialization within marine and freshwater/estuarine food webs (Matich et al. 2011), and

dolphins are known to exhibit considerably different foraging tactics among individuals and populations (e.g., Sargeant et al. 2005, 2007; Torres and Read 2009). The high degree of individual variation and specialization among individuals is not unexpected in resource-limited environments (e.g., Cherel et al. 2008; Kiszka et al. 2015). In fact, within resource-limited ecosystems, behavioral and morphological diversity among generalist predators may be more important in promoting food web and community stability than functional redundancy compared to more productive ecosystems, especially if predators within productive systems have similar morphologies, foraging behaviors, and/or life histories (e.g., Vaudo and Heithaus 2011). Niche partitioning through character displacement enables the coexistence of similar species, and can promote greater species diversity, as well as functional diversity within and across populations in ecosystems with limited productivity (e.g., Dayan and Simberloff 2005; Pfennig and Pfennig 2009). As such, niche partitioning within both populations and communities can lead to low functional redundancy during predictable conditions, but in the event of species declines or loss, expansion of ecological niches by individuals and/or populations may promote resilience and stability (Chase and Leibold 2003). Quantifying predator and prey population sizes, and using natural perturbations and designed experiments (e.g., predator and prey exclusions and translocations) to test the abilities of predators with specific foraging behaviors, life histories, and inherent levels of behavioral variation to adjust foraging tactics and fill vacant niche space will be an important step forward in testing ecological theory, predicting the effects of climate change and human disturbance, and increasing our understanding of how management of species and/or environmental conditions may alter community dynamics.

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Conflict of Interest

None declared.