Diet shift and site-fidelity of oceanic whitetip sharks *Carcharhinus longimanus* along the Great Bahama Bank

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ABSTRACT: Identifying the driving forces behind oceanic pelagic shark movements is key to a better understanding of their life history. Some oceanic pelagic shark species have been shown to aggregate in specific regions to mate and/or exploit abundant food resources. The oceanic whitetip shark *Carcharhinus longimanus*, a subtropical, ectothermic, oceanic pelagic shark that has experienced severe population declines, aggregates seasonally around Cat Island (CI) in The Bahamas. Large pelagic teleosts (e.g. billfish, tunas, and dolphinfish) are abundant in this region and oceanic whitetips are anecdotally reported to feed heavily on recreationally caught teleosts. However, it was unknown whether feeding habits at CI substantially differ from longer-term feeding habits. We used tag-recapture to assess site-fidelity of adult oceanic whitetips to CI and stable isotope analysis (SIA) of 2 different tissues (blood plasma and white muscle) to compare short- and long-term feeding patterns. The relatively high recapture rate (20.3%) confirmed that individual whitetips exhibit site-fidelity to CI. The aggregation consisted of adult individuals; females were more common, more than half were gravid, and no physical or behavioral evidence of mating or parturition was observed at CI. SIA-based Bayesian mixing model estimates of short-term (near CI) diets showed more large pelagic teleosts (72%) than in long-term diets (47%), showing a spatiotemporal difference in oceanic whitetip feeding habits. This suggests that availability of large teleost prey is a possible mechanism underpinning site-fidelity and aggregation of whitetips at CI. These results provide insight into the function of one of the last known aggregations of this once-abundant top predator.

KEY WORDS: Stable isotope · Elasmobranch · Endangered · Tag · Pelagic · Bayesian mixing model

INTRODUCTION

Oceanic pelagic sharks, defined as sharks that are not closely associated with the seafloor and live their lives exclusively or partially in ocean basins far from continental landmasses, make some of the longest migrations of any vertebrates (Compagno 2008, Dulvy et al. 2008). The driving forces of these movements are the subject of increasing research attention given the need to sustainably manage fisheries that exploit these species, coupled with the realization that migrations are likely to be affected by global

climate change (Dulvy et al. 2008, Block et al. 2011). The migratory cycles of sharks that live primarily in neritic and coastal habitats often involve predictable and repeated movements between a series of geospatially fixed locations ('site-fidelity') (Hueter et al. 2005, Speed et al. 2010, Bond et al. 2012, Feldheim et al. 2014, Chapman et al. 2015). In contrast, oceanic pelagic sharks often orient to mobile environmental features such as oceanographic fronts, although site-fidelity to fixed locations does occur in oceanic pelagic species that complete part of their life-cycle over the continental shelf, along the coast, or at offshore bathymetric features such as seamounts (Casey & Kohler 1992, Bigelow et al. 1999, Litvinov 2008, Block et al. 2011).

The oceanic whitetip shark *Carcharhinus longimanus* is one of 21 elasmobranch species characterized as 'oceanic pelagic' (Dulvy et al. 2008), and is one of few shark species that can potentially complete its entire life cycle in the open ocean. In the Northwest Atlantic, oceanic whitetips make long-distance migrations, and some have shown periods of seasonal residency within the Bahamian archipelago along the eastern edge of the Great Bahama Bank (Howey-Jordan et al. 2013). One specific location along this bank (Cat Island, or CI) is known to harbor relatively high densities of this species over successive winter and spring seasons (Howey-Jordan et al. 2013). This raises the question as to whether the predictable aggregation of this species at CI is driven by individual site-fidelity, and, if so, what motivates individuals to orient to this fixed location as opposed to other similar surrounding islands or to mobile oceanic features. Coastal sharks and oceanic pelagic sharks that complete part of their life cycle along the coast have demonstrated site-fidelity to fixed locations for purposes of reproduction, e.g. when individuals home to their natal nursery site to give birth, or 'natal philopatry' (Feldheim et al. 2014), or repeatedly return to the same mating aggregation sites (Pratt et al. 2001). Gallagher et al. (2014) reported oceanic whitetip swimming in 'nose-to-tail' formation at CI during spring and speculated that this could be related to courtship (Gallagher et al. 2014). However, this behavior was observed in all-female groups, and other studies have observed similar behavior in immature sharks (Guttridge et al. 2011).

Individual sharks also practice site-fidelity when they are able to predict and intercept spatially fixed feeding opportunities (e.g. prey spawning aggregations or parturition sites; Weng et al. 2008, Jorgensen et al. 2009). Many large predatory pelagic fish, including dolphinfish, wahoo, billfish, and tunas (col-

lectively referred to as 'sportfish'), are common at CI during the winter and spring, where they are targeted by recreational sportfishers that operate out of one of very few large marinas in this region of The Bahamas. Previous diet studies of oceanic whitetips from various regions (5 studies, n = 108 individuals) suggest a diet comprised primarily of cephalopods (44%) and teleosts (43%), with a small proportion of their diet (13%) comprised of a broad mix of birds, molluscs, crustaceans, and mammals (Cortés 1999). Based on these studies, the estimated trophic level (TL) of oceanic whitetips (TL = 4.2) is similar to, and sometimes below, those of large pelagic teleosts that occur around CI, including blackfin tuna *Thunnus atlanticus* (TL = 4.1), skipjack tuna *Katsuwonus pelamis* (3.8), dolphinfish *Coryphaena hippurus* (4.4), blue marlin *Makaira nigricans* (4.5), yellowfin tuna *T. albacares* (4.3), and wahoo *Acanthocybium solandri* (4.4). Oceanic whitetips may therefore return to CI to feed on the same prey (forage fish and squids) that support these large pelagic teleosts at this site. Another possibility is that oceanic whitetips repeatedly return to CI to prey on these large pelagic predators, as they can potentially capture large, free-swimming pelagic fish (Backus et al. 1956). Recreational fishermen observe oceanic whitetips partially or wholly consuming hooked sportfish, primarily tunas, dolphinfish, wahoo, and billfish, and oceanic whitetips are also offered carcasses by local sportdiving operations, supplementing natural prey sources. These recreational operations may provide consistent opportunities for oceanic whitetips to feed on large teleosts at CI. Thus, this region may provide a rich feeding ground for oceanic whitetips to prey on large pelagic fish, as opposed to other regions where they feed (based on previous diet studies) on much smaller forage fish and squids. Oceanic whitetips in the Atlantic Ocean are highly depleted (IUCN Red List: 'Critically Endangered'; Baum et al. 2006), with estimated declines of ~99% over 50 yr in the Gulf of Mexico (Baum & Myers 2004). As CI is one of the few known aggregation sites for oceanic whitetips, it is important to understand the function of this region in oceanic whitetip biology and ecology.

We hypothesized that large pelagic predators are proportionally more abundant in oceanic whitetip diet while they aggregate at CI than in their long-term diet. Direct analysis of stomach contents is not possible for ethical reasons given the status of this species in the northwestern Atlantic. Stable isotope analysis (SIA) has proven to be a useful non-lethal tool to examine shark feeding ecology over various timeframes (Estrada et al. 2003, Logan & Lutcavage

2010, Hussey et al. 2012). We therefore used SIA (δ^{13}C and δ^{15}N) of 2 tissues to examine short-term (blood plasma) and long-term (muscle tissue) feeding habits. SIA uses the ratio of heavy to light isotopes in an organism to represent long-term integration of diet into various tissues (Fry 2006). In elasmobranchs, blood plasma has been shown to represent relatively short (70 to 200 d) periods of time (Matich et al. 2011, Kim et al. 2012b), while muscle tissue represents diet over longer (400 to 600 d) timeframes (MacNeil et al. 2006, Matich et al. 2011, Kim et al. 2012b). Oceanic whitetips return to The Bahamas in October to November, and sharks were sampled at CI in early May (Howey-Jordan et al. 2013); thus, sharks had likely been at CI for several months (i.e. ~180 to 210 d prior to sampling), allowing for blood plasma to reflect a diet change at CI.

The primary goals of this study were 2-fold. First, we conducted a tagging study over 4 yr in April/May to describe the demographic structure of the aggregation and assess the level of individual site-fidelity to CI. Second, we compared the short-term (several months, representing diet at CI) to longer-term (>1 yr) feeding habits of oceanic whitetips. Based on the hypothesis of more extensive feeding on large pelagic predators by whitetips at CI, we predicted that blood plasma would have higher δ^{15}N values compared to white muscle and that Bayesian mixing model diet estimates would show significantly higher contributions of large pelagic teleosts to short-term than to long-term diet of oceanic whitetips. We also compared δ^{13}C and δ^{15}N across shark size, between gender, and between pregnant and non-pregnant females (determined by ultrasound) to assess the potential feeding differences between these groups.

MATERIALS AND METHODS

Animal capture, handling, and tagging

Four 10 d fishing expeditions were made to CI, The Bahamas (Fig. 1), between 1 May 2011 and 9 May 2014. Oceanic whitetips were attracted to the research vessel using a chum crate containing fresh pieces of dolphinfish and Atlantic bonito *Sarda sarda*. Baited hand-lines were deployed after sharks were sighted. These lines consisted of 8 m of nylon line (6 mm diameter) with a large float (37 cm diameter) attached at one end, an 18/0 non-offset carbon circle hook with approximately 80 cm of steel leader attached to the other end, and a second smaller float (20 cm diameter) attached to the line approximately

1.5 m from the leader to provide additional flotation to the gear. Once hooked and brought alongside the vessel, all sharks were measured and their gender was visually determined by the presence or absence of claspers. In 2014 both uteri of all female sharks were examined via ultrasonography using the Ibex Pro (E.I. Medical Imaging), a water-resistant, portable ultrasound unit, equipped with a 5 to 2.5 MHz, 60 mm curved linear array transducer with a 24 cm scan depth. This enabled determination of whether or not females were gravid at the time of capture. Two uniquely numbered external tags were deployed on all captured sharks: a Rototag® attached to the upper third of the first dorsal fin (Dalton Tags) and a stainless steel M-type dart tag inserted in the basolateral dorsal musculature (Hallprint). Previously captured sharks ('recaptures') were identified using these tags. We were also able to obtain photographs of free-swimming tagged sharks from dive operations. When we were able to verify the tag number from the photograph, we considered this a 'resighting' of that individual (see Table 1).

Sampling and analysis of shark tissues

Shark tissue samples were collected in conjunction with tagging protocols at CI, The Bahamas, as described in Howey-Jordan et al. (2013). Blood (3 ml) was collected via caudal venipuncture using sterile syringes and 16-gauge needles, transferred to sterile vacuum tubes containing acid citrate dextrose (ACD) anticoagulant modfied for use with elasmobranchs (Walsh & Luer 2004), and temporarily stored on ice. For all sharks possible (n = 13), white muscle tissue was also collected from the hypaxial dorsal musculature using stainless steel biopsy punches (custommade by DJM).

Blood was centrifuged for 5 min at 1300 × *g* to separate plasma, which was stored in 1 ml aliquots at −20°C. White muscle tissue was immediately stored in cryovials and frozen at −5°C. Muscle tissue samples were thawed and thoroughly rinsed in DI water (3× sonication) to extract urea (e.g. Kim et al. 2012b). Samples were then frozen at −80°C for 24 h, lyophilized for 72 h, and homogenized using a Wig-L-Bug (Sigma Aldrich). Analyses of δ^{13}C and δ^{15}N were performed at the University of Hawaii using an online C-N analyzer coupled with a Delta XP isotope ratio mass spectrometer. Replicate reference materials of atmospheric nitrogen and Vienna Pee Dee Belemnite (V-PDB) were analyzed between approximately 10 samples. Values of δ^{13}C for blood plasma
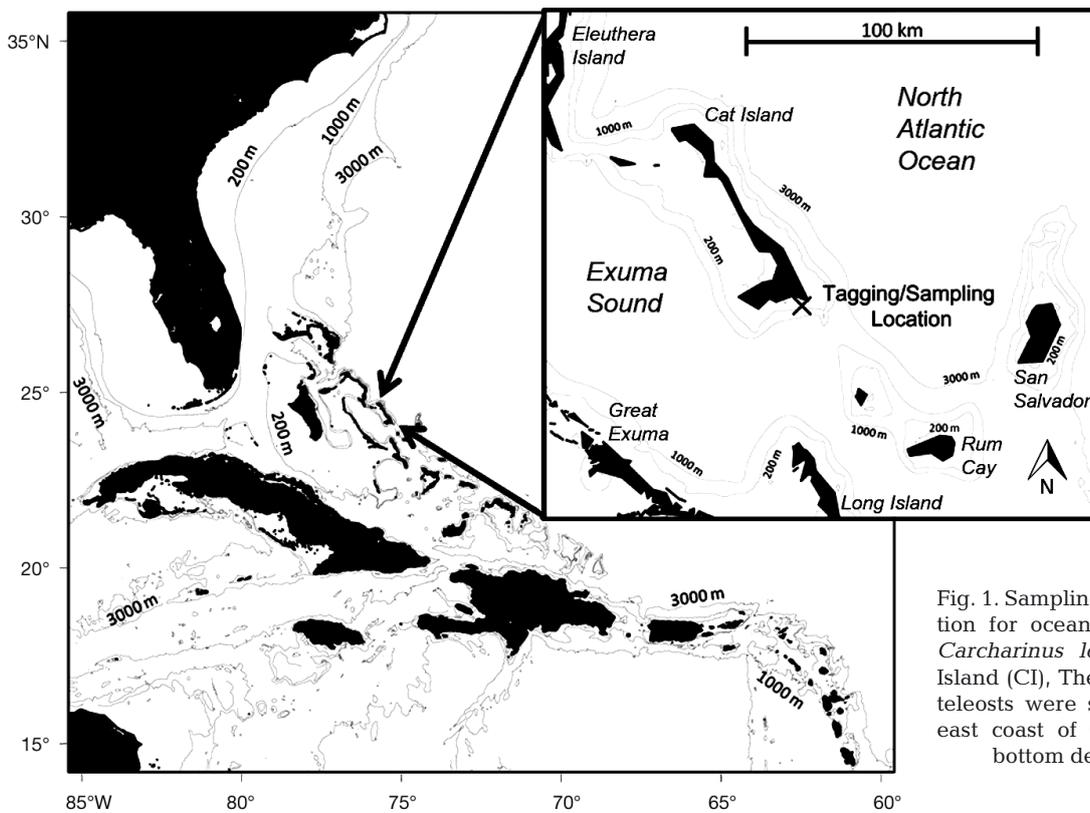
Fig. 1. Sampling and tagging location for oceanic whitetip sharks *Carcharinus longimanus* at Cat Island (CI), The Bahamas. Pelagic teleosts were sampled along the east coast of CI. Isobaths show bottom depth in meters

have been shown to be affected by storage in ACD (Lemons et al. 2012); δ^{13}C values of blood plasma were thus corrected by −1.2‰ (Lemons et al. 2012). Values of δ^{13}C and δ^{15}N for white muscle tissue and blood plasma were adjusted for different tissue-specific diet tissue discrimination factor (DTDF) values (Kim et al. 2012a) based on captive leopard sharks *Triakis semifasciata* (see subsection 'Statistical and diet analyses'). We did not perform chemical or arithmetic lipid extractions/corrections since C:N ratios for all tissues were <3.5 (Post et al. 2007; see Table 2) and lipid extractions have been shown to have little effect on shark muscle tissue (Hussey et al. 2010a).

Sampling and analysis of potential prey tissues

Oceanic whitetips are known to feed on a wide range of prey, from small teleosts and cephalopods to large pelagic predators. Large pelagic predators (tuna species, dolphinfish, and wahoo) were collected by hook-and-line aboard the research vessel or sampled from local private fishing vessels. Smaller prey (e.g. flying fish, larval fish, and squids) were collected from the stomach contents of landed sportfish (tunas, dolphinfish, and wahoo); only intact, recently

consumed (completely undigested) prey were sampled for muscle tissue.

For large pelagic fish, white muscle (WM) was sampled from the dorsal musculature approximately 20 cm beneath the skin. For forage fish, WM was sampled from the dorsal musculature just below the skin. For squids, a section of mantle tissue was taken. Tissue samples were frozen at −5°C, then frozen at −80°C for 24 h, lyophilized for 72 h, and homogenized using a Wig-L-Bug (Sigma Aldrich). Analyses of δ^{13}C and δ^{15}N were performed at the University of Hawaii, as described in the previous subsection.

Statistical and diet analyses

The δ^{13}C and δ^{15}N values of oceanic whitetip white muscle and plasma samples were compared to assess differences between short-term (70 to 200 d; plasma) and long-term (400 to 600 d; muscle) diet. In order to account for tissue-specific differences in DTDFs, we corrected both muscle and plasma for DTDFs determined in a controlled laboratory study (Kim et al. 2012a). We chose DTDFs according to Kim et al. (2012a) for 2 reasons. First, it is the only study to date that has assessed the DTDFs of both muscle and plasma in sharks, from both tissues in the same ani-

mals, in controlled laboratory settings. Also, DTDF values for $\delta^{15}N$ ($\Delta^{15}N_{tissue}$) have been shown to correlate negatively with $\delta^{15}N$ values of predator diet; fish and sharks feeding on prey with lower $\delta^{15}N$ values tend to have higher $\Delta^{15}N_{tissue}$ or DTDF (Caut et al. 2009, Olin et al. 2013). Prey in the CI region were shown to have relatively low $\delta^{15}N$ values, making the high DTDF values found in Kim et al. (2012a) appropriate. We used the non-parametric Mann-Whitney U-test to compare plasma and muscle $\delta^{13}C$ and $\delta^{15}N$ values, with significance at $p < 0.05$.

Relative inputs of large pelagic teleosts (tunas, wahoo, dolphinfish, and billfish), forage fish (flying fish), and squids were assessed using the Bayesian mixing model MixSIR (Moore & Semmens 2008). The $\delta^{13}C$ and $\delta^{15}N$ values for samples of wahoo, dolphinfish, and skipjack, blackfin, and yellowfin tunas were grouped, and mean $\delta^{13}C$ and $\delta^{15}N$ values ($\pm SD$) were calculated to represent large pelagic teleosts. Mean $\delta^{13}C$ and $\delta^{15}N$ values ($\pm SD$) were calculated for both flying fish and various squids. Since it is not known which squid species are specifically consumed by whitetips, we assumed that pelagic predator (tunas, dolphinfish, and wahoo) stomach contents adequately sampled the squid prey species available, and we did not identify the squid samples to the species level. We used DTDFs from Kim et al. (2012a) and mean prey SIA values (see Table 2) to generate median and 95% confidence interval estimates for the proportion of large pelagic teleosts, forage fish, and squids in the short-term diet of oceanic whitetips using blood plasma $\delta^{13}C$ and $\delta^{15}N$ values and in the long-term diet using white muscle $\delta^{13}C$ and $\delta^{15}N$ values using the Bayesian mixing model MixSIR. We ran 10^6 iterations and uninformed priors when generating mixing model estimates.

We compared the $\delta^{13}C$ and $\delta^{15}N$ values for both blood plasma and muscle to shark fork length (FL, cm) to assess dietary changes with animal size using linear regression; we used Pearson's correlation coefficient to assess the relative strength of potential correlations. Differences in mean $\delta^{13}C$ and $\delta^{15}N$ values between pregnant and non-pregnant females were assessed using the non-parametric Mann-Whitney U-test with significance at $p < 0.05$.

RESULTS

Fifty-nine oceanic whitetips (48 ♀, FL = 197 ± 21 cm; 11 ♂, FL = 187 ± 14 cm; mean ± SD) were tagged over three ~10 d expeditions starting in the first week of May 2011, 2012 and 2013 at Cat Island

(Fig. 1). All of these individuals were at or above the known size at maturity for the species (Lessa et al. 1999), and all of the males had long, calcified claspers. None of the females had a hematose cloaca or recent bite wounds that could be attributed to mating, although 1 female had well-healed bite scars that could have occurred during courtship, mating, or intraspecific aggression in the previous months. None of the males had hematose claspers or sperm present in the clasper. Over 2012, 2013, and 2014, a total of 12 individuals were recaptured and/or re-sighted (20.3%) from 1 to 3 yr after capture (Table 1). Two individuals were recaptured or resighted over 3 consecutive years (Table 1). Eleven of 19 (58%) females examined with ultrasound in late April/early May 2014 (the period of tissue sampling for SIA) were gravid.

Muscle samples were obtained from 13 (11 ♀, 2 ♂) and blood plasma from 19 (16 ♀, 3 ♂) individual oceanic whitetips. Muscle samples were taken from 39 large pelagic teleosts including blackfin tuna (n = 11), dolphinfish (n = 21), yellowfin tuna (n = 3), skipjack tuna (n = 2), and wahoo (n = 2) (Table 2). These species are all occasionally consumed by oceanic whitetips at CI after being hooked by sportfishers (authors' pers. obs.). Prey items in the stomachs of captured pelagic teleosts (tunas, dolphinfish, and wahoo) were dominated by squids and flying fish, and muscle samples were obtained from 9 squid and 7 flying fish (Table 2). Pelagic forage fish and squid $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SD) were relatively low (Table 2). Large pelagic teleosts had similar mean $\delta^{13}C$ and $\delta^{15}N$ values (Table 2, Fig. 2a), with an overall mean of −16.5‰ (±0.5‰) and 8.4‰ (±1.0‰)

Table 1. Recaptures of tagged oceanic whitetip sharks *Carcharhinus longimanus* at Cat Island, The Bahamas. FL: fork length at initial capture

ID no.	Date tagged (mo/d/yr)	Recapture date (mo/d/yr)	Resighting date (mo/d/yr)	Sex	FL (cm)
851	5/5/11	5/8/13	4/23/12	F	204
1124	5/1/11	4/27/14		F	224
448	5/7/12	4/26/14		F	212
868	5/10/12	5/5/14		F	184
490	5/11/12	5/12/13		F	203
865	5/9/12	5/8/13	5/6/14	F	210
715	5/8/13	4/26/14		F	216
725	5/8/13	4/29/14		M	198
471	5/1/13	5/6/14		F	174
1063	5/8/13	5/5/14		F	203
870	5/10/12		5/1/13	F	204
901	5/12/12		5/1/13	F	203

Table 2. Values of $\delta^{13}C$ and $\delta^{15}N$ for species collected for this study at Cat Island, The Bahamas. Lengths refer to standard fork length for all species except squid (mantle length). Mean isotopic values for prey groupings used in mixing models shown in *italics*. Oceanic whitetip (OWT; *Carcharhinus longimanus*) muscle and blood plasma 'corr' values represent $\delta^{13}C$ and $\delta^{15}N$ values corrected for diet tissue discrimination factors according to Kim et al. (2012a)

Species	Mean $\delta^{13}C$ (SD)	Mean $\delta^{15}N$ (SD)	C:N (SD)	Mean length (SD) (cm)	n
Flying fish species	−16.9 (0.3)	5.5 (0.7)	3.1 (0.03)	17.7 (1.1)	7
Squid species	−18.9 (0.9)	5.1 (0.8)	3.4 (0.4)	4.2 (4.5)	9
Pelagic forage species	*−18.0 (1.2)*	*5.3 (0.8)*	*3.2 (0.2)*	*−*	*16*
Dolphinfish	−16.3 (0.5)	8.7 (0.9)	3.1 (0.04)	100.5 (7.3)	21
Wahoo	−16.7 (0.2)	8.5 (0.6)	3.2 (0.1)	102.5 (9.2)	2
Blackfin tuna	−16.9 (0.4)	8.1 (1.1)	3.2 (0.2)	54.6 (3.6)	11
Skipjack tuna	−16.4 (0.1)	7.9 (1.1)	3.1 (0.1)	55.9 (7.2)	2
Yellowfin tuna	−16.4 (0.5)	7.3 (0.3)	3.2 (0.2)	66.7 (10.6)	3
Large pelagic teleost species	*−16.5 (0.5)*	*8.4 (1.0)*	*3.2 (0.1)*	*−*	*39*
OWT (muscle)	−15.9 (0.6)	10.4 (0.7)	3.2 (0.2)	202.8 (18.7)	13
OWT (plasma)	−14.5 (0.4)	10.2 (0.6)	1.8 (0.2)	201.1 (19.1)	19
OWT (muscle)$_{corr}$	−17.6 (0.6)	6.7 (0.7)	3.2 (0.2)	202.8 (18.7)	13
OWT (plasma)$_{corr}$	−17.3 (0.4)	8.0 (0.6)	1.8 (0.2)	201.1 (19.1)	19

(Table 2, Fig. 2a). Oceanic whitetip muscle $\delta^{13}C$ and $\delta^{15}N$ values ranged from −16.6 to −14.0‰ and 8.5 to 11.6‰, respectively (−15.9 ± 0.6; 10.4 ± 0.7‰). Blood plasma $\delta^{13}C$ (ACD-corrected) and $\delta^{15}N$ values ranged from −15.6 to −13.9‰ and 9.5 to 11.5‰, respectively (−14.5 ± 0.4; 10.2 ± 0.6‰) (Table 2).

After tissue-specific DTDF correction, oceanic whitetip muscle (−17.6 ± 0.6 and 6.7 ± 0.7) and plasma (−17.3 ± 0.4 and 8.0 ± 0.6) (Table 2) $\delta^{13}C$ and $\delta^{15}N$ values were significantly different (Mann-Whitney U-test, $p < 0.01$ for $\delta^{13}C$ and $\delta^{15}N$; Fig. 2a). Individual shark muscle $\delta^{13}C$ and $\delta^{15}N$ values overlapped little with individual shark plasma values (Fig. 2a), with plasma having higher $\delta^{13}C$ and $\delta^{15}N$ values that were more consistent with large pelagic teleosts than forage prey (Fig. 2a). Compared to individual shark blood plasma $\delta^{13}C$ and $\delta^{15}N$ values, muscle $\delta^{13}C$ and $\delta^{15}N$ values were more consistent across individual sharks and were more similar to forage prey (squids and flying fish) at CI, suggesting that muscle reflects more feeding on small forage prey (Fig. 2a).
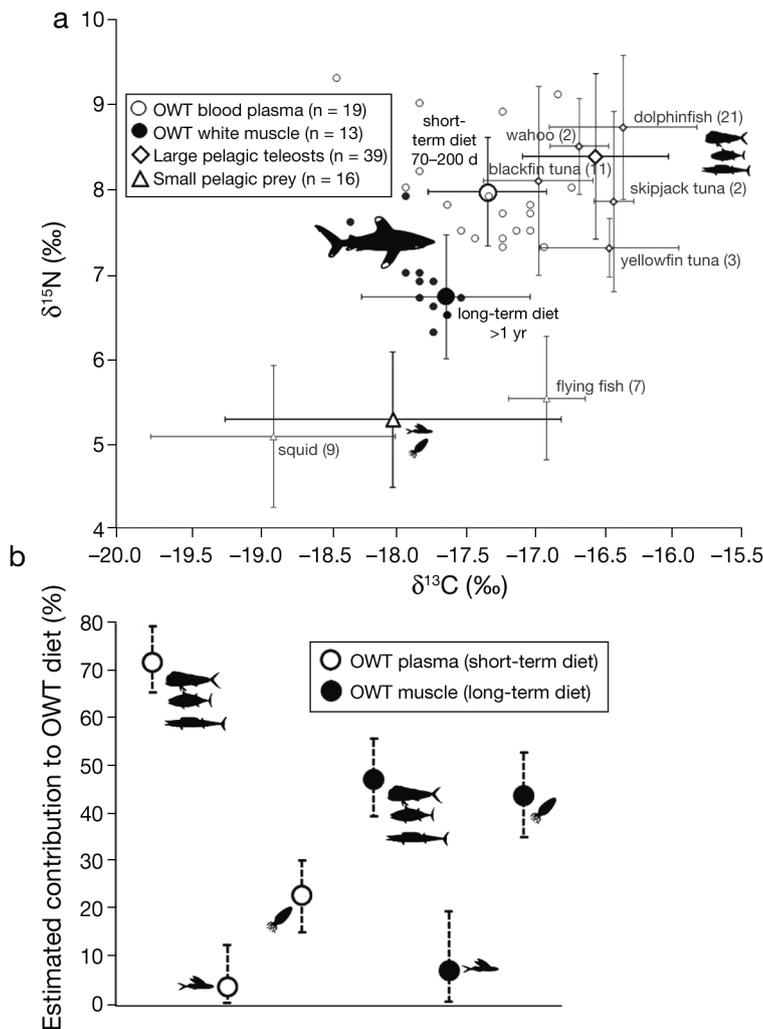
Fig. 2. (a) Biplot of $\delta^{13}C$ and $\delta^{15}N$ values for oceanic whitetip sharks *Carcharhinus longimanus* (OWT) and potential prey items at Cat Island (CI), The Bahamas. Pelagic predators (◇) are commonly caught pelagic teleosts at CI, and 'small pelagic prey' is represented by squids and flying fish (△). Large symbols with error bars represent mean $\delta^{13}C$ and $\delta^{15}N$ values (±SD); sample size indicated by number in parentheses. Individual shark plasma (○) and muscle (●) values also shown (smaller circles). OWT muscle and blood plasma values are diet tissue discrimination factor-corrected based on values from Kim et al. (2012a). (b) Estimates of dietary inputs of large pelagic predators (larger icons: dolphinfish, tuna, wahoo) and small pelagic forage prey (smaller icons: flying fish and squid) into diet of OWT. Estimates are from a Bayesian mixing model (MixSIR) and based on 2 tissues, blood plasma and muscle, which represent short-term and long-term OWT diet, respectively. Error bars represent 95% confidence intervals, as reported by MixSIR analyses

Mixing model results indicated clear differences between oceanic whitetip diet estimated from plasma (short-term diet) and muscle (long-term diet) (Fig. 2b). Median estimated input of large pelagic teleosts to short-term diet was 72% (95% confidence interval: 65 to 79%), with 23% from squids (15 to 30% confidence interval) and low inputs from small forage fish (4%; 0 to 13% confidence interval). In contrast, muscle-derived diet estimates suggested a long-term diet consisting of 47% large teleosts, 44% squid, and 8% small forage fish (40 to 56%, 35 to 53%, and 1 to 20% confidence interval, respectively). Distributions of posterior probabilities of diet input values from the Bayesian mixing model were fairly narrow, with 95% confidence intervals that were well constrained (Fig. 2b).

There was a moderate increase of $\delta^{15}N$ values of both muscle and blood plasma with shark size, though the trends were not statistically significant (Fig. 3). There were no apparent differences in $\delta^{13}C$ and $\delta^{15}N$ between males and females (though sample size for males was low; n = 2 and n = 3 for muscle and plasma, respectively), nor were there differences in $\delta^{13}C$ and $\delta^{15}N$ values between pregnant (n = 11) and non-pregnant (n = 5) females (Mann-Whitney U-test, p > 0.5).
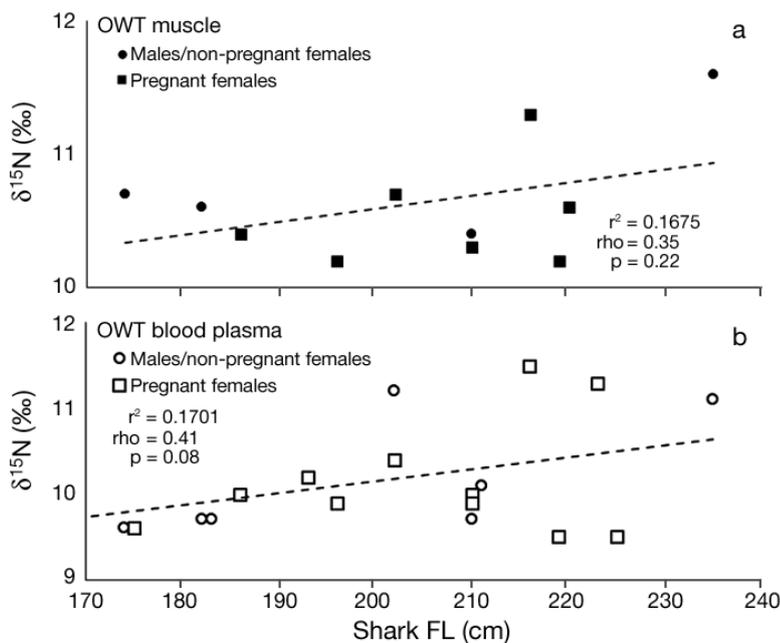

Fig. 3. Fork length (FL; cm) versus $\delta^{15}N$ for (a) muscle and (b) blood plasma in oceanic whitetip sharks *Carcharhinus longimanus* (OWT) in Cat Island, The Bahamas. Dashed line represents linear regression fit to data. Positive correlations of size and muscle/blood plasma $\delta^{15}N$ values were not significant at the $\alpha = 0.05$ level (p-values shown). Rho-values show Pearson's correlation coefficient. There was no apparent trend for size versus $\delta^{13}C$ in either tissue (data not shown)

DISCUSSION

Shark movements

Four consecutive years of tagging oceanic whitetips at CI demonstrate that adult females, most of which are gravid, and a smaller number of adult males are consistently present at this site in the spring. There is currently no definitive evidence (e.g. presence of neonates or juveniles, observations of sharks with physical signs of mating) that parturition or mating occurs there. We recaptured or resighted 20% of tagged oceanic whitetips, demonstrating that some individuals exhibit seasonal site-fidelity to CI. Howey-Jordan et al. (2013) previously showed that oceanic whitetips depart from CI in the summer, with peak displacement occurring during the late summer and fall; this movement is potentially attributed to reproduction and/or the favorable expansion of warm water to more northerly latitudes (Howey-Jordan et al. 2013). In the fall and winter, oceanic whitetips returned to The Bahamas, potentially coinciding with an influx of large prey, including dolphinfish which show large-scale movements similar to those of oceanic whitetips (Howey-Jordan et al. 2013, Merten et al. 2014). Our study extends observations in Howey-Jordan et al. (2013) by confirming that some individuals return to CI and can be found in almost exactly the same location over successive years (up to at least 3 consecutive years in 2 individuals; Table 1). Although we cannot confirm that other tagged sharks also returned to CI, our recapture rate is very high for an oceanic pelagic shark; recapture rates for 3 pelagic shark species (blue shark *Prionace glauca*, shortfin mako *Isurus oxyrinchus*, and porbeagle *Lamna nasus*) by the US National Marine Fisheries Service Cooperative Shark Tagging Program were 5.9, 11.4, and 11.0%, respectively, though these involved basin-wide, year-round commercial and recreational fishing recapture effort (Kohler et al. 2002). The recapture rate of oceanic whitetips is particularly high when considering the short and geographically limited effort (~10 d yr^{-1} at a single location) to recapture and/or resight them. Thus, 20% is a conservative estimate of the percentage of whitetips that return to CI. Oceanic whitetips are a true oceanic pelagic species in that they can potentially complete their entire life-

cycle in the open ocean (Bonfil et al. 2008). These tagging results extend our understanding of the movement ecology of this species and oceanic pelagic sharks in general by revealing that fine-scale site-fidelity to fixed island features can be a part of their migratory cycle, which has generally been thought to be driven more by shifting oceanographic features (Block et al. 2011, Queiroz et al. 2012). If seasonally predictable orientation to, and aggregation at, geo-spatially fixed features is a common trait of oceanic pelagic sharks, it suggests vulnerability to targeted exploitation while visiting these sites, which could be reduced by fisheries time–area closures during period(s) of residence.

Shark diet

Stable isotope analysis of muscle provides new information on present-day feeding habits (compared to diet data from ~50 years ago) of oceanic whitetips in the North Atlantic. Mixing model diet estimates from muscle suggest a nearly equal mix of squids (44%) and larger pelagic teleosts (47%) (Fig. 2b), with minimal inputs (8%) of small forage fish. Oceanic whitetip movement data recorded by archival satellite tags (Howey-Jordan et al. 2013) revealed that they primarily occupy the epipelagic zone but make consistent, though relatively infrequent, excursions into the mesopelagic zone. These excursions are typical of animals that dive to feed on deep-scattering layer organisms such as squids, as has been observed in blue sharks (Carey et al. 1990, Howey 2010), pantropical spotted dolphins *Stenella attenuata* (Baird et al. 2001), and short-finned pilot whales *Globicephala macrorhynchus* (Baird et al. 2002). Oceanic whitetips have been observed to associate with pilot whales, which are primarily squid feeders (Gannon et al. 1997a,b, Mintzer et al. 2008), and once corrected for marine mammal-specific DTDFs, $\delta^{13}C$ and $\delta^{15}N$ values of short-finned pilot whales sampled in The Bahamas (D. E. Claridge et al. pers. comm.) are extremely similar to DTDF-corrected oceanic whitetip muscle values. Although previous diet information for oceanic whitetips is minimal and largely qualitative, Backus et al. (1956) provided basic information from 41 captured individuals, reporting mostly squid and blackfin tuna, though some of these sharks were captured on tuna longlines and thus were potentially biased towards fisheries-caught tuna. Backus et al. (1956) also reported oceanic whitetips feeding on large commercially captured (long-lined) fish, including a 500 lb

(~230 kg) tuna that was almost completely consumed. In conjunction, deep-diving behavior, observed association and isotopic similarity with squid-feeding marine mammals, and early studies that report squid in oceanic whitetip diet suggest that these sharks may be primarily squid predators that opportunistically feed on large teleosts when made available. Based on results presented here, conditions at CI may greatly increase possibilities for such opportunistic feeding.

The results from isotopic analysis of blood plasma suggest increased input of pelagic teleost predators in oceanic whitetip diet when they are in The Bahamas and around CI. Approximately 72% of recent (70 to 200 d) diet was estimated to be comprised of tunas, dolphinfish, and wahoo (Fig. 2b), species that are commonly caught by recreational fishermen at CI and consumed by oceanic whitetips. It is unclear if, or why, CI presents more opportunities for sharks to feed on recreational sportfish than other islands in The Bahamas, but there are no known accounts of such high abundances of oceanic whitetips from surrounding islands. There is evidence that blue marlin, and potentially other pelagic teleosts, aggregate in Exuma Sound near CI to spawn (Serafy et al. 2003), so large pelagic fish density may be particularly high along the Great Bahama Bank. Coupled with observations of common depredation of sportfish by oceanic whitetips, this suggests that CI presents an opportunity for these sharks to feed on large, calorically rich prey. Although our analyses cannot definitively link oceanic whitetip residency to high feeding success, it is possible that the abundant food resources available at CI have contributed to a high degree of individual site-fidelity to CI.

Shark feeding aggregations

Seasonal site-fidelity of a highly migratory oceanic shark due to abundant food resources is plausible given similar documented behaviors in migratory, partially oceanic shark species. Tiger sharks *Galeocerdo cuvier* tagged in Shark Bay, Australia, exhibit a mix of migratory patterns, with some sharks remaining local while one shark potentially migrated at least 8000 km to southeast Africa (Heithaus et al. 2007). Despite their capacity for such long migrations, many of these sharks are seasonally residential to Shark Bay, when their main prey (sea snakes, dugongs *Dugong dugon*, and green sea turtles *Chelonia mydas*) densities are high (Heithaus 2001). Whale sharks

Rhincodon typus have been shown to seasonally aggregate to feed on dense zooplankton blooms, coral spawn, and fish spawn in regions of eastern Africa, Central America, Australia, Mexico, and the North Pacific Ocean (Clark & Nelson 1997, Taylor & Pearce 1999, Eckert & Stewart 2001, Heyman et al. 2001, Rowat et al. 2007). Salmon sharks *Lamna ditropis*, capable of migrating through subarctic, temperate, and subtropical waters (Weng et al. 2008), aggregate at salmon spawning sites in both the western and eastern North Pacific Ocean to feed on this abundant prey resource from spring to autumn (Nagasawa 1998, Weng et al. 2008). Finally, white sharks *Carcharodon carcharias* are known to migrate between coastal regions of both North America and New Zealand and oligotrophic, oceanic waters adjacent to these regions (Boustany et al. 2002, Weng et al. 2007, Domeier & Nasby-Lucas 2008, Duffy et al. 2012). White sharks are known to forage extensively on pinnipeds, an energy-rich food resource, at nearshore haulout sites in New Zealand in the South Pacific (Duffy et al. 2012) and at the Farallone Islands and Guadalupe Island in the eastern North Pacific (ENP; Weng et al. 2007, Domeier & Nasby-Lucas 2008, Jorgensen et al. 2009). Furthermore, stable isotope analyses showed that in the ENP, white shark feeding success was much higher at nearshore aggregation sites than at offshore habitats (Carlisle et al. 2012). The high philopatry and relative importance of white shark feeding success at seasonal pinniped haulouts demonstrates that, although such predators are capable of migrating long distances and feeding on diverse prey, seasonal aggregations occur in regions that are particularly important to energy budgets of migratory, partially oceanic sharks. This study suggests that the same may be true for certain oceanic pelagic shark populations.

We found that the differences between short- and long-term diet seemed to apply to all sharks (Fig. 3). Shark size or gender did not seem to influence feeding patterns. There was no difference between pregnant and non-pregnant sharks; this suggests that feeding on large pelagic predators is not substantially skewed towards sharks with higher caloric needs due to pregnancy. However, the relationship between shark size and blood plasma $\delta^{15}N$ values was nearly significant (p = 0.08), with a moderate Pearson's correlation coefficient (rho-value = 0.41; Fig. 3). Since sample size (n = 19) was relatively low, it is possible that sampling of more individuals would reveal a significant relationship. This would suggest that, while at CI, larger oceanic whitetips prey on larger pelagic teleosts, more pelagic teleosts, or both.

Potential effects of provisioning

While the net effect of oceanic whitetip feeding on large teleosts on shark fitness, behavior, and movements is difficult to quantify, it is possible to speculate on potential positive and negative effects. Deep dives (sometimes exceeding 1000 m) to obtain squid or other organisms associated with the deep scattering layer are by nature energetically costly. In contrast, consumption of whole large pelagic fish likely comes at lower energetic costs (when the prey is fatigued by sportfishing), as consumption of large prey increases the ratio of consumed tissue mass to prey item captured (Kerr 1971, Griffiths 1975, Gill 2003). Thus, feeding on large teleosts likely provides a net energetic benefit. In addition to natural foraging, oceanic whitetips are also offered pelagic teleost prey by local dive operators (intentional provisioning to attract sharks), and recreational sportboats report losing hooked tunas, billfish, wahoo, and dolphinfish to oceanic whitetips (unintentional provisioning). By default, occasional association with dive- and sportboats increases interactions between humans and oceanic whitetips. We do not know to what extent, if at all, dive operations and recreational fishing attract oceanic whitetips by making large teleosts available for capture and consumption. If these activities attract whitetips to CI, this intentional and unintentional provisioning of whitetips could impact their life history. In sharks, changes in feeding behavior, aggression, and movement patterns have been suggested and/or demonstrated as a result of provisioning (Fitzpatrick et al. 2011, Maljkoviè & Côté 2011, Bruce & Bradford 2013, Brunnschweiler & Barnett 2013). Modification of migratory patterns in response to provisioning has been demonstrated in other shark species (Bruce & Bradford 2013), as has a lack of response to provisioning (Hammerschlag et al. 2012). While increased feeding on large pelagic teleosts may be occurring in The Bahamas region in general (and not just CI), CI has a large, well-used marina and there are no reports of similarly high densities of oceanic whitetips at surrounding islands. However, this marina is largely inactive when oceanic whitetips first return to CI in late fall/early winter (Howey-Jordan et al. 2013). This suggests that provisioning does not drive the initial return of oceanic whitetips to CI, but the possibility that provisioning at CI has contributed to site-fidelity cannot be ruled out. The site-fidelity of oceanic whitetips demonstrated here potentially mitigates catch of oceanic whitetips (by-catch and/or targeted) while inhabiting The Bahamas as long-lining operations are prohibited within their exclusive economic zone (EEZ).

SIA: caveats and considerations

Several aspects of our analytical approach should be considered when interpreting the SIA results presented here. Comparisons of diet from muscle and blood plasma, and the diet reconstructions generated using Bayesian mixing models, are sensitive to the predator- and tissue-specific DTDFs used for both $\delta^{13}C$ and $\delta^{15}N$ (Caut et al. 2009, Hussey et al. 2010b, Olin et al. 2013). Ideally, multiple DTDFs are used to generate multiple mixing model estimates that can be quantitatively and qualitatively compared. In this case, only one study exists that calculated elasmobranch DTDFs for $\delta^{13}C$ and $\delta^{15}N$ in both muscle and blood plasma from the same individuals (Kim et al. 2012a), so analyses were limited to the DTDFs from that study. It is thus possible that DTDFs more specific to oceanic pelagic sharks would produce different mixing model results. However, the main purpose of this study was to compare results of muscle (long-term diet) and blood plasma (short-term diet); therefore, it is the relationship between these DTDFs (i.e. $\Delta^{15}N_{muscle} > \Delta^{15}N_{plasma}$) that influences comparative results from these 2 tissues. Studies that report tissue-specific DTDFs have shown that relative differences between 2 tissues generally have a consistent relationship; for example, in fish, $\Delta^{15}N_{muscle}$ is consistently higher than $\Delta^{15}N_{liver}$ (Caut et al. 2009). Assuming that the relationship found in Kim et al. (2012a) between the DTDFs of muscle and blood plasma ($\Delta^{15}N_{muscle} > \Delta^{15}N_{plasma}$) generally holds true for sharks, the feeding pattern we found (more large, pelagic teleosts in the short-term diet) would also hold true. Different DTDF values would result in different mixing model estimates, but as long as $\Delta^{15}N_{muscle} > \Delta^{15}N_{plasma}$ then our results would demonstrate higher inputs of large teleosts in short-term diet regardless of the absolute values of $\Delta^{15}N_{muscle}$ and $\Delta^{15}N_{plasma}$. Of course, as in many studies that interpret isotopic data from wild animals, the lack of multiple DTDFs for plasma in shark species comparable to oceanic whitetips (e.g. large carcharhinids) points to the value and importance of further controlled studies on large captive predators to more accurately quantify these important parameters.

We attempted to sample as many pelagic species as possible, and the available pelagic prey base was not particularly diverse. Sampling of large pelagic teleosts was limited to 5 species and 39 individuals, and pelagic forage prey to 2 prey types and 16 individuals (Table 2, Fig. 2a). However, mean muscle and plasma $\delta^{13}C$ and $\delta^{15}N$ values for sharks, once corrected for tissue-specific DTDFs (Kim et al. 2012a), fell within these prey values in $\delta^{13}C$ versus $\delta^{15}N$ 'isospace' (Fig. 2a), suggesting that these prey could explain $\delta^{13}C$ and $\delta^{15}N$ values for both tissues. Mean $\delta^{13}C$ and $\delta^{15}N$ values of large teleosts were reasonably similar (Fig. 2a), and we assume that other unsampled, potentially consumed sportfish (e.g. marlins) are represented by this group isotopically due to trophic similarities. Similarly, the prey base (squids and flying fish) represent small zooplanktivorous (flying fish) and zooplanktivorous/piscivorous (squids) prey available to predators at CI. We assume that other biologically and trophically similar species (e.g. other squids and other similarly sized pelagic forage fish) would have similar isotopic values and are thus adequately represented by this prey base.

Recent migration patterns (i.e. recent feeding on different regional prey bases) can influence isotopic values, as has been demonstrated in other highly migratory fish (Carlisle et al. 2012, Madigan et al. 2014). In the above studies, white sharks migrated between highly productive coastal and oligotrophic offshore habitats (Carlisle et al. 2012), and Pacific bluefin tuna *Thunnus orientalis* migrated from a largely oligotrophic pelagic environment (waters near Japan) to a pelagic region highly impacted by seasonal upwelling (waters of the California Current) (Madigan et al. 2012, 2014). In contrast, oceanic whitetips have been shown to largely remain in offshelf, pelagic waters, and their migrations are largely confined to oceanographically similar waters (oligotrophic sub-tropical systems) (Howey-Jordan et al. 2013). If oceanic whitetip migratory routes led to substantial feeding on isotopically different prey, this would likely be evident in the SIA data, as DTDF-corrected oceanic whitetip data would not fit within prey resources in isospace. However, the prey isotopic values seemed to encapsulate well the DTDF-corrected $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 2a). It is possible, however, that observed intra-specific differences in muscle and/or blood plasma reflect the timing of migration into the CI region, where lower $\delta^{13}C$ and $\delta^{15}N$ values reflect more recent entry into The Bahamas EEZ and thus fewer large pelagic fish reflected in recent diet. Future studies of oceanic whitetips in the CI region will combine tissue analyses and electronic tagging data for sharks tagged in consecutive years, allowing retrospective movement and isotopic analyses.

It is important to note that, while muscle and blood plasma represent diet over different time periods, the timeframes of dietary estimates using each of these tissues are not mutually exclusive. As a tissue that integrates diet over an estimated 400 to 600 d, muscle

includes diet both within and outside the CI region. Similarly, blood plasma values may also reflect diet outside of the CI region, particularly if a sampled shark has moved into the CI region fairly recently. Consequently, differences in feeding behavior in the CI region and elsewhere will potentially be diluted by the fact that the 2 tissues analyzed may partially reflect feeding behaviors both within and outside the CI region. Due to this dilution effect, it is possible that differences in feeding within the CI region (high inputs of large pelagic teleosts) and outside the CI region (higher inputs of small pelagic forage prey) (Fig. 2b) are even more pronounced than results suggest.

Conclusions

In conjunction, tag-recapture and stable isotope results confirm the electronic tag data-based assertion that CI is an important aggregation site for oceanic whitetips, and suggest high food availability as an important factor that drives aggregation. Like pinniped haulouts for white sharks and salmon spawning aggregations for salmon sharks, high abundance of pelagic teleosts likely attracts oceanic whitetips to this region in a seasonally and geographically predictable manner. Results here provide insight into the function of one of the last known aggregation sites for a heavily exploited top predator that was once extremely abundant. The study region represents a unique location to study the movements (via tagging studies) and diet (via SIA) of oceanic whitetip sharks. Subsequent coupling of electronic tagging and stable isotope data will lend further insight into the drivers of movement patterns in this highly migratory shark species.

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