Species co-occurrence affects the trophic interactions of two juvenile reef shark species in tropical lagoon nurseries in Moorea (French Polynesia)

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ABSTRACT

Food web structure is shaped by interactions within and across trophic levels. As such, understanding how the presence and absence of predators, prey, and competitors affect species foraging patterns is important for predicting the consequences of changes in species abundances, distributions, and behaviors. Here, we used plasma δ^{13}C and δ^{15}N values from juvenile blacktip reef sharks (*Carcharhinus melanopterus*) and juvenile sicklefin lemon sharks (*Negaprion acutidens*) to investigate how species co-occurrence affects their trophic interactions in littoral waters of Moorea, French Polynesia. Co-occurrence led to isotopic niche partitioning among sharks within nurseries, with significant increases in δ^{15}N values among sicklefin lemon sharks, and significant decreases in δ^{15}N among blacktip reef sharks. Niche segregation likely promotes coexistence of these two predators during early years of growth and development, but data do not suggest coexistence affects life history traits, such as body size, body condition, and ontogenetic niche shifts. Plasticity in trophic niches among juvenile blacktip reef sharks and sicklefin lemon sharks also suggests these predators are able to account for changes in community structure, resource availability, and intra-guild competition, and may fill similar functional roles in the absence of the other species, which is important as environmental change and human impacts persist in coral reef ecosystems.

1. Introduction

Understanding the factors that shape animal behavior and foraging decisions is important for predicting how environmental changes may affect ecological communities in the event of disturbance (Duffy, 2002; Heithaus et al., 2008). Within food webs, the presence or absence of species that serve as predators, prey, and/or competitors play a crucial role in shaping the trophic interactions, and thus the niches that species fill (Paine, 1966; Polis and Strong, 1996). These interspecific interactions can be especially important among juvenile animals that must face food-risk trade-offs during early periods of growth and development (Heithaus, 2007). For example, juvenile Atlantic salmon (*Salmo salar*) exhibit reduced foraging areas and foraging activities in response to proximate predators (Metcalf et al., 1987), whereas juvenile stone loach (*Barbatula barbatula*) decrease consumption rates when predators are present (Nilsson et al., 2010). In Laurentian Shield lakes, Canada, the presence of yellow perch (*Perca flavescens*) causes juvenile brook trout (*Salvelinus fontinalis*) to switch from littoral to pelagic prey (Browne and Rasmussen, 2009), and competition leads to a decrease in prey size selected by upland bullies (*Gobiomorphus breviceps*) in controlled settings (James and Poulin, 1998).

Competitive interactions can lead to reductions in occupied niche space, as well as increase dietary plasticity within trophic guilds (Chase and Leibold, 2003; Holt, 2009; Pfennig and Pfennig, 2009). Indeed, the presence of competitors can lead to niche

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segregation and expansion among herbivores (e.g. Stewart et al., 2003; Kartzinel et al., 2015) and predators (e.g. Fedriani et al., 2000; Elboch et al., 2015; Matich et al., 2017), potentially changing the roles species play within their respective food webs. Investigating the importance of competitive interactions, however, can be challenging for large-bodied species, and using ecosystems and conditions that serve as natural experiments provides the opportunity to test and refine hypotheses that stem from studies of smaller-bodied species, and develop predictive frameworks concerning species co-occurrences and declines (Schoener, 1983; Sih et al., 1985).

Globally, coastal marine ecosystems serve as nurseries for sharks in temperate, subtropical, and tropical latitudes, and nursery habitats can support more than one juvenile shark species (reviewed by Heithaus, 2007; Heupel et al., 2007). These nurseries are generally small and discrete, and their accessibility has provided opportunities to better understand the behavior, movements and trophic interactions of a diversity of shark species (McCandless et al., 2007; Heupel et al., 2007; Grubbs, 2010). Since nurseries can either be mono- or multi-specific (i.e. they support either one or several species, respectively), they provide an opportunity to investigate the potential influence of species co-occurrence on the trophic interactions of sharks. However, a lack of replicate ecosystems where environmental conditions and food webs are similar limits our ability to investigate the impacts juvenile sharks have on one another (but see e.g. Hueter and Tyminski, 2007; Yates et al., 2015). Worldwide declines in elasmobranchs necessitates understanding how the loss of sharks may affect communities and, ultimately, the function of marine ecosystems (Ferretti et al., 2010; Dulvy et al., 2014). Thus, understanding how the presence or absence of one species affects the behavior and ecology of other sharks is of great interest from ecological and conservation perspectives. Here, we used stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values from juvenile blacktip reef sharks (*Carcharhinus melanopterus*) and juvenile sicklefin lemon sharks (*Negaprion acutidens*) to investigate how species co-occurrence affects trophic interactions of these sharks within the shallow lagoons of Moorea, French Polynesia. We test the hypothesis that niche segregation occurs in response to potential competition for food resources between co-occurring shark species within their nursery habitats (Chase and Leibold, 2003; Holt, 2009; Pfennig and Pfennig, 2009).

2. Methods

2.1. Field and laboratory sampling

Moorea, French Polynesia (S 17°30′, W 149°51′) is located west of Tahiti in the Society Islands, and is surrounded by an array of lagoons bordered by fringing reef (Fig. 1). These shallow lagoons provide protection from large predatory sharks, and serve as nurseries for juvenile blacktip reef sharks and sicklefin lemon sharks, hereafter lemon sharks (Mourier and Planes, 2013; Mourier et al., 2013a). Sampling was conducted from January 2012 to January 2013 across nine nurseries previously identified (Mourier and Planes, 2013; Mourier et al., 2013a), six of which only supported blacktip reef sharks, one of which only supported lemon sharks, and two of which supported juvenile sharks of both species (J. Mourier unpublished data; Fig. 1).

Sharks were caught using small gillnets placed perpendicularly to the shoreline at dusk and during early evening hours (from 17:00 to 21:00), in waters 50—100 cm deep. Upon capture, sharks were externally tagged using numbered spaghetti identification tags implanted next to the dorsal fin. Shark total length was measured to the nearest 0.5 cm, and body mass was measured to the nearest 0.1 kg. An 18-gauge needle was used to collect 3 mL of blood from the caudal vein during each capture. Blood samples were placed into BD Vacutainer blood collection vials without anticoagulants, and immediately separated into components, including plasma, using a centrifuge spun for one minute at 3000 rpm. Plasma samples were put on ice and frozen before laboratory preparations.

All samples were dried and homogenized for stable isotopic analysis at Florida International University's Stable Isotope Laboratory, during which variation among standards was 0.07‰ and 0.08‰ ± SD for δ^{13}C and δ^{15}N, respectively. Mean C:N of plasma
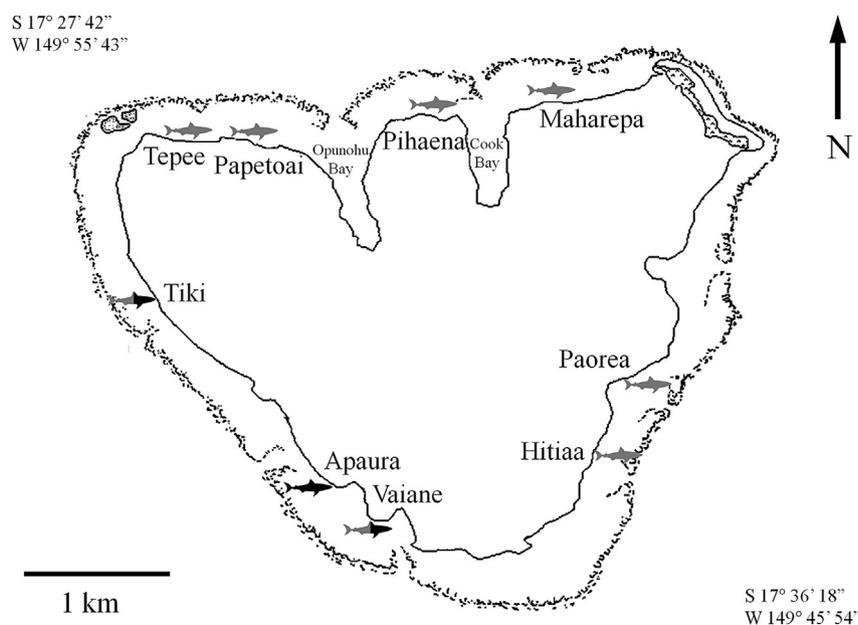
Fig. 1. The island of Moorea, French Polynesia is surrounded by fringing reef. Shark silhouettes denote sampling locations. Gray silhouettes identify monospecific blacktip reef shark nurseries, black silhouettes identify monospecific lemon shark nurseries, and black and gray silhouettes identify multispecific nurseries.

were 1.95 ± 0.22 for blacktip reef sharks, and 1.84 ± 0.15 for lemon sharks, therefore lipids were not extracted (Post et al., 2007).

2.2. Quantitative analysis

Plasma stable isotope values were plotted on $\delta^{13}C$-$\delta^{15}N$ biplots, and MANOVA was used to test for differences across species. Plasma exhibits a much faster turnover rate (isotopic half-life: $\delta^{13}C$ = ~22 days; $\delta^{15}N$ = ~33 days; Kim et al., 2012) than other tissues that can be sampled from sharks non-lethally (MacNeil et al., 2006; Kim et al., 2012; Vander Zanden et al., 2015), and therefore provided the most recent indications of trophic interactions among sharks. MANOVA was also employed to quantify significant differences in $\delta^{13}C$ and $\delta^{15}N$ values for each species across lagoons, and the effects of species co-occurrence on $\delta^{13}C$ and $\delta^{15}N$ values, with subsequent ANOVAs and post hoc Tukey's tests. $\delta^{13}C$ and $\delta^{15}N$ values were individually plotted against shark total length (TL), and potential ontogenetic shifts in trophic interactions across the size ranges found in nurseries were quantified using linear regression. Two-tailed t-tests at α = 0.05 assessed differences in slopes across species, and between monospecific and multi-specific nurseries - sample sizes were not large enough to test for differences across all lagoons.

To ensure shark size did not bias results, ANOVAs were used to test for significant differences in shark size and body condition across lagoons. Body conditions were calculated using residuals from regression of body length vs. body mass. All analyses were performed in IBM SPSS 22.

3. Results

From January 2012—May 2012, and November 2012—January 2013, 99 juvenile blacktip reef sharks and 56 juvenile lemon sharks were sampled, ranging from 55 to 86 cm total length (TL) and 58—87 cm TL, respectively (Table 1). No significant differences were found in shark sizes or body conditions between monospecific and multi-specific nurseries for blacktip reef sharks ($F_{1,92}$ = 0.05, p = 0.82, $F_{1,67}$ = 0.61, p = 0.44, respectively) or lemon sharks ($F_{1,54}$ = 1.19, p = 0.28, $F_{1,14}$ = 0.03, p = 0.86).
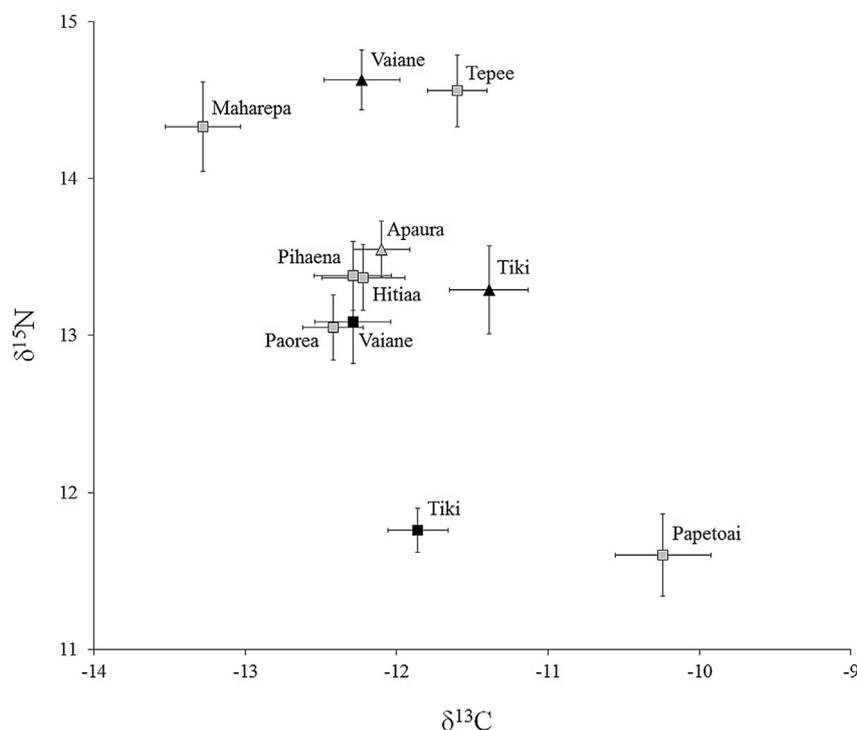
Blacktip reef sharks and lemon sharks exhibited wider ranges of $\delta^{15}N$ values (9.91‰—17.28‰, and 12.13‰—17.24‰, respectively) than $\delta^{13}C$ values (−14.37‰ to −8.20‰, and −13.88‰ to −10.65‰, respectively; Fig. 2A, Table 1). Lemon sharks had significantly higher $\delta^{15}N$ values than blacktip reef sharks ($F_{1,153}$ = 16.78, p < 0.01). Blacktip reef sharks exhibited significant differences in $\delta^{13}C$ and $\delta^{15}N$ across study sites ($F_{7,91}$ = 8.76, p < 0.01, $F_{7,91}$ = 17.30,

Table 1
Summary of data for blacktip reef sharks and sicklefin lemon sharks sampled in monospecific (only one shark species present) and multi-specific nurseries (species co-occur), including sample sizes, capture dates, range of total lengths (in cm), mean $\delta^{13}C$ and $\delta^{15}N$ ± SD (in ‰), and slope of best fit line for regression of $\delta^{13}C$ and $\delta^{15}N$ with shark total length (in ‰/cm TL).

Species	Nursery type	n	Capture dates	TL range	$\delta^{13}C$	$\delta^{15}N$	Slope TL v $\delta^{13}C$	Slope TL v $\delta^{15}N$
C. melanopterus	monospecific	84	Jan 2012—May 2012	55.0—85.5	−11.79 ± 1.30	13.69 ± 1.50	0.104	−0.111
C. melanopterus	multispecific	20	Jan 2012—May 2012	58.0—70.0	−11.97 ± 0.75	12.09 ± 0.80	0.147	−0.111
N. acutidens	monospecific	11	Jan 2012—May 2012	62.0—87.0	−12.10 ± 0.62	13.55 ± 0.59	0.026	−0.022
N. acutidens	multispecific	45	Jan 2012—Jan 2013	58.0—87.0	−12.15 ± 0.82	14.51 ± 1.21	0.006	−0.085
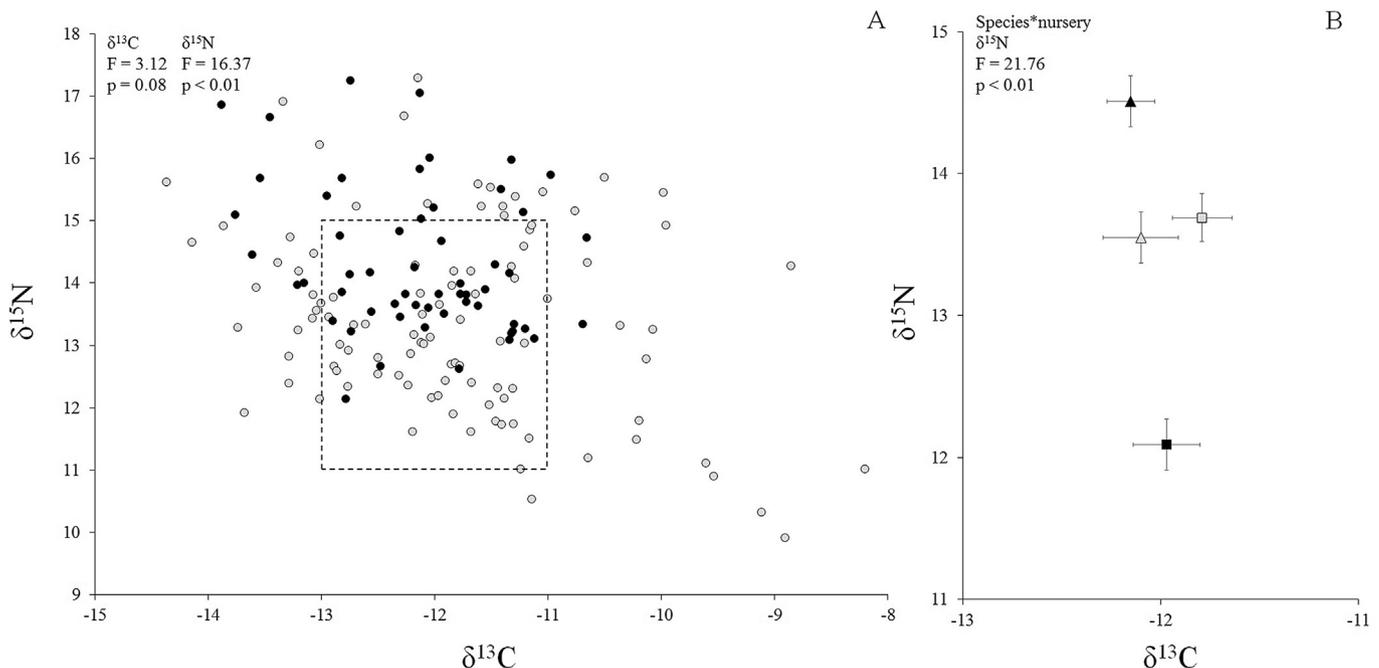
Fig. 2. Isotopic biplot (in ‰) for A) all blacktip reef sharks (gray circles) and all lemon sharks (black circles), which exhibited significant differences in $\delta^{15}N$ values. The dashed box represents the area of panel B) Mean $\delta^{13}C$ and $\delta^{15}N$ values (with SEs) for blacktip reef sharks (squares) and lemon sharks (triangles) in monospecific nurseries (gray symbols), and multi-specific nurseries (black symbols).

Fig. 3. Mean $\delta^{13}C$ and $\delta^{15}N$ values (in ‰, with SE) for blacktip reef sharks (squares) and lemon sharks (triangles) for each nursery - monospecific nurseries are gray squares and triangles, and multi-specific nurseries are black squares and triangles.

p < 0.01, respectively), and lemon sharks exhibited significant differences in $\delta^{15}N$ across study sites ($F_{2,53} = 6.40$, p < 0.01; Fig. 3, Appendices A, B & C). Differences in $\delta^{15}N$ were driven by patterns in species co-occurrence - blacktip reef sharks exhibited significantly lower $\delta^{15}N$ values in multi-specific nurseries than monospecific nurseries ($F_{1,97} = 22.69$, p < 0.01), and lemon sharks exhibited significantly higher $\delta^{15}N$ values in multi-specific nurseries than monospecific nurseries ($F_{1,54} = 6.50$, p = 0.01; Fig. 2B). There were no significant differences in $\delta^{13}C$ values among blacktip reef sharks or lemon sharks based on nursery type ($F_{1,97} = 0.33$, p = 0.57, $F_{1,54} = 0.04$, p = 0.85, respectively; Fig. 2B). Differences in blacktip reef shark $\delta^{13}C$ values were attributed to the depletion of ^{13}C among sharks caught in Maharepa, and the enrichment of ^{13}C among sharks caught in Papetoai (Fig. 3, Appendices A, B & C).

An ontogenetic shift in $\delta^{13}C$ occurred among blacktip reef sharks within nurseries. Both blacktip reef sharks and lemon sharks in nurseries became more depleted in ^{15}N with total length (Fig. 4). There were no significant differences in ontogenetic niche shifts between multi-specific and monospecific nurseries for blacktip reef sharks ($t_{97} = 0.75$, p = 0.46, $t_{97} = 0.04$, p = 0.97, for $\delta^{13}C$ and $\delta^{15}N$, respectively), nor lemon sharks ($t_{54} = 0.94$, p = 0.35 for $\delta^{15}N$). Blacktip reef sharks did exhibit significantly faster depletions in ^{15}N than lemon sharks in monospecific nurseries ($t_{87} = 2.18$, p = 0.02; Table 1).

4. Discussion

Understanding species interactions and how they are shaped by co-occurrence patterns is critical for elucidating the impacts that changes in species abundances and distributions will have on marine communities (Duffy, 2002; Bascompte et al., 2005; Estes et al., 2011). Our results suggest that juvenile blacktip reef sharks and lemon sharks of similar sizes exhibit similar trophic interactions within shallow lagoon food webs of Moorea when the other species is absent. In contrast, co-occurrence and potential competition leads to lemon sharks feeding at higher trophic levels, and blacktip reef sharks feeding at lower trophic levels (based on differences in $\delta^{15}N$ values; Hussey et al., 2012), segregating trophic niche space, and suggesting these species exhibit flexibility in their trophic interactions.

Within food webs, particularly in resource-limited contexts, sympatric species are expected to exhibit distinct resource use patterns in order to coexist (Pianka, 1974; Schluter and McPhail, 1992), thus niche segregation among blacktip reef sharks and lemon sharks was not unexpected. Trophic niche segregation can be facilitated by species foraging on different prey species, at different time periods, and/or in different habitats (e.g. Pianka, 1974). Within Moorea, co-occurrence of blacktip reef sharks and lemon sharks occurred in two of the nine nurseries surveyed. However, 67% of lagoons where juvenile lemon sharks were found (n = 3) supported juvenile blacktip reef sharks, suggesting that spatial segregation is not the only means through which competition is reduced between these two shark species. Indeed, not only did blacktip reef sharks and lemon sharks caught concurrently exhibit significantly different $\delta^{15}N$ values from one another, but lemon sharks caught in monospecific nurseries exhibited significantly more depleted $\delta^{15}N$ values than those caught in multi-specific nurseries, and blacktip reef sharks caught in monospecific nurseries exhibited significantly more enriched $\delta^{15}N$ values than those caught in multi-specific nurseries, with no significant difference among lemon sharks and blacktip reef sharks in monospecific nurseries. These findings suggest that sharks may fill similar ecological roles within food webs when species occur individually, and undergo shifts in $\delta^{15}N$ when they overlap spatially, partitioning food resources at different trophic levels, assuming that $\delta^{15}N$ is an accurate indicator of trophic level (Post, 2002; Layman et al., 2012). Lemon sharks are born at larger body sizes (55–66 cm TL; Mourier et al., 2013a) than blacktip reef sharks
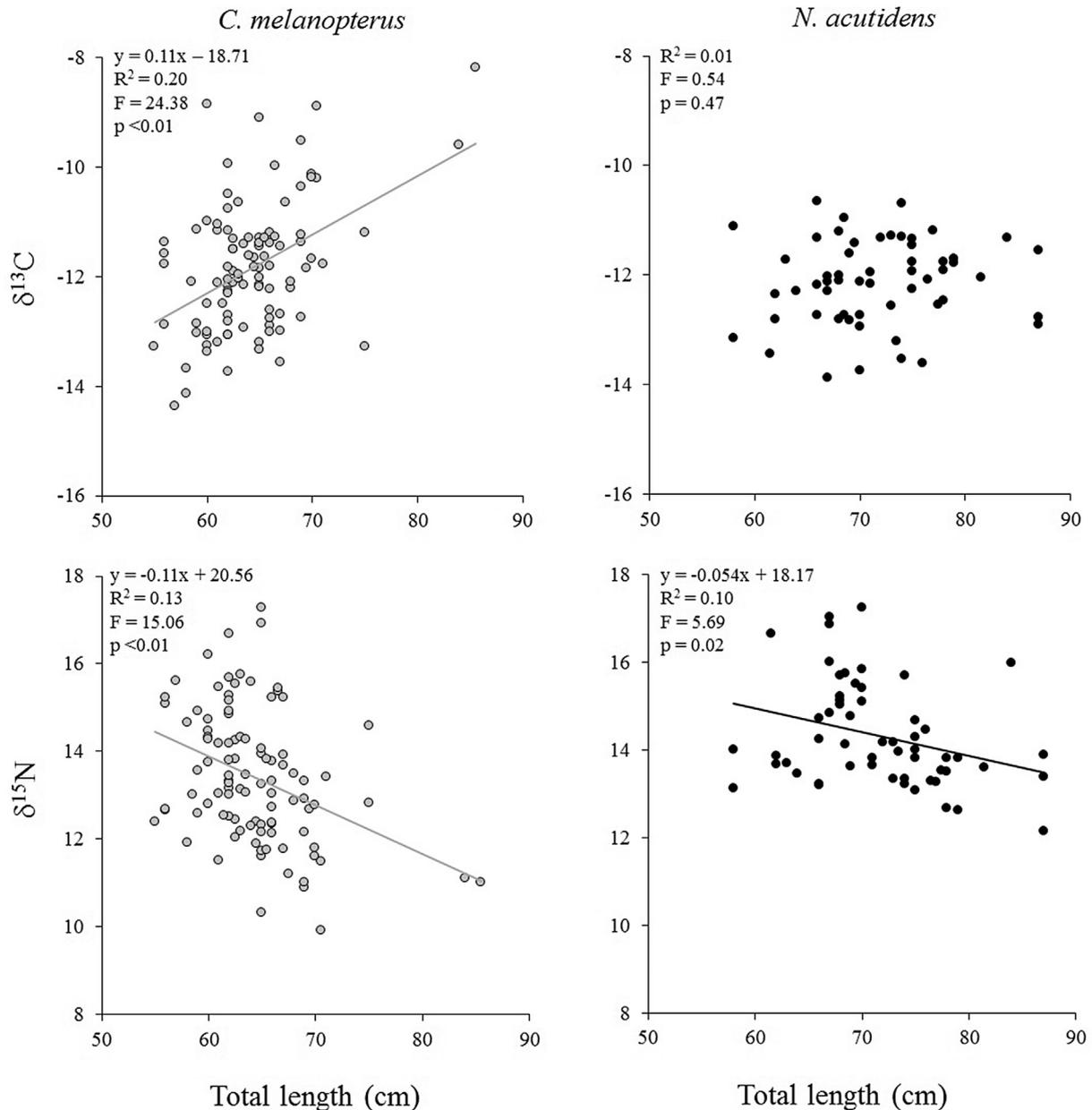
Fig. 4. Blacktip reef sharks exhibited a significant enrichment in ^{13}C with shark total length and a significant depletion in ^{15}N with shark total length. Lemon sharks exhibited a significant depletion in ^{15}N with shark total length. Stable isotope values are in ‰.

(33−52 cm TL; Mourier et al., 2013b), which may facilitate lemon sharks in consuming larger prey items at higher trophic levels, and thus with higher δ^{15}N values than blacktip reef sharks when they co-occur (Hussey et al., 2012). Strong patterns of reproductive philopatry in both species (Mourier and Planes, 2013; Mourier et al., 2013a), and site fidelity among young juvenile sharks in Moorea nurseries (Mourier and Planes, 2013; Mourier et al., 2013a; Matich et al., 2015), also suggest that niche segregation within nurseries is consistent across years, and presents the hypothesis that these patterns may persist outside of nursery habitats as sharks grow due to continued spatial overlap on reef habitats.

Studies investigating trophic overlap among elasmobranchs in other ecosystems have shown similar segregation among species (e.g. Carrassón and Cartes, 2002; Domi et al., 2005; Barría et al., 2015; Shaw et al., 2016), while others have shown high levels of

trophic overlap among sharks (e.g. Preciado et al., 2009; Pethybridge et al., 2011; Heithaus et al., 2013; Kiszka et al., 2014, 2015; Churchill et al., 2015), suggesting trophic niche segregation is not ubiquitous. Yet, the number of studies investigating elasmobranch community trophic interactions currently limits our ability to discern broad-scale patterns in niche overlap (e.g. based on region or ecosystem-type), and its implications on shark populations. Our results suggest that co-occurrence has nominal effects on early stages of life history among sharks in Moorea. Both blacktip reef sharks and lemon sharks undergo ontogenetic shifts in δ^{15}N, but neither species exhibited significant differences in ontogenetic shifts based on the presence or absence of the other species. Blacktip reef sharks and lemon sharks also did not exhibit significant differences in shark size or in body condition between mono- and multi-specific nurseries, suggesting that co-occurrence may

have limited consequences concerning growth and development during early years, but growth rate studies are needed to test this hypothesis.

The ecological consequences resultant of niche partitioning among sharks within lagoon food webs, however, suggest co-occurrence may play a large part in shaping the ecological roles blacktip reef sharks and lemon sharks play in Moorea. Sharks serve as predators within their respective ecosystems (Heithaus et al., 2010). However, variability in food web structure, including the presence of competitors, can lead to variability in species' trophic interactions (Paine, 1966; Polis and Strong, 1996). Sympatric sharks species (*Carcharhinus amblyrhynchos*, *C. galapagensis*, *C. plumbeus*, *Galeocerdo cuvier*) in Hawaii vary in their trophic overlap with one another based on difference in potential competition and intraguild predation, illustrating the importance of studying trophic interactions across various contexts (Papastamatiou et al., 2006). Characids in the Amazon exhibit similar trophic shifts, and promote coexistence among species with similar trophic niches through niche width reductions (Barros et al., 2016). When functionally similar species coexist, competition can lead to niche partitioning when resources are limited, masking functional redundancy and the potential for species to fill vacant niche space, which can be consequential for making predictions concerning food web stability (Walker, 1992; Rastetter et al., 1999). Indeed, quantifying trophic interactions within multi-specific nurseries in Moorea alone would suggest juvenile blacktip reef sharks and juvenile lemon sharks exhibit different trophic ecologies and ecological roles within Moorea, and therefore limited functional redundancy. In the event of a disturbance and species decline(s), a lack of functional redundancy could have important implications within lagoon food web(s) through the loss of essential ecological role(s) of the declining species (e.g. Downing et al., 2012; Mouillot et al., 2013). However, when monospecific nurseries are considered with multi-specific nurseries, blacktip reef sharks and lemon sharks appear plastic in their trophic interactions, converging to similar isotopic niches in the absence of the other species. As such, assuming sympatric species have consistently different ecological roles could lead to under-estimations of functional redundancy, and thus resilience within food webs (e.g. Kitchell et al., 2002; Hayward and Kerley, 2008). While greater investigation across different contexts is needed, future studies investigating how species co-occurrence affects trophic niche space and position (Layman et al., 2007; Jackson et al., 2011) will improve our understanding of the effects of competition on food web structure and predator-prey interactions, as well as the conditions under which niche partitioning promotes and obstructs the coexistence of functionally redundant species.

In light of our findings, it is important to consider that spatial variability in $\delta^{15}N$ values may have been attributed to differences in food availability, food web structure, or other extrinsic factors, which are currently under investigation at the community level. Stable isotopes also do not provide the taxanomic resolution of stomach contents, and multiple trophic pathways can lead to individuals or species having similar stable isotope values despite different diets (Martinez del Rio et al., 2009). Because of the invasive nature of gastric lavage, we did not collect stomach contents, and cannot decisively conclude that sharks with similar stable isotope values fed on similar prey items. However, differences in $\delta^{15}N$ are informative of niche partitioning (Martinez del Rio et al., 2009), and thus are informative of trophic differences among blacktip reef sharks and lemon sharks in multi-specific nurseries, and shifts in trophic interactions across nurseries. Species-specific and temporally variable isotopic discrimination values may also lead to differences within and among shark $\delta^{15}N$ values (reviewed by McCutchan et al., 2003; Vanderklift and Ponsard, 2003). However, samples were collected from similar temporal periods, thus temporal differences are unlikely, and elasmobranchs appear to exhibit similarities in isotopic discrimination despite large morphological differences (MacNeil et al., 2006; Logan and Lutcavage, 2010; Kim et al., 2012; Malpica-Cruz et al., 2012; Caut et al., 2013). Maternal meddling may have also influenced $\delta^{13}C$ and $\delta^{15}N$ values by inflating values due to embryonic isotope discrimination, (McMeans et al., 2009; Matich et al., 2010; Vaudo et al., 2010; Olin et al., 2011), however we would expect similar effects across each nursery based on their proximity in Moorea.

Despite these caveats, data show that lemon sharks and blacktip reef sharks exhibit similarities in trophic interactions when the other species is absent in Moorea nurseries. Yet, when both species overlap in habitat use, trophic niche space is segregated, and each species experiences an apparent shift in trophic level based on $\delta^{15}N$ values. Our results are encouraging that each species has the potential to be flexible in their foraging patterns to account for changes in community composition, and potential functional redundancy among these juvenile sharks provides insight into the resilience of Moorea food webs (Peterson et al., 1998; Chase and Leibold, 2003). Future investigations of interspecific interactions among these sharks across wider spatial and temporal scales, and across different life history stages will provide insight into the role these predators play within lagoon and reef food webs, as well as the impact population declines and expansions may have in coral reef ecosystems.

Acknowledgments

Appendix A. Results from ANOVAs for differences in $\delta^{13}C$ and $\delta^{15}N$ across lagoons. Significant p-values (in bold) are p < 0.05

C. melanopterus

	SS	df	MSS	F-value	p-value
$\delta^{13}C$	61.79	7	8.83	9.95	**<0.01**
$\delta^{15}N$	137.50	7	19.64	19.70	**<0.01**

N. acutidens

	SS	df	MSS	F-value	p-value
$\delta^{13}C$	2.59	2	1.29	2.23	0.12
$\delta^{15}N$	14.66	2	7.33	6.38	**<0.01**

Appendix B. Tukey's post hoc results for differences in C. melanopterus δ^{13}C and δ^{15}N values across lagoons. Significant p-values (in bold) are $p < 0.05$

	Lagoon	δ^{13}C		δ^{15}N	
		Mean difference	p-value	Mean difference	p-value
Hitiaa	Maharepa	1.06	0.37	−0.96	0.59
	Paorea	0.21	>0.99	0.32	>0.99
	Papetoai	−1.98	**<0.01**	1.77	**0.01**
	Pihaena	0.07	>0.99	−0.01	>0.99
	Tepee	−0.61	0.82	−1.18	0.14
	Tiki	−0.36	>0.99	1.61	**0.03**
	Vaiane	0.08	>0.99	0.28	>0.99
Maharepa	Hitiaa	−1.06	0.37	0.96	0.59
	Paorea	−0.86	0.65	1.27	0.22
	Papetoai	−3.04	**<0.01**	2.72	**<0.01**
	Pihaena	−0.99	0.28	0.94	0.41
	Tepee	−1.67	**<0.01**	−0.23	>0.99
	Tiki	−1.42	**<0.01**	2.57	**<0.01**
	Vaiane	−0.99	0.55	1.24	0.33
Paorea	Hitiaa	−0.21	>0.99	−0.32	>0.99
	Maharepa	0.86	0.65	−1.27	0.22
	Papetoai	−2.18	**<0.01**	1.45	0.08
	Pihaena	−0.14	>0.99	−0.33	>0.99
	Tepee	−0.82	0.52	−1.50	**0.02**
	Tiki	−0.56	0.92	1.30	0.14
	Vaiane	−0.13	>0.99	−0.04	>0.99
Papetoai	Hitiaa	1.98	**<0.01**	−1.77	**0.01**
	Maharepa	3.04	**<0.01**	−2.72	**<0.01**
	Paorea	2.18	**<0.01**	−1.45	0.08
	Pihaena	2.05	**<0.01**	−1.79	**<0.01**
	Tepee	1.37	**<0.01**	−2.95	**<0.01**
	Tiki	1.62	**<0.01**	−0.15	>0.99
	Vaiane	2.06	**<0.01**	−1.49	0.10
Pihaena	Hitiaa	−0.07	>0.99	0.01	>0.99
	Maharepa	0.99	0.28	−0.94	0.41
	Paorea	0.14	>0.99	0.33	>0.99
	Papetoai	−2.05	**<0.01**	1.78	**<0.01**
	Tepee	−0.68	0.49	−1.17	**0.03**
	Tiki	−0.42	0.95	1.63	**<0.01**
	Vaiane	0.01	>0.99	0.29	>0.99
Tepee	Hitiaa	0.61	0.82	1.18	0.14
	Maharepa	1.67	**<0.01**	0.23	>0.99
	Paorea	0.82	0.52	1.50	**0.02**
	Papetoai	−1.37	**<0.01**	2.95	**<0.01**
	Pihaena	0.68	0.49	1.17	**0.03**
	Tiki	0.26	0.99	2.80	**<0.01**
	Vaiane	0.69	0.79	1.46	0.06
Tiki	Hitiaa	0.36	0.99	−1.61	**0.03**
	Maharepa	1.42	**<0.01**	−2.57	**<0.01**
	Paorea	0.56	0.92	−1.30	0.14
	Papetoai	−1.62	**<0.01**	0.15	>0.99
	Pihaena	0.42	0.95	−1.63	**<0.01**
	Tepee	−0.26	0.99	−2.80	**<0.01**
	Vaiane	0.43	0.99	−1.33	0.17
Vaiane	Hitiaa	−0.08	>0.99	−0.28	>0.99
	Maharepa	0.99	0.55	−1.24	0.33
	Paorea	0.13	>0.99	0.04	>0.99
	Papetoai	−2.06	**<0.01**	1.49	0.10
	Pihaena	−0.01	>0.99	−0.29	>0.99
	Tepee	−0.69	0.79	−1.46	0.06
	Tiki	−0.43	0.99	1.33	0.17

Appendix C. Tukey's post hoc results for differences in N. acutidens δ^{15}N values across lagoons. Significant p-values (in bold) are $p < 0.05$

	Lagoon	δ^{15}N	
		Mean difference	p-value
Apaura	Tiki	0.26	0.91
	Vaiane	−1.08	**0.01**
Tiki	Apaura	−0.26	0.91
	Vaiane	−1.34	**<0.05**
Vaiane	Apaura	1.08	**0.01**
	Tiki	1.34	**<0.05**

References

Barría, C., Coll, M., Navarro, J., 2015. Unravelling the ecological role and trophic relationships of uncommon and threatened elasmobranchs in the western Mediterranean Sea. Mar. Ecol. Prog. Ser. 539, 225—240.

Barros, G., Zuanon, J., Deus, C., 2016. Effects of species co-occurrence on the trophic-niche breadth of characids in Amazon forest streams. J. Fish Biol. 90, 326—340.

Bascompte, J., Melian, C.J., Sala, E., 2005. Interaction strength combinations and the overfishing of a marine food web. Proc. Natl. Acad. Sci. 102, 5443—5447.

Browne, D.R., Rasmussen, J.B., 2009. Shifts in the trophic ecology of brook trout resulting from interactions with yellow perch: an intraguild predator-prey interaction. Trans. Am. Fish. Soc. 138, 1109—1122.

Carrassón, M., Cartes, J.E., 2002. Trophic relationships in a Mediterranean deep-sea fish community: partition of food resources, dietary overlap and connections within the benthic boundary layer. Mar. Ecol. Prog. Ser. 241, 41—55.

Caut, S., Jowers, M.J., Michel, L., Lepoint, G., Fisk, A.T., 2013. Diet- and tissue-specific incorporation of isotopes in the shark Scyliorhinus stellaris, a North Sea meso-predator. Mar. Ecol. Prog. Ser. 492, 185—198.

Chase, J.M., Leibold, M.A., 2003. Ecological Niches. Linking Classical and Contemporary Approaches. University of Chicago Press.

Churchill, D.A., Heithaus, M.R., Vaudo, J.J., Grubbs, R.D., Gastrich, K., Castro, J.I., 2015. Trophic interactions of common elasmobranchs in deep-sea communities of the Gulf of Mexico revealed through stable isotope and stomach content analysis. Deep-Sea Res. II 115, 92—102.

Domi, N., Bouquegneau, J.M., Das, K., 2005. Feeding ecology of five commercial shark species of the Celtic Sea through stable isotope and trace metal analysis. Mar. Environ. Res. 60, 551—569.

Downing, A.S., van Nes, E.H., Mooij, W.M., Scheffer, M., 2012. The resilience and resistance of an ecosystem to a collapse of diversity. PLoS one 7, e46135.

Duffy, J.E., 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99, 201—219.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N.K., Fordham, S.V., Francis, M.P., Pollock, C.M., Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J.V., Ebert, D.A., Gibson, C., Heupel, M.R., Livingstone, S.R., Sanciangco, J.C., Stevens, J.D., Valenti, S., White, W.T., 2014. Extinction risk and conservation of the world's sharks and rays. eLife 3, e00590.

Elbroch, L.M., Lendrum, P.E., Newby, J., Quigley, H., Thompson, D.J., 2015. Recolonizing wolves influence the realized niche of resident cougars. Zool. Stud. 54, 41.

Estes, J., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. Science 333, 301—306.

Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., York, E.C., 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125, 258—270.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R., Lotze, H.K., 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecol. Lett. 13, 1055—1071.

Grubbs, R.D., 2010. Ontogenetic shifts in movements and habitat use. In: Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), Sharks and Their Relatives. II. Biodiversity, Adaptive Physiology, and Conservation. CRC Press, pp. 319—350.

Hayward, M.W., Kerley, G.I.H., 2008. Prey preferences and dietary overlap amongst Africa's large predators. South Afr. J. Wildl. Res. 38, 93—108.

Heithaus, M.R., 2007. Nursery areas as essential shark habitats: a theoretical perspective. Am. Fish. Soc. Symp. 50, 3—13.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23, 202—210.

Heithaus, M.R., Frid, A., Vaudo, J.J., Worm, B., Wirsing, A.J., 2010. Unraveling the ecological importance of elasmobranchs. In: Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), Sharks and Their Relatives. II. Biodiversity, Adaptive Physiology, and Conservation. CRC, Boca Raton, pp. 611—637.

Heithaus, M.R., Vaudo, J.J., Kreicker, S., Layman, C.A., Krützen, M., Burkholder, D.A., Gastrich, K., Bessey, C., Sarabia, R., Cameron, K., Wirsing, A., Thomson, J.A., Dunphy-Daly, M.M., 2013. Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. Mar. Ecol. Prog. Ser. 481, 225—237.

Heupel, M.R., Carlson, J.K., Simpfendorfer, C.A., 2007. Shark nursery areas: concepts, definition, characterization and assumptions. Mar. Ecol. Prog. Ser. 337, 287—297.

Holt, R.D., 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. Proc. Natl. Acad. Sci. 106, 19659—19665.

Hueter, R.E., Tyminski, J.P., 2007. Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off peninsular Florida and Texas. Am. Fish. Soc. Symp. 50, 193—223.

Hussey, N.E., MacNeil, M.A., Olin, J.A., McMeans, B.C., Kinney, M.J., Chapman, D.D., Fisk, A.T., 2012. Stable isotopes and elasmobranchs: tissue types, methods, applications, and assumptions. J. Fish Biol. 80, 1449—1484.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comapring isotopic niche widths among and within communities: SIBER - stable isotope Bayesian ellipses in R. J. Animal Ecol. 80, 595—602.

James, K.E.S., Poulin, R., 1998. The effects of perceived competition and parasitism on the foraging behaviour of the upland bully (Eleotridae). J. Fish Biol. 53, 827—834.

Kartzinel, T.R., Chen, P.A., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L., Rubenstein, D.I., Wang, W., Pringle, R.M., 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. Proc. Natl. Acad. Sci. 112, 8019—8024.

Kim, S.L., Martinez del Rio, C., Casper, D., Koch, P.L., 2012. Isotopic incorporation rates for shark tissues from a long-term captive feeding study. J. Exp. Biol. 215, 2495—2500.

Kiszka, J.J., Charlot, K., Hussey, N.E., Heithaus, M.R., Simon-Bouhet, B., Humber, F., Caurant, F., Bustamante, P., 2014. Trophic ecology of common elasmobranchs exploited by artisanal shark fisheries off south-western Madagascar. Aquat. Biol. 23, 29—38.

Kiszka, J.J., Aubail, A., Hussey, N.E., Heithaus, M.R., Caurant, F., Bustamante, P., 2015. Plasticity of trophic interactions among sharks from the oceanic south-western Indian Ocean revealed by stable isotope and mercury analyses. Deep-Sea Res. I 96, 49—58.

Kitchell, J.F., Essington, T.E., Boggs, C.H., Schindler, D.E., Walters, C.J., 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. Ecosystems 5, 202—216.

Layman, C.A., Arrington, D.A., Montana, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88, 42—48.

Layman, C.A., Araujo, M.S., Boucek, R., Harrison, E., Jud, Z.R., Matich, P., Hammerschlag-Peyer, C.M., Rosenblatt, A.R., Vaudo, J.J., Yeager, L.A., Post, D., Bearhop, S., 2012. Applying stable isotopes to examine food web structure: an overview of analytical tools. Biol. Rev. 87, 542—562.

Logan, J.M., Lutcavage, M.E., 2010. Stable isotope dynamics in elasmobranch fishes. Hydrobiologia 644, 231—244.

MacNeil, M.A., Drouillard, K.G., Fisk, A.T., 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. Can. J. Fish. Aquatic Sci. 63, 345—353.

Malpica-Cruz, L., Herzka, S.Z., Sosa-Nishizaki, O., Lazo, J.P., 2012. Tissue-specific isotope trophic discrimination factors and turnover rates in a marine elasmobranch: empirical and modeling results. Can. J. Fish. Aquatic Sci. 69, 551—564.

Martinez del Rio, C., Wolf, N., Carleton, S.A., Gannes, L.Z., 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biol. Rev. 84, 91—111.

Matich, P., Heithaus, M.R., Layman, C.A., 2010. Size-based variation in intertissue comparisons of stable carbon and nitrogen isotopic signatures of bull sharks (Carcharhinus leucas) and tiger sharks (Galeocerdo cuvier). Can. J. Fish. Aquatic Sci. 67, 877—885.

Matich, P., Kiszka, J.J., Heithaus, M.R., Mourier, J., Planes, S., 2015. Short-term shifts of stable isotope (δ^{13}C, δ^{15}N) values in juvenile sharks within nursery areas suggest rapid shifts in energy pathways. J. Exp. Mar. Biol. Ecol. 465, 83—91.

Matich, P., Ault, J.S., Boucek, R.E., Bryan, D.R., Gastrich, K.R., Harvey, C.L., Heithaus, M.R., Kiszka, J.J., Paz, V., Rehage, J.S., Rosenblatt, A.E., 2017. Ecological niche partitioning within a large predator guild in a nutrient-limited estuary. Limnol. Oceanogr. http://dx.doi.org/10.1002/lno.10477.

McCandless, C.T., Kohler, N.E., Pratt Jr., H.L., 2007. Shark Nursery Grounds of the Gulf of Mexico and the East Coast Waters of the United States. American Fisheries Society, Bethesda, Maryland. Symposium 50.

McCutchan Jr., J.H., Lewis Jr., W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102, 378—390.

McMeans, B.C., Olin, J.A., Benz, G.W., 2009. Stable-isotope comparisons between embryos and mothers of a placentatrophic shark species. J. Fish Biol. 75, 2464—2474.

Metcalf, N.B., Huntingford, F.A., Thorpe, J.E., 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. Anim. Behav. 35, 901—911.

Mouillot, D., Graham, N.A.J., Villeger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbance. Trends Ecol. Evol. 28, 167—177.

Mourier, J., Planes, S., 2013. Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (Carcharhinus melanopterus) in French Polynesia. Mol. Ecol. 22, 201—214.

Mourier, J., Buray, N., Schultz, J.K., Clua, E., Planes, S., 2013a. Genetic network and breeding patterns of a sicklefin lemon shark (Negaprion acutidens) population in the society Islands, French Polynesia. PLoS one 8, e73899.

Mourier, J., Mills, S.C., Planes, S., 2013b. Population structure, spatial distribution and life history traits of blacktip reef sharks Carcharhinus melanopterus. J. Fish Biol. 82, 979—993.

Nilsson, E., Persson, A., Nilsson, P.A., 2010. Interspecific competition and predation: relative effects on foragers and their densities. Behav. Ecol. Sociobiol. 64, 729—736.

Olin, J.A., Hussey, N.E., Fritts, M., Heupel, M.R., Simpfendorfer, C.A., Poulakis, G.R., Fisk, A.T., 2011. Maternal meddling in neonatal sharks: implications for interpreting stable isotopes in young animals. Rapid Commun. Mass Spectrom. 25, 1008—1016.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65—75.

Papastamatiou, Y.P., Wetherbee, B.M., Lowe, C.G., Crow, G.L., 2006. Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Mar. Ecol. Prog. Ser. 320, 239—251.

Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1, 6—18.

Pethybridge, H., Daley, R.K., Nichols, P.D., 2011. Diet of demersal sharks and chimaeras inferred by fatty acid profiles and stomach content analysis. J. Exp. Mar. Biol. Ecol. 409, 290—299.

Pfennig, K.S., Pfennig, D.W., 2009. Character displacement: ecological and reproductive responses to a common evolutionary problem. Q. Rev. Biol. 84, 253—276.

Pianka, E.R., 1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. 71, 2141—2145.

Polis, G.A., Strong, D.R., 1996. Food web complexity and community dynamics. Am. Nat. 147, 813—846.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703—718.

Post, D.M., Arrington, D.A., Layman, C.A., Takimoto, G., Quattrochi, J., Montaña, C.G., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179—189.

Preciado, I., Cartes, J.E., Serrano, A., Velasco, F., Olaso, I., Sánchez, F., Frutos, I., 2009. Resource utilization by deep-sea sharks at the Le Danois Bank, Cantabrian Sea, north-east Atlantic Ocean. J. Fish Biol. 75, 1331—1355.

Rastetter, E.B., Gough, L., Hartley, A.E., Herbert, D.A., Nadelhoffer, K.J., Williams, M., 1999. A revised assessment of species redundancy and ecosystem reliability. Conserv. Biol. 13, 440—443.

Schluter, D., McPhail, J.D., 1992. Ecological character displacement and speciation in sticklebacks. Am. Nat. 140, 85—108.

Schoener, T.W., 1983. Field experiments on interspecific competition. Am. Nat. 122, 240—285.

Shaw, A.L., Frazier, B.S., Kucklick, J.R., Sancho, G., 2016. Trophic ecology of a predatory community in a shallow-water, high-salinity estuary assessed by stable isotope analysis. Mar. Coast. Fish. 8, 46—61.

Sih, A., Crowley, P., McPeek, M., Petranka, J., Strohmeir, K., 1985. Predation, competition, and prey communities: a review of field experiments. Annu. Rev. Ecol. Syst. 16, 269—311.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Dick, B.L., Ben-David, M., 2003. Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? Ecoscience 10, 297—302.

Vanderklift, M.A., Ponsard, S., 2003. Source of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. Oecologia 136, 169—182.

Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., Weidel, B.C., 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS one 10, e0116182.

Vaudo, J.J., Matich, P., Heithaus, M.R., 2010. Mother—offspring isotope fractionation in two species of placentatrophic sharks. J. Fish Biol. 77, 1724—1727.

Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18—23.

Yates, P.M., Heupel, M.R., Tobin, A.J., Simpfendorfer, C.A., 2015. Ecological drivers of shark distributions along a tropical coastline. PLoS One 10, e0121346.