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Energetic connectivity of diverse elasmobranch populations – implications for ecological resilience

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Understanding the factors shaping patterns of ecological resilience is critical for mitigating the loss of global biodiversity. Throughout aquatic environments, highly mobile predators are thought to serve as important vectors of energy between ecosystems thereby promoting stability and resilience. However, the role these predators play in connecting food webs and promoting energy flow remains poorly understood in most contexts. Using carbon and nitrogen isotopes, we quantified the use of several prey resource pools (small oceanic forage, large oceanics, coral reef, and seagrass) by 17 species of elasmobranch fishes ($n = 351$ individuals) in The Bahamas to determine their functional diversity and roles as ecosystem links. We observed remarkable functional diversity across species and identified four major groups responsible for connecting discrete regions of the seascape. Elasmobranchs were responsible for promoting energetic connectivity between neritic, oceanic and deep-sea ecosystems. Our findings illustrate how mobile predators promote ecosystem connectivity, underscoring their functional significance and role in supporting ecological resilience. More broadly, strong predator conservation efforts in developing island nations, such as The Bahamas, are likely to yield ecological benefits that enhance the resilience of marine ecosystems to combat imminent threats such as habitat degradation and climate change.

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1. Introduction

How ecosystems respond to human-induced stressors and disturbance regimes has the potential to alter their ecological functions [1]. Conserving the processes that promote ecological resilience in the face of these changes is, therefore, key [2]. Ecological resilience can be defined, in part, by the propensity of ecological systems to rebound following disturbances [3], and is strongly mediated by levels of biodiversity, functional complexity [4] and the diversity of energetic resource pools supporting food-webs [5]. A critical mechanism proposed to support high levels of ecological resilience is the maintenance of strong energy and nutrient flow across habitats [5,6]. This can be facilitated by passive processes, such as current- and wind-based transport of nutrients [7], or more active ecological processes, such as the movements and foraging interactions of large mobile consumers [8–10]. Predators that feed across resource channels help link energy pathways, and aid in the stability and resilience of food webs [5]. For example, Rooney *et al*. [5] illustrated how food-web stability is strongly mediated by predatory multi-channel feeding, whereby individuals may feed across a distinct energetic pathway with different rates of productivity and turnover.

Animals like whales and sharks that feed across multiple food webs, migrate long distances or occupy diverse habitats, connect disparate regions of the ocean [11]. Yet these widespread functional roles often make them vulnerable to individual- and population-level threats, including human impacts. While some species of marine megafauna are highly protected and are recovering (e.g. some whale and sea turtle species, [12,13]), many sharks continue to experience high levels of overexploitation resulting in population declines [14]. Given that sharks display a variety of functional roles, including top-down control of food webs and connecting trophic levels through their foraging behaviour [15], their ongoing removal is likely to have long-term effects on the structure and function of marine ecosystems [16]. This therefore remains a critical area of research.

Quantifying how mobile marine predators serve as energetic vectors is inherently challenging, owing to their cryptic lifestyles combined with a lack of techniques that can reliably resolve patterns of energy flow. However, the application of biochemical tracers, such as naturally occurring stable isotopes, can provide a non-lethal means for discerning patterns of predator-mediated energy flow among ecosystems [17]. This is because carbon isotope values of animal tissues reflect primary production pathways supporting the base of food-webs, which are isotopically distinct across major producer groups (e.g. C_3 versus C_4 photosynthetic versus chemoautotrophic production). Nitrogen isotopes complement carbon isotopes because of predictable, stepwise ^{15}N fractionation between predator and prey that reflects a consumer's trophic position within food webs [17]. When combined with isotopic end members (prey species that represent a single energetic resource channel, [18]), an animal's or population's reliance on multiple energetic pathways can be discerned, provided they are isotopically distinct [17,19]. This offers a means for determining the extent to which consumers connect ecosystems themselves [9].

Among target areas for research on trophic coupling, marine seascapes within subtropical and tropical latitudes offer a valuable opportunity to understand patterns of predator-mediated ecosystem connectivity, due to the diversity of species and distinct ecosystems that exist across very small spatial scales [20]. In The Bahamas, acoustic telemetry and biologging revealed that tiger sharks connect coral reef, carbonate banks and seagrass meadows throughout their home range [21], whereby the intermediary seagrass habitats appear to serve as strategic navigation routes and connective pathways between ecosystems [22,23]. At Palmyra Atoll, blacktip reef sharks (*Carcharhinus melanopterus*), grey reef sharks (*C. amblyrhynchos*) and red snapper (*Lutjanus fulvus*) were shown to derive energy from lagoon, forereef and oceanic environments, with grey reef sharks connecting forereef and oceanic components and potentially linking the epipelagic and deep-water environment [9]. More broadly, similar patterns of ecosystem connectivity have been observed across other marine ecosystems such as estuaries (fishes and dolphins [24]), open ocean (whales [25]) and the deep sea (dolphins and whales [26]). However, a critical evaluation of predator-mediated connectivity has yet to be undertaken at any great scale, with most studies focusing on a relatively low number of species. This precludes a comprehensive understanding of predator-mediated ecosystem connectivity and the implications this may have for patterns of ecological resilience.

Here, we compile a large carbon and nitrogen stable isotope dataset to quantify functional diversity displayed across seventeen species of elasmobranch. Specifically, we establish (1) how species use and therefore connect major energetic resource pools and (2) key functional groups defined by interspecific resource use patterns. We use The Bahamas as a case study system, where commercial longlining was banned in 1993 and the exclusive economic zone designated a shark sanctuary in 2011. Bahamian ecosystems, therefore, provide a unique opportunity to understand the functional role of elasmobranchs in the absence of significant fishing pressure. We discuss our results within the context of ecosystem function and patterns of ecological resilience.

2. Methods

(a) Declarations

All sampling was conducted between 2009 and 2020 under research permits issued by the Bahamas Ministry of Agriculture and Marine Resources, Department of Marine Resources.

(b) Compilation of elasmobranch stable isotope values

We compiled elasmobranch carbon and nitrogen stable isotope values from several published studies [27–29], in addition to several unpublished datasets. Animals were captured using a variety of techniques including scientific longlines [30–32], drum lines [21,22,33], gillnets [34], handlines [35,36], hand nets [37] and benthic traps [28]. This included 351 individuals from 17 species sampled from around the Bahamian islands of New Providence, Cat Island, Southern Exuma, South Eleuthera, Andros and Bimini (figure 1). Deep-sea species were exclusively sampled in northeast Exuma Sound and deep waters west of North Bimini (figure 1). Specific information on animal capture, sampling and stable isotope analyses for unpublished datasets can be found in the electronic supplementary material (electronic supplementary material, appendix S1).

Species were grouped based on their major habitat association [38]. Neritic species (i.e. those commonly associated with shallow ocean overlaying the continental shelf) included blacknose sharks (*Carcharhinus acronotus*), Caribbean reef sharks (*C. perezi*), lemon sharks (*Negaprion brevirostris*), nurse sharks (*Ginglymostoma cirratum*), bull sharks (*C. leucas*), southern

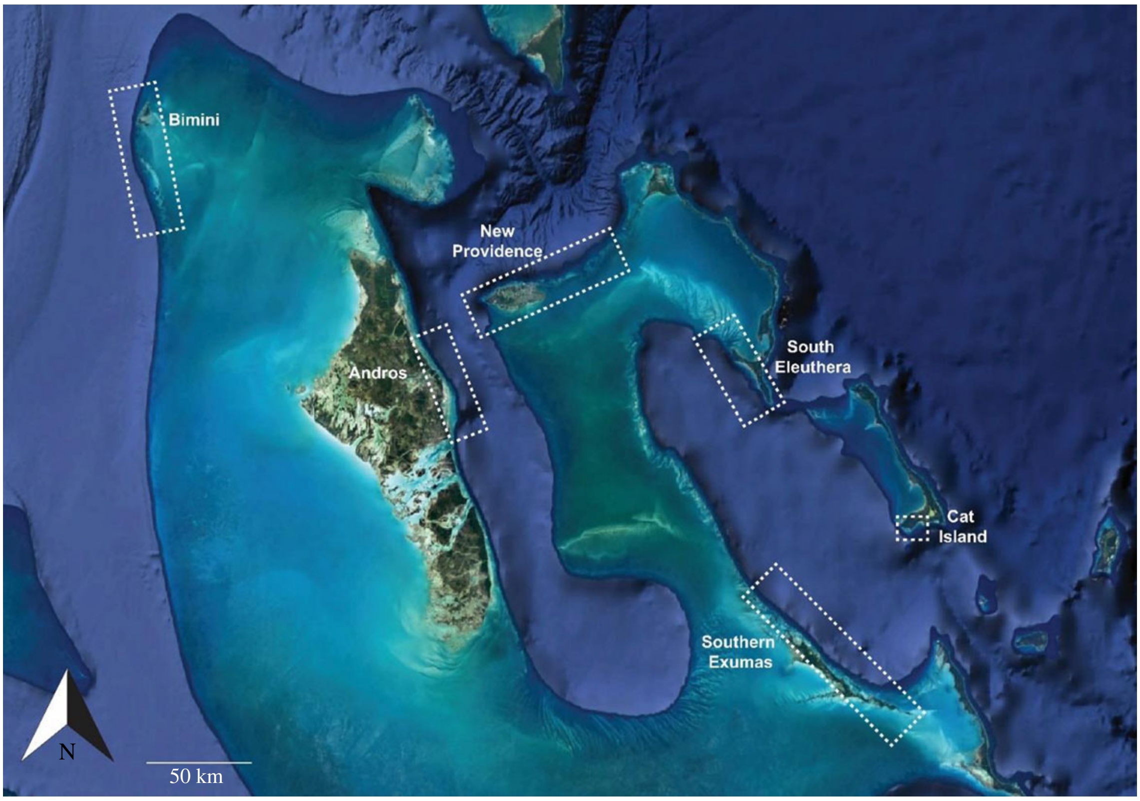

Figure 1. General sampling locations (white hashed lines) of elasmobranchs included in this study. Species were sampled from a variety of neritic and oceanic habitats from Bimini, New Providence, Andros, Southern Exumas, South Eleuthera and Cat Island.

stingrays (*Hypanus americanus*) and Atlantic chupare (*Styracura schmardae*). Oceanic/semi-oceanic species included silky sharks (*C. facliformis*), oceanic whitetip sharks (*C. longimanus*) and tiger sharks (*Galeocerdo cuvier*). Deep-sea associated species included Cuban dogfish (*Squalus cubensis*), smooth dogfish (*Mustelus canis insularis*), Mead's catsharks (*Scyliorhinus meadi*), gulper sharks (*Centrophorus* spp.), Atlantic sixgill sharks (*Hexanchus vitulus*), bluntnose sixgill sharks (*H. griseus*) and sharpnose sevengill sharks (*Heptranchias perlo*). Given similar habitat characteristics between Bahamian islands and similar prevailing biological oceanography (e.g. water temperature, primary production pathways), it was assumed that stable isotope values of elasmobranchs and primary producers would not differ significantly between islands (see [29]).

The goal of this study was to address overall, long-term patterns of resource use, therefore we only included data from tissues with longer isotopic incorporation rates that are relatively insensitive to short-term (i.e. seasonal) fluctuations in energetic resource use. These included red blood cells (herein 'RBCs', $T_{95} = 41–582$ days, [39,40]), white muscle ($T_{95} = 173–1014$ days, [39,41–43]) and fin tissue ($T_{95} = 30–726$ days). Because there were several species for which data were generated from multiple tissues, all isotope values were corrected for trophic discrimination prior to statistical analyses (see electronic supplementary material, appendix S1, electronic supplementary material, table S1). Given the lack of trophic discrimination factor values for elasmobranchs, we first used weighted averages from all published studies for each tissue (electronic supplementary material, appendix S1; electronic supplementary material, table S2). However, the weighted averages for muscle tissue resulted in many species falling beyond the isotopic mixing space, indicating that this value was an inappropriate estimate for many species in this study. As a result, we assigned discrimination values for muscle tissue generated for adult lemon sharks, which resulted in most species falling well within the isotopic mixing space [18,44]. We selected this species due to the close taxonomic relatedness to many species included in this study. For RBCs, muscle, and fin clips we assigned trophic discrimination factors of $\Delta^{13}C = 1.88‰$; $\Delta^{15}N = 2.44‰$, $\Delta^{13}C = 1.3‰$; $\Delta^{15}N = 3.2‰$ and $\Delta^{13}C = 3.6‰$; $\Delta^{15}N = 0.4‰$, respectively (electronic supplementary material, appendix S1, electronic supplementary material, table S1).

Lipids and urea have known isotopic effects that can alter ecological interpretation (reviewed by [17,45]). For legacy datasets, however, it is often unattainable to ensure all samples are treated in a uniform manner. However, we ensured that all datasets accounted for potential effects of lipids and/or urea in some manner, either through chemical treatment or mathematical normalization (for lipids only) where C:N was high (following DI water rinses to remove urea; [46]). Chemical treatment was not conducted on muscle tissue of a single bluntnose sixgill shark, however the C:N ratio and bulk isotope values fell within the range of lipid-extracted samples for closely related deep-water species [47,48].

(c) Elasmobranch-mediated energy flow

We used stable isotope mixing models to evaluate how elasmobranchs connect ecosystems through energetic resource use (per [9]). Thus, we adopted a well-established isotopic 'end-member' approach [9,18,49] to evaluate the reliance of elasmobranchs on four major resource pools – oceanic forage, large oceanic predators (herein 'large oceanics'), coral reefs, and seagrass. The isotopic mixing space was constructed from resampling published means and s.d.s ($n = 100$) of key prey species [50] sampled from The Bahamas that are known to derive most energy from a single resource pool. Prey isotope values spanned several geographical areas including Eleuthera [51–53], Cat Island [27], Bimini [54], Inagua and Long Island [55]. Oceanic forage species ($\delta^{13}C = 18.0‰ \pm 1.2‰$, $\delta^{15}N = 5.3‰ \pm 0.7‰$) included squid (unidentified spp.) and flying fish (family Exocoetidae). Large oceanics ($\delta^{13}C = -16.7‰ \pm 0.6‰$, $\delta^{15}N = 8.6‰ \pm 1.2‰$) were composed of offshore piscivorous fishes including wahoo (*Acanthocybium solandri*), dolphinfish (*Coryphaena hippurus*), blackfin tuna (*Thunnus* *atlanticus*), skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*). Coral reef endmembers ($\delta^{13}C = -12.5‰ \pm 1.7‰$, $\delta^{15}N = 8.3‰ \pm 0.4‰$) included mostly piscivorous reef fishes that exhibit high fidelity to large coral reefs, including bar jack (*Caranx ruber*), graysby grouper (*Cephalopholis cruentata*), Nassau grouper (*Epinephelus striatus*), schoolmaster snapper (*Lutjanus apodus*), yellowtail snapper (*Ocyurus chrysurus*) and lane snapper (*Lutjanus synagris*). Seagrass endmembers ($\delta^{13}C = -8.4‰ \pm 1.9‰$, $\delta^{15}N = 5.2‰ \pm 3.0‰$) included several populations of green sea turtles (*Chelonia mydas*) and juvenile and adult bonefish (*Albula vulpes*). Mean $\delta^{13}C$ and $\delta^{15}N$ (±s.d.) for all endmember species can be found in the electronic supplementary material (electronic supplementary material, appendix 1; electronic supplementary material, table S2).

Bayesian mixing models were implemented in the R package *MixSIAR* [56], which offers greater flexibility than traditional mixing models by allowing for the inclusion of model covariates. Here, we ran species-specific mixing models which included a random effect of individual to quantify intraspecific variation in resource use. These were compared to a null model (i.e. no covariates) that assumes a uniform resource use distribution across all individuals using leave one out cross validation and Akaike weights [56]. Models were run for 100 000 iterations across three Markov chains with a burn-in of 50 000 and thinning interval of 50. Model convergence was assessed via Gelman-Rubin diagnostics and Geweke statistics [56]. We also assessed multiplicative error terms to ensure carbon and nitrogen isotope data were sufficiently explained by model covariates [56]. For sharpnose sevengill sharks, two energy channels were removed from the mixing model to improve model convergence. This was justified given that this species fell extremely close to a single endmember (large oceanics) [18].

To further evaluate the degree to which different species connected multiple resource pools we calculated Pielou's evenness [57]. This was calculated using the proportional contributions of each resource pool to species diet and provides values between 0 and 1, where = 0 low evenness (i.e. a species relies solely upon a single resource channel), and 1 = high evenness (i.e. a species relies similarly on all available resource pools). Species exhibiting high evenness values are assumed to be greater ecosystem connectors.

(d) Functional diversity of elasmobranchs

We adopted hierarchical K-means clustering using the R package *NbClust* [58] to determine the diversity of functional roles displayed by elasmobranch species. Median estimates of energetic resource use were calculated from all individuals, for each species and normalized to Euclidean distances prior to clustering. The most appropriate number of clusters was explored using mean within sum-of-squares (WSS) and average silhouette width [58]. The final cluster designation was based on the results of preprocessing algorithms combined with visual scrutiny of the resulting dendrogram. We removed species with low sample sizes ($n = 1$ or 2) from clustering, which included the bluntnose sixgill shark, sharpnose sevengill shark and Mead's catshark.

Finally, we evaluated isotopic niche area for each functional group (as inferred through hierarchical clustering) as a proxy for trophic niche variation [59]. We calculated estimates of niche area and proportional pairwise overlap using 95% kernel utilization distributions (KUDs) in the R package *rKIN* [59,60].

3. Results

Carbon and nitrogen stable isotope values were compiled for 17 elasmobranch species ($n = 351$ individuals) that associate with neritic, oceanic/semi-oceanic and deep-water ecosystems (table 1). Across sampled elasmobranchs, raw $\delta^{13}C$ and $\delta^{15}N$ values (i.e. prior to TDF correction) ranged from −17.1‰ (silky shark) to −5.4‰ (nurse shark) and 2.5‰ (Atlantic chupare) to 14.4‰ (bull shark), respectively (figure 2). The greatest ranges of $\delta^{13}C$ and $\delta^{15}N$ values (where $n > 3$) were observed for nurse sharks ($\delta^{13}C = -14.8‰$ to −5.4‰) and bull sharks ($\delta^{15}N = 10.0‰$ to 14.4‰), and the lowest ranges were observed for gulper sharks ($\delta^{13}C = -16.4‰$ to −15.8‰; $\delta^{15}N = 10.3‰$ to 11.0‰) (figure 2).

(a) Elasmobranch-mediated energy flow

Bayesian isotope mixing models revealed that elasmobranch species were generally reliant upon a mixture of energetic resource channels (figure 3). High resource use diversity was observed for many neritic species including blacknose, nurse and Caribbean reef sharks (figure 3). Most oceanic species were heavily reliant upon large oceanic and oceanic forage species, with little use of neritic resource channels (e.g. coral reefs and seagrass). Several deep-water species, such as the Atlantic sixgill and smooth dogfish exhibited use of both neritic and oceanic prey resources (figures 2 and 3). We observed the highest intraspecific variation in resource use by lemon sharks, nurse sharks, and Cuban dogfish (figure 3). Uniform resource use (i.e. consistent reliance upon the same resource pools across individuals) was observed across many neritic, oceanic and deep-water species, particularly oceanic whitetip sharks, silky sharks and tiger sharks (figure 3). Across the fourteen species included in hierarchical cluster analysis, Pielou's evenness values were generally high and ranged from 0.55 (gulper shark) to 0.99 (smooth dogfish) (figure 4).

(b) Functional diversity of elasmobranchs

Hierarchical cluster analysis revealed at least four distinct species clusters based on the average use of available prey resource channels (figure 5; electronic supplementary material, appendix S1 and figure S1). The first cluster was defined as *neritic ecosystem connectors* (herein, NECs) and comprised neritic species, including blacknose sharks, nurse sharks, southern stingrays and Atlantic chupares, which derived most energy from seagrass and coral reef prey (figure 5). The second cluster, *neritic–oceanic connectors* (herein, NOCs), included neritic, oceanic/semi-oceanic and deep-sea associated species that use all available resource channels. NOCs included Cuban dogfish, smooth dogfish, Caribbean reef sharks and lemon sharks. A third cluster, *oceanic omnivores* (i.e. trophic omnivores; herein, OOs), included oceanic whitetip sharks, silky sharks and gulper sharks. Oceanic omnivores displayed a mixed reliance on oceanic forage and large oceanic resource channels, thereby connecting lower and upper components of oceanic food webs. The final group was defined as *higher oceanic predators* (herein, HOPs) and comprised species displaying a strong reliance on the large oceanic resource channel. This group comprised tiger sharks, Atlantic sixgill sharks and bull sharks.

The largest niche area was observed for NECs ($41.8‰^2$), followed by HOPs ($41.3‰^2$), NOCs ($19.4‰^2$) and OOs ($4.9‰^2$) (table 2, figure 5). Pairwise isotopic overlap was greatest between NOCs and NECs (greater than 50%), OOs and HOPs (greater than 70%) (table 3), and NECs and HOPs (greater than 78%). Moderate niche overlap was observed between NECs and NOCs, NECs and HOPs, OOs and NOCs, HOPs and NECs, and HOPs and NOCs (27–34%). Low niche overlap was observed between NECs

Table 1. Primary habitat association, size range, sample size and mean (± 1 s.d.) carbon and nitrogen stable isotope values (bulk and TDF corrected) for 17 species of elasmobranch sampled from The Bahamas.

scientific name	common name	habitat	total length (cm)	*n*	$\delta^{13}C$	$\delta^{13}C_{TDF}$	$\delta^{15}N$	$\delta^{15}N_{TDF}$	reference
Carcharhinus acronotus	blacknose shark	neritic	103–119	9	−10.7	−12.2 (0.8)	9.6	6.7 (0.5)	this study
Carcharhinus leucas	bull shark	neritic	227–278	7	−13.8	−15.2 (1.3)	13.1	10.0 (1.3)	this study
Carcharhinus perezi	Caribbean reef shark	neritic	81–190	69	−11.6	−13.5 (1.0)	9.0	6.5 (0.7)	this study
Ginglymostoma cirratum	nurse shark	neritic	113–246	53	−9.9	−11.4 (2.6)	8.9	6.1 (0.9)	[29]; this study
Styracura schmardae	Atlantic chupare	neritic	25–120	20	−9.6	−13.3 (1.3)	4.8	4.4 (1.1)	[29]
Hypanus americanus	southern stingray	neritic	45–102	20	−8.1	−11.8 (0.7)	7.0	6.6 (1.1)	[29]
Negaprion brevirostris	lemon shark	neritic	65–269	46	−12.4	−14.2 (1.5)	8.8	6.3 (0.7)	this study
Carcharhinus falciformis	silky shark	oceanic/ semi-oceanic	106–212	13	−16.0	−17.3 (0.9)	9.7	6.5 (0.7)	this study
Carcharhinus longimanus	oceanic whitetip shark	oceanic/ semi-oceanic	194–307	38	−15.5	−17.2 (0.2)	9.4	6.5 (0.7)	[27]; this study
Galeocerdo cuvier	tiger shark	oceanic/ semi-oceanic	155–304	26	−12.7	−14.5 (1.6)	10.1	7.5 (1.2)	this study
Centrophorus spp.	gulper shark	deep sea	70–104	9	−16.1	−17.4 (0.2)	10.6	7.5 (0.2)	[28]
Heptranchias perlo	sharpnose sevengill shark	deep sea	63–87	2	−16.5	−17.8 (0.5)	12.8	9.6 (0.6)	[28]
Hexanchus vitulus	Atlantic sixgill shark	deep sea	120–151	4	−13.8	−15.1 (0.6)	11.2	8.1 (0.0)	[28]
Hexanchus griseus	bluntnose sixgill shark	deep sea	> 300	1	−12.1	−14.0	8.9	6.5	this study
Mustelus canis insularis	smooth dogfish	deep sea	78–107	11	−11.7	−13.9 (1.5)	9.1	7.0 (1.2)	[28]; this study
Scyliorhinus meadi	Mead's catshark	deep sea	50	1	−14.1	−15.4	8.0	4.9	[28]
Squalus cubensis	Cuban dogfish	deep sea	39–77	22	−14.1	−15.4 (0.7)	10.0	6.8 (0.7)	[28]

and OOs (1% – 7%), OOs and NECs, and HOPs and OOs (less than 10% (table 3, figure 5).

4. Discussion

As climate change and human impacts continue to threaten ecosystem stability, management and conservation groups in many regions have been increasingly forced to set priorities, such as the increased expansion of marine protected areas [63]. As such, some habitats, like coral reefs, have been given more attention than others despite the inherent connectivity between ecosystems. Here we provide an evaluation of predator-mediated ecosystem connectivity from The Bahamas archipelago, highlighting the functional connections facilitated by sharks and rays between disparate habitats. We observed functional diversity within and across elasmobranch species which were found to energetically couple neritic and oceanic waters, including the deep-sea. Patterns of evenness suggested that most species are

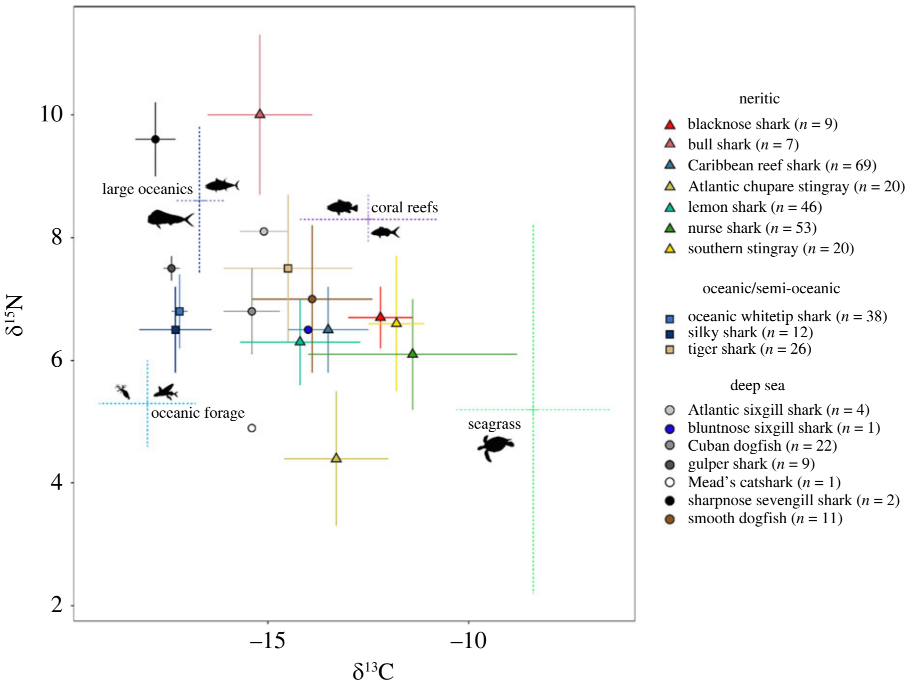

Figure 2. Mean δ^{13}C and δ^{15}N values (± 1 s.d.) adjusted for trophic discrimination for 17 species of elasmobranch spanning neritic (triangles), oceanic/semi-oceanic (squares), and deep-water (circles) associated habitats. Values are shown relative to four major prey resource pools: large oceanics, oceanic forage, coral reefs, and seagrass/banks.

rarely reliant on a single resource pool, and therefore connect at least two different ecosystems in space and time. These findings underscore the value of predator biodiversity in facilitating the conditions required to ensure ecological resilience, specifically energy and nutrient flow across habitats [3,64].

(a) Ecosystem connectivity and functional diversity of Bahamian elasmobranchs

Neritic ecosystem connectors (NECs) comprised species that facilitated energy flow between seagrass and coral reef environments and included blacknose sharks, nurse sharks and two larger-bodied stingray species. These findings align with the known habitat use of these species and their physical mobility between neritic regions of the seascape [37], which comprise a large portion of The Bahamas Exclusive Economic Zone [21,22]. Individuals within this functional group were not homogeneous, with NECs exhibiting the broadest isotopic niche and significant overlap with other functional groups. This suggests considerable variation among individuals—a trend that was particularly evident within nurse sharks. Such variation indicates that not all sharks and rays in this functional group link coral reef and seagrass habitats equally, and individual differences may buffer populations from disturbance events, such as habitat degradation [65], climate change [66] and species invasions [67]. We thus draw two major conclusions from NECs: (1) this functional group is critical for facilitating energetic transfer between seagrass and coral reef environments, and (2) species within this group may be buffered from environmental disturbance due to the use of multiple prey resource pools [5] provided energetic needs can be adequately sustained by remaining undisturbed pools.

The second functional group, neritic–oceanic connectors (NOCs) comprised species that predominantly relied upon coral reef and oceanic-derived energy (figure 5), which is supported by existing knowledge of vertical movement behaviors (reviewed by [68]). Caribbean reef sharks relied upon energy derived from seagrass, coral reef and oceanic forage species, reflecting their movements across ecotones [21–23,29]. Their reliance on oceanic forage species may also, in part, explain the functionality of commonly observed deep-diving behaviours [62,68,69]. Several deep-sea elasmobranchs, namely Cuban dogfish and smooth dogfish were assigned to this group, because both species were reliant upon oceanic and coral reef-derived energy. In regions such as the Exuma Sound, these dogfishes typically occupy depths of 300–900 m along the slope [31,61], which probably receives significant inputs of carbonate matter washed off shallow banks and algal-covered reef walls. Based on vertical habitat preferences [31,61], it is plausible that both species may provide a connection between the neritic extent of the slope (abutting the near-vertical reef wall) and deep benthic environments, which could be particularly important for deep-sea habitats that typically exhibit low levels of productivity. Our findings here suggest that this connectivity may, in part, be mediated by the vertical movements of both large- and smaller-bodied sharks within this functional group.

Oceanic omnivores (OOs) such as oceanic whitetip sharks and silky sharks relied upon a mix of oceanic forage and larger oceanic prey [27]. Despite their large body sizes, these findings suggest that these species may not constitute true apex predators in offshore, oceanic ecosystems of The Bahamas, but rather feed across multiple trophic levels. This is certainly true for silky sharks, for which data were only available for juvenile and subadult individuals. This functional group exhibited the narrowest isotopic niche and lowest overlap with other functional groups, which suggests a uniform functional role among individuals that is largely divergent from other sampled taxa. These species likely serve as connectors of lower and upper trophic levels within oceanic food webs. For oceanic whitetip sharks, which routinely perform mesopelagic excursions [35,36,70], individuals may facilitate energetic connectivity between epi- and mesopelagic zones.

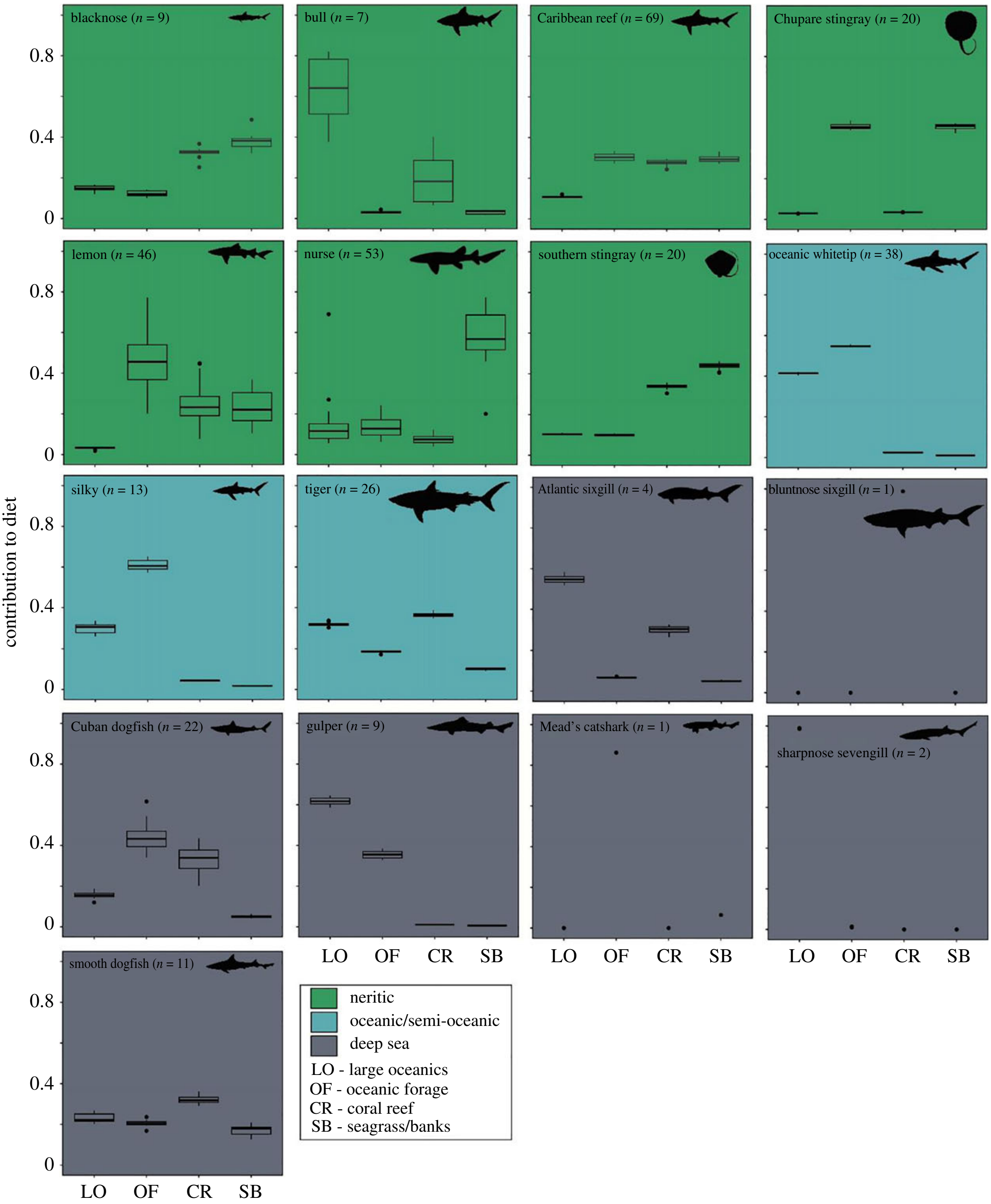

Figure 3. Relative use of large oceanic (LO), oceanic forage (OF), coral reef (CR), and seagrass/banks (SB) energetic resource pools by 17 species of elasmobranchs from The Bahamas ($n = 351$). Colours represent primary habitat associations where green = neritic, blue = oceanic/semi-oceanic, and grey = deep-sea. Boxplots comprise median estimates from each individual, for each species, derived from 100 000 posterior draws.

Higher oceanic predators (HOPs), the fourth functional group, comprised bull sharks, tiger sharks, and Atlantic sixgill sharks, which exhibited a strong reliance on large oceanic prey. For Atlantic sixgill sharks, it is likely that cluster designations may in part, represent opportunistic reliance upon larger sinking carrion such as whales and larger fishes, which are commonly observed in deep-water environments of the eastern Bahamas [71], rather than active hunting of large pelagic fishes. A surprising assignment was that of bull sharks to this group, which commonly traverse neritic ecosystems [72]. This observation could be explained by their common occurrence in Bahamian marinas where they are highly provisioned with offshore offal (O.N.S. 2023, personal communication), or by known movements across the oceanic environment of the Florida straits during migrations between The Bahamas and Florida [73].

From an energy flow perspective, it remains unclear the extent to which these species connect regions of the oceanic food web, given the lack of empirical data on vertical habitat preference and movement trajectories. Based on the high $\delta^{15}N$ values of HOPs, it could be inferred that these species occupy apex positions throughout oceanic food webs, but the moderate body sizes of individuals sampled (TL = 120–304 cm), suggest that this is unlikely. Instead, we predict that bluntnose sixgill sharks, deep-diving great hammerhead

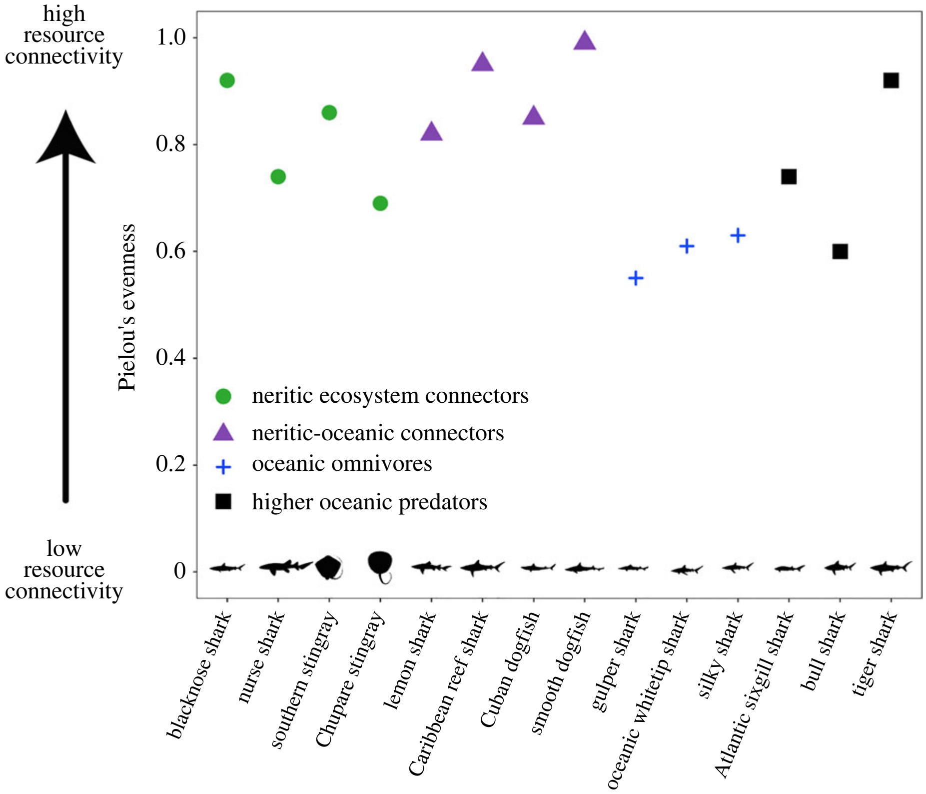

Figure 4. Pielou's evenness for fourteen species of elasmobranchs sampled from The Bahamas. High evenness values indicate even use of available resource pools, whereas low values indicate dominant use of a single resource pool. Colours and symbols indicate functional groups derived from Bayesian mixing models and hierarchical clustering: neritic ecosystem connectors (green circles), neritic–oceanic connectors (purple triangles), oceanic omnivores (blue crosses) and higher oceanic predators (black squares).

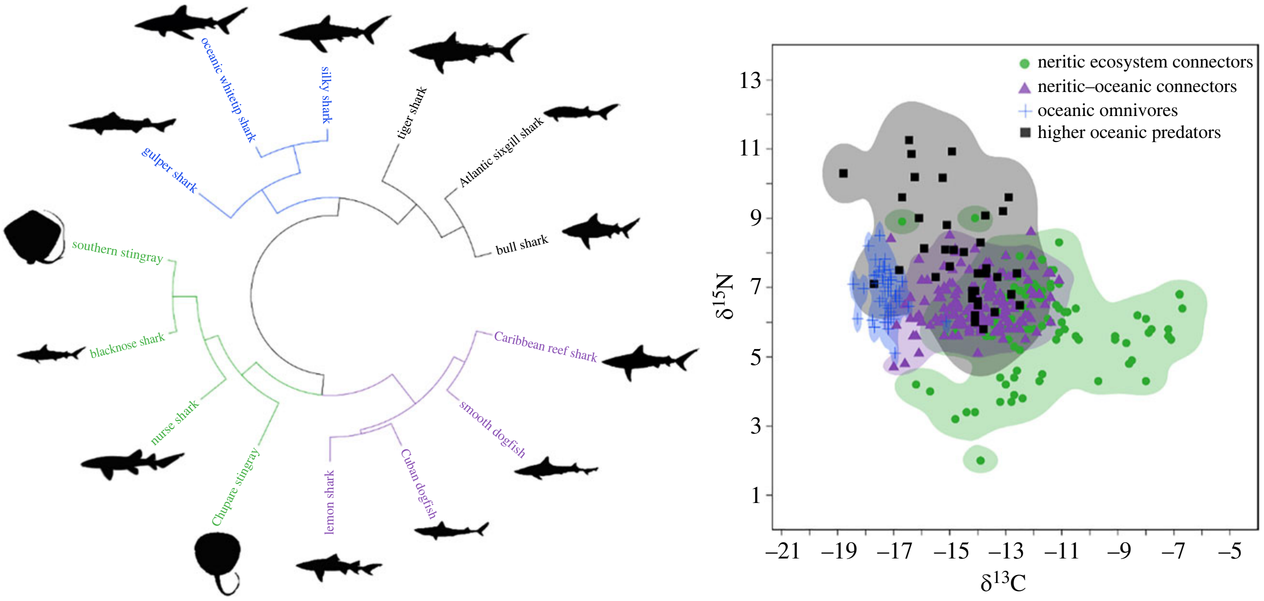

Figure 5. *Left*: Functional groupings of 14 elasmobranch species based on their relative use of energetic resource pools. Four major functional clusters were identified including neritic ecosystem connectors (green), neritic–oceanic connectors (purple), oceanic omnivores (dark blue) and higher oceanic predators (dark grey). Note: bluntnose sixgill sharks, sharpnose sevengill sharks and Mead's catsharks were not included due to low sample sizes ($n = 1$ or 2). *Right*: Isotopic niche width of functional groupings were calculated using 95% kernel utilization distributions (KUDs). Isotope values are corrected for tissue-specific trophic discrimination.

sharks (*Sphyrna mokarran*), and toothed whales may assume this role for the deeper oceanic environment in The Bahamas [31]. However, we did not have sufficient data to support this inference within the confines of this study. Further, these regions also support a variety of large, deep-diving toothed whales [74] that may fill this ecological role. Despite assessing 14 different species, expanding the taxonomic resolution of mobile predators studied in the context of energy flow is clearly required for a more holistic understanding of ecosystem structure and function. For Bahamian elasmobranchs, this may include greater attention on the collection of samples from species such as blacktip sharks (*C. limbatus*), great hammerhead sharks (*Sphyrna mokarran*), bonnethead sharks (*Sphyrna tiburo*) and yellow stingrays (*Urobatis jamaicensis*).

Table 2. Isotopic niche area of four elasmobranch functional groups identified through use of four primary production channels. Areas are based on 95% kernel utilization distributions.

functional group	species composition	$n_{\text{individuals}}$	niche area (‰^{2})
neritic ecosystem connectors (NECs)	blacknose shark, nurse shark, southern stingray, Chupare stingray	102	41.8
neritic–oceanic connectors (NOCs)	lemon shark, Caribbean reef shark, Cuban dogfish, smooth dogfish,	148	19.4
oceanic omnivores (OOs)	oceanic whitetip shark, silky shark, gulper shark	60	4.9
higher oceanic predators (HOPs)	Atlantic sixgill shark, tiger shark, bull shark	37	41.3

Table 3. Isotopic niche overlap between four elasmobranch functional groups identified through use of four primary production channels. Overlap estimates are proportions (0–1) based on 95% Kernel Utilization Distributions (KUDs).

functional group	neritic ecosystem connectors	neritic–oceanic connectors	oceanic omnivores	higher oceanic predators
neritic ecosystem connectors	—	0.312	0.004	0.332
neritic–oceanic connectors	0.67	—	0.070	0.786
oceanic omnivores	0.036	0.277	—	0.725
higher oceanic predators	0.336	0.369	0.086	—

When considering deep water elasmobranchs in the fourth functional group, physiological processes such as tissue catabolism could be responsible for high δ^{15}N values [75]. Similarly, the nitrogen physiology of deep-water sharks is unique relative to other vertebrates, whereby individuals must balance concentrations of urea and trimethylamine *n*-oxide to maintain osmotic balance under high hydrostatic pressures [76]. If this requires alteration to overall nitrogen balance [77], such as the mobilization of nitrogen from structural tissues to synthesize urea and/or TMAO, this may leave the residual δ^{15}N values of tissues ^{15}N-enriched. While the δ^{15}N patterns of deep-sea elasmobranchs may be linked to both physiological and ecological processes [48], low δ^{13}C values for species such as Atlantic sixgill and sharpnose sevengill sharks indicate an exclusive reliance upon oceanic resource pools, suggesting these species are unlikely to be critical connectors of ecosystems.

(b) Implications for connectivity and resilience

Although these findings have specific implications for Bahamian seascapes (as outlined above), they are highly relevant when considering the broader role of marine predators in terms of ecosystem connectivity and resilience. Our results highlight how, when faced with diverse energetic resource pools, mobile predators are rarely reliant upon energy derived from a single energetic pathway, as reflected in consistently high Pielou's evenness values (all > 0.5). These observations agree with those reported across a variety of marine, freshwater and terrestrial settings and are strongly tied to theories of ecosystem structural asymmetry and stability [78]. For example, previous work has suggested that the use of phytoplanktonic and detrital energy channels by predators, diversifies ecosystem linkages and can increase overall stability [5,6]. Similarly, the ecological coupling of marine and freshwater food webs by highly mobile predators may increase the resilience of estuarine systems that frequently experience extreme weather events (e.g. [24]). This is due to disparity of productivity and energetic turnover between distinct energetic pathways, which buffers against long-term perturbations. Although the overall rate of energetic turnover has yet to be determined for energy channels supporting many sub-tropical ecosystems, this offers a challenging, albeit critical avenue for further work. Similarly, exploring how predators may shift resource acquisition in response to environmental and anthropogenic cues is required to fully appreciate the mechanisms driving stability [79]. Such information is essential for predicting the long-term, ecosystem-wide effects of chronic stressors, such as climate change.

(c) Caveats and considerations

While previous research on our study species supports the inferences we draw from our results, we must acknowledge several important assumptions. We acknowledge that for many species, individuals may display ontogenetic shifts in diet, which may explain the relatively high individual-level variability seen within lemon sharks, nurse sharks and Cuban dogfish (figure 2). The goal of this study, however, was to provide a general species-level overview of energetic resource use. For many species (i.e. deep-sea and oceanic/semi-oceanic), the use of specific primary production channels is unlikely to change across ontogeny. Future studies should aim to investigate how the functional role of different species changes across size, to develop conservation strategies for specific life-history stages. Second, we recognize that several shark species did not fall directly within the isotopic mixing space [18,80], including bull sharks and sharpnose sevengill sharks (figure 2). However, isotope values of most individuals were extremely close to a single end member, promoting high confidence that individuals use a specific energetic resource channel. This observation partly reflects challenges associated with the use of a unified mixing space for seventeen different species comprising data generated from multiple tissues and associated TDFs, which remain poorly defined for elasmobranchs. Moreover, this pattern could be driven by variation in isotopic baselines between sampling locations, most likely due to localized nutrient dynamics [81]. If this were the case, baseline $\delta^{15}N$ values would be most impacted among islands of varying population densities with notable differences in run-off and sewage treatment. While we are not able to explicitly explore differences in isotopic baselines among islands using the data presented, the relatively low standard deviations of most elasmobranchs and literature-derived prey stable isotope values used to derive the mixing space, indicate these effects are relatively small. Work by Shipley *et al*. [29] provides the only known compilation of baseline isotope values for the wider Bahamas, which suggested relatively low spatial variation, at least for some primary producers referenced in this study (e.g. seagrass). Further work exploring baseline differences among islands would greatly improve knowledge of local nutrient dynamics and how this impacts isotopic baseline composition, which provides a useful avenue for future work. Finally, we acknowledge the relatively low sample sizes for some species, which pertain largely to species captured from deep-sea environments, such as bluntnose sixgill shark, Atlantic sixgill shark and Mead's catshark. This reflects the logistical challenges associated with sampling deep-water species in remote regions of The Bahamas; this gap will be filled by focused sampling of deep-water species in the future.

5. Conclusion

Across The Bahamas, the assemblage of sub-tropical elasmobranch species occupies a diversity of functional roles that facilitate energy flow across discrete components of the seascape. The observed energetic connectivity between disparate ecosystems, such as connecting neritic waters and the deep-sea are considered to increase overall stability through asynchronous ecosystem effects (see [5]). Marine protected areas, such as The Bahamas shark sanctuary, will have ecological spillover effects extending well beyond habitat and ecosystem boundaries due to the mobile nature of many elasmobranch species [21,22,28,35,36,47,48,61,62,82]. Successful predator conservation efforts in island nations, including the shark sanctuary of The Bahamas, will potentially yield ecological benefits for ecosystem structure, function and resilience, which may catalyze the broader adoption of similar measures across other countries. This is imperative, given many small developing, low-lying nations face continued threats from overfishing [83] combined with the severe effects of global climate change [84], which is likely to intensify throughout much of the Anthropocene. However, despite conservation efforts, many large mobile predators are still being removed from ocean ecosystems in vast quantities [85,86]. Our findings strongly suggest that large-scale removal of predators may decouple intrinsic energetic linkages that are critical for long-term stability.

Ethics. Research was conducted under permits granted from The Bahamas Ministry of Agriculture and Marine Resources (including MAF/FIS/9, MAF/FIS/17 and MAF/FIS/34).

Data accessibility. All data and code supporting this submission can be accessed through the electronic supplementary material.

The data are provided in electronic supplementary material [87].

Authors' contributions. O.N.S.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing; P.M.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; N.E.H.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, writing—original draft, writing—review and editing; A.M.L.B.: data curation, funding acquisition, investigation, resources, writing—review and editing; D.C.: data curation, funding acquisition, investigation, methodology, resources, writing—review and editing; M.G.F.: data curation, funding acquisition, investigation, resources, supervision, writing—review and editing; A.E.G.: data curation, funding acquisition, resources, writing—review and editing; T.L.G.: conceptualization, data curation, funding acquisition, investigation, resources, validation, writing—review and editing; L.A.H.: data curation, funding acquisition, investigation, resources, validation, writing—review and editing; S.K.: data curation, investigation, project administration, resources, validation, writing—review and editing; D.J.M.: data curation, funding acquisition, investigation, methodology, resources, validation, writing—review and editing; O.O.: data curation, funding acquisition, resources, validation, writing—review and editing; N.V.P.: data curation, funding acquisition, investigation, resources, validation, writing—review and editing; M.P.: data curation, funding acquisition, investigation, resources, writing—review and editing; M.J.S.: data curation, funding acquisition, investigation, resources, validation, writing—review and editing; E.V.C.S.: data curation, funding acquisition, investigation, resources, validation, writing—review and editing; B.D.S.: data curation, investigation, resources, validation, writing—review and editing; B.S.T.: data curation, formal analysis, investigation, resources, validation, writing—review and editing; M.W.: data curation, investigation, resources, writing—review and editing; E.J.B.: data curation, funding acquisition, project administration, resources; A.J.G.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Duarte CM *et al.* 2020 Rebuilding marine life. *Nature* **580**, 39–51. (doi:10.1038/s41586-020-2146-7)
2. Tittensor DP *et al.* 2019 Integrating climate adaptation and biodiversity conservation in the global ocean. *Sci. Adv.* **5**, eaay9969. (doi:10.1126/sciadv.aay9969)
3. Bernhardt JR, Leslie HM. 2013 Resilience to climate change in coastal marine ecosystems. *Annu. Rev. Mar. Sci.* **5**, 371–392. (doi:10.1146/annurev-marine-121211-172411)
4. Hooper DU *et al.* 2005 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35. (doi:10.1890/04-0922)
5. Rooney N, McCann K, Gellner G, Moore JC. 2006 Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–269. (doi:10.1038/nature04887)
6. Rooney N, McCann KS. 2012 Integrating food web diversity, structure and stability. *Trends Ecol. Evol.* **27**, 40–46. (doi:10.1016/j.tree.2011.09.001)
7. O'Leary BC, Roberts CM. 2018 Ecological connectivity across ocean depths: implications for protected area design. *Glob. Ecol. Conserv.* **15**, e00431. (doi:10.1016/j.gecco.2018.e00431)
8. Lundberg J, Moberg F. 2003 Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* **6**, 0087–0098. (doi:10.1007/s10021-002-0150-4)
9. McCauley DJ, Young HS, Dunbar RB, Estes JA, Semmens BX, Micheli F. 2012 Assessing the effects

of large mobile predators on ecosystem connectivity. *Ecol. Appl.* **22**, 1711–1717. (doi:10.1890/11-1653.1)

10. Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B. 2016 Megafaunal impacts on structure and function of ocean ecosystems. *Annu. Rev. Environ. Resour.* **41**, 83–116. (doi:10.1146/annurev-environ-110615-085622)
11. Doughty CE, Roman J, Faurby S, Wolf A, Haque A, Bakker ES, Malhi Y, Dunning Jr JB, Svenning JC. 2016 Global nutrient transport in a world of giants. *Proc. Natl Acad. Sci. USA* **113**, 868–873. (doi:10.1073/pnas.1502549112)
12. Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB, Ehrhart LM, Limpus CJ, Suganuma H, Troëng S, Yamaguchi M. 2008 Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Glob. Ecol. Biogeogr.* **17**, 297–304. (doi:10.1111/j.1466-8238.2007.00367.x)
13. Fleming A, Jackson JA. 2011 *Global review of humpback whales (megaptera novaeangliae)*. NOAA Technical Memorandum NMFS-SWFSC-474. La Jolla, CA: Southwest Fisheries Science Center.
14. Dulvy NK *et al.* 2021 Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Curr. Biol.* **31**, 4773–4787. (doi:10.1016/j.cub.2021.08.062)
15. Hammerschlag N *et al.* 2019 Ecosystem function and services of aquatic predators in the Anthropocene. *Trends Ecol. Evol.* **34**, 369–383. (doi:10.1016/j.tree.2019.01.005)
16. Jorgensen SJ *et al.* 2022 Emergent research and priorities for shark and ray conservation. *Endanger. Species Res.* **47**, 171–203. (doi:10.3354/esr01169)
17. Shipley ON, Matich P. 2020 Studying animal niches using bulk stable isotope ratios: an updated synthesis. *Oecologia* **193**, 27–51. (doi:10.1007/s00442-020-04654-4)
18. Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ. 2014 Best practices for use of stable isotope mixing models in food-web studies. *Can. J. Zool.* **92**, 823–835. (doi:10.1139/cjz-2014-0127)
19. Newsome SD, Yeakel JD, Wheatley PV, Tinker MT. 2012 Tools for quantifying isotopic niche space and dietary variation at the individual and population level. *J. Mammal.* **93**, 329–341. (doi:10.1644/11-MAMM-S-187.1)
20. Atwood TB, Connolly RM, Ritchie EG, Lovelock CE, Heithaus MR, Hays GC, Fourqurean JW, Macreadie PI. 2015 Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Change* **5**, 1038–1045. (doi:10.1038/nclimate2763)
21. Gallagher AJ *et al.* 2021a Spatial connectivity and drivers of shark habitat use within a large marine protected area in the Caribbean, The Bahamas Shark Sanctuary. *Front. Mar. Sci.* **1223**, 1–15.
22. Gallagher AJ, Alsudairy NA, Shea BD, Payne NL, Duarte CM. 2021b First Application of 360-Degree Camera Technology to Marine Predator Bio-Logging. *Front. Mar. Sci.* **8**, 707376. (doi:10.3389/fmars.2021.707376)
23. Gallagher AJ *et al.* 2022 Tiger sharks support the characterization of the world's largest seagrass ecosystem. *Nat. Commun.* **13**, 6328. (doi:10.1038/s41467-022-33926-1)
24. Rosenblatt AE, Heithaus MR, Mather ME, Matich P, Nifong JC, Ripple WJ, Silliman BR. 2013 The roles of large top predators in coastal ecosystems: New insights from long term ecological research. *Oceanography* **26**, 155–167. (doi:10.5670/oceanog.2013.59)
25. Lavery TJ, Roudnew B, Gill P, Seymour J, Seuront L, Johnson G, Mitchell JG, Smetacek V. 2010 Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proc. R. Soc. B* **277**, 3527–3531. (doi:10.1098/rspb.2010.0863)
26. Visser F, Merten VJ, Bayer T, Oudejans MG, de Jonge DSW, Puebla O, Reusch TBH, Fuss J, Hoving HJT. 2021 Deep-sea predator niche segregation revealed by combined cetacean biologging and eDNA analysis of cephalopod prey. *Sci. Adv.* **7**, eabf5908.
27. Madigan DJ, Brooks EJ, Bond ME, Gelsleichter J, Howey LA, Abercrombie DL, Brooks A, Chapman DD. 2015 Diet shift and site-fidelity of oceanic whitetip sharks Carcharhinus longimanus along the Great Bahama Bank. *Mar. Ecol. Prog. Ser.* **529**, 185–197. (doi:10.3354/meps11302)
28. Shipley ON, Polunin NV, Newman SP, Sweeting CJ, Barker S, Witt MJ, Brooks EJ. 2017a Stable isotopes reveal food web dynamics of a data-poor deep-sea island slope community. *Food Webs* **10**, 22–25. (doi:10.1016/j.fooweb.2017.02.004)
29. Shipley ON *et al.* 2018 Trophic niche dynamics of three nearshore benthic predators in The Bahamas. *Hydrobiologia* **813**, 177–188.
30. Brooks EJ, Sims DW, Danylchuk AJ, Sloman KA. 2013 Seasonal abundance, philopatry and demographic structure of Caribbean reef shark (Carcharhinus perezi) assemblages in the north-east Exuma Sound, The Bahamas. *Mar. Biol.* **160**, 2535–2546. (doi:10.1007/s00227-013-2246-0)
31. Brooks EJ, Brooks AM, Williams S, Jordan LK, Abercrombie D, Chapman DD, Howey-Jordan LA, Grubbs RD. 2015 First description of deep-water elasmobranch assemblages in the Exuma Sound, The Bahamas. *Deep Sea Res. Part II* **115**, 81–91. (doi:10.1016/j.dsr2.2015.01.015)
32. Smukall MJ, Guttridge TL, Dhellemmes F, Seitz AC, Gruber SH. 2021 Effects of leader type and gear strength on catches of coastal sharks in a longline survey around Bimini, The Bahamas. *Fish. Res.* **240**, 105989. (doi:10.1016/j.fishres.2021.105989)
33. Gallagher AJ, Staaterman ER, Cooke SJ, Hammerschlag N. 2017 Behavioural responses to fisheries capture among sharks caught using experimental fishery gear. *Can. J. Fish. Aquat. Sci.* **74**, 1–7. (doi:10.1139/cjfas-2016-0165)
34. Hussey NE *et al.* 2017 Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions. *Proc. R. Soc. B* **284**, 20170166. (doi:10.1098/rspb.2017.0166)
35. Howey-Jordan LA, Brooks EJ, Abercrombie DL, Jordan LK, Brooks A, Williams S, Gospodarczyk E, Chapman DD. 2013 Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (Carcharhinus longimanus) in the western North Atlantic. *PLoS ONE* **8**, e56588. (doi:10.1371/journal.pone.0056588)
36. Howey LA *et al.* 2016 Into the deep: the functionality of mesopelagic excursions by an oceanic apex predator. *Ecol. Evol.* **6**, 5290–5304. (doi:10.1002/ece3.2260)
37. O'Shea OR, Ward CRE, Brooks EJ. 2017 Range extension in Styracura (= Himantura) schmardae (Caribbean whiptail stingray) from The Bahamas. *Caribb. Nat.* **38**, 1–8.
38. Ebert DA, Dando M, Fowler S. 2021 *Sharks of the world*. Princeton, NJ, USA: Princeton University Press.
39. Kim SL, del Rio CM, Casper D, Koch PL. 2012 Isotopic incorporation rates for shark tissues from a long-term captive feeding study. *J. Exp. Biol.* **215**, 2495–2500. (doi:10.1242/jeb.070656)
40. Caut S, Jowers MJ, Michel L, Lepoint G, Fisk AT. 2013 Diet-and tissue-specific incorporation of isotopes in the shark Scyliorhinus stellaris, a North Sea mesopredator. *Mar. Ecol. Prog. Ser.* **492**, 185–198. (doi:10.3354/meps10478)
41. MacNeil MA, Drouillard KG, Fisk AT. 2006 Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. *Can. J. Fish. Aquat. Sci.* **63**, 345–353. (doi:10.1139/f05-219)
42. Malpica-Cruz L, Herzka SZ, Sosa-Nishizaki O, Lazo JP. 2012 Tissue-specific isotope trophic discrimination factors and turnover rates in a marine elasmobranch: empirical and modeling results. *Can. J. Fish. Aquat. Sci.* **69**, 551–564. (doi:10.1139/f2011-172)
43. Galvan DE, Jañez J, Irigoyen AJ. 2016 Estimating tissue-specific discrimination factors and turnover rates of stable isotopes of nitrogen and carbon in the smallnose fanskate Sympterygia bonapartii (Rajidae). *J. Fish Biol.* **89**, 1258–1270. (doi:10.1111/jfb.13024)
44. Hussey NE, Brush J, McCarthy ID, Fisk AT. 2010 Δ15N and Δ13C diet–tissue discrimination factors for large sharks under semi-controlled conditions. *Comp. Biochem. Physiol. A: Mol. Integr. Physiol.* **155**, 445–453. (doi:10.1016/j.cbpa.2009.09.023)
45. Hussey NE, MacNeil MA, Olin JA, McMeans BC, Kinney MJ, Chapman DD, Fisk AT. 2012 Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. *J. Fish Biol.* **80**, 1449–1484. (doi:10.1111/j.1095-8649.2012.03251.x)
46. Carlisle AB, Litvin SY, Madigan DJ, Lyons K, Bigman JS, Ibarra M, Bizzarro JJ. 2017 Interactive effects of urea and lipid content confound stable isotope analysis in elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* **74**, 419–428. (doi:10.1139/cjfas-2015-0584)
47. Shipley ON *et al.* 2017b Polar compounds preclude mathematical lipid correction of carbon stable isotopes in deep-water sharks. *J. Exp. Mar. Biol. Ecol.* **494**, 69–74. (doi:10.1016/j.jembe.2017.05.002)
48. Shipley O, Brooks EJ, Madigan DJ, Sweeting CJ, Dean Grubbs R. 2017c Stable isotope analysis in deep-sea chondrichthyans: recent challenges,

ecological insights, and future directions. *Rev. Fish Biol. Fish.* **27**, 481–497. (doi:10.1007/s11160-017-9466-1)

49. Hamilton BR, Shipley ON, Grubbs RD. 2022 Multi-channel feeding by migratory sharks in a fluvial-dominated estuary. *Estuarine Coastal Shelf Sci*. **275**, 107977.
50. Madigan DJ, Shipley ON, Carlisle AB, Dewar H, Snodgrass OE, Hussey NE. 2021 Isotopic tracers suggest limited trans-oceanic movements and regional residency in North Pacific blue sharks (*Prionace glauca*). *Front. Mar. Sci.* **8**, 653606. (doi:10.3389/fmars.2021.653606)
51. Murchie KJ, Haak CR, Power M, Shipley ON, Danylchuk AJ, Cooke SJ. 2019 Ontogenetic patterns in resource use dynamics of bonefish (*Albula vulpes*) in the Bahamas. *Environ. Biol. Fishes* **102**, 117–127. (doi:10.1007/s10641-018-0789-0)
52. Shipley ON, Lee CS, Fisher NS, Burruss G, Frisk MG, Brooks EJ, Zuckerman ZC, Herrmann AD, Madigan DJ. 2019 Trophodynamics and mercury bioaccumulation in reef and open-ocean fishes from The Bahamas with a focus on two teleost predators. *Mar. Ecol. Prog. Ser.* **608**, 221–232. (doi:10.3354/meps12798)
53. Zhu Y, Newman SP, Reid WD, Polunin NV. 2019 Fish stable isotope community structure of a Bahamian coral reef. *Mar. Biol.* **166**, 1–14. (doi:10.1007/s00227-018-3447-3)
54. Gillis AJ, Ceriani SA, Seminoff JA, Fuentes MM. 2018 Foraging ecology and diet selection of juvenile green turtles in the Bahamas: insights from stable isotope analysis and prey mapping. *Mar. Ecol. Prog. Ser.* **599**, 225–238. (doi:10.3354/meps12635)
55. Vander Zanden HB, Arthur KE, Bolten AB, Popp BN, Lagueux CJ, Harrison E, Campbell CL, Bjorndal KA. 2013 Trophic ecology of a green turtle breeding population. *Mar. Ecol. Prog. Ser.* **476**, 237–249. (doi:10.3354/meps10185)
56. Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX. 2018 Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* **6**, e5096. (doi:10.7717/peerj.5096)
57. Pielou EC. 1975 *Ecological diversity*. New York, NY: John Wiley & Sons.
58. Charrad M, Ghazzali N, Boiteau V, Niknafs A. 2014 NbClust: an R package for determining the relevant number of clusters in a data set. *J. Stat. Softw.* **61**, 1–36. (doi:10.18637/jss.v061.i06)
59. Eckrich CA, Albeke SE, Flaherty EA, Bowyer RT, Ben-David M. 2020 rKIN: Kernel-based method for estimating isotopic niche size and overlap. *J. Anim. Ecol.* **89**, 757–771. (doi:10.1111/1365-2656.13159)
60. Albeke SE. 2017 *rKIN: (kernel) isotope niche estimation*. R package version 0.1.
61. Shipley ON, Howey LA, Tolentino ER, Jordan LK, Brooks EJ. 2017e Novel techniques and insights into the deployment of pop-up satellite archival tags on a small-bodied deep-water chondrichthyan. *Deep Sea Res. Part I* **119**, 81–90. (doi:10.1016/j.dsr.2016.11.005)
62. Shipley ON, Howey LA, Tolentino ER, Jordan LK, Ruppert JL, Brooks EJ. 2017d Horizontal and vertical movements of Caribbean reef sharks (*Carcharhinus perezi*): conservation implications of limited migration in a marine sanctuary. *R. Soc. Open Sci.* **4**, 160611. (doi:10.1098/rsos.160611)
63. Gallagher AJ, Amon DJ, Bervoets T, Shipley ON, Hammerschlag N, Sims DW. 2020 The Caribbean needs big marine protected areas. *Science* **367**, 749–749. (doi:10.1126/science.abb0650)
64. Mumby PJ, Hastings A. 2008 The impact of ecosystem connectivity on coral reef resilience. *J. Appl. Ecol.* **45**, 854–862. (doi:10.1111/j.1365-2664.2008.01459.x)
65. Manlick PJ, Maldonado K, Newsome SD. 2021 Competition shapes individual foraging and survival in a desert rodent ensemble. *J. Anim. Ecol.* **90**, 2806–2818. (doi:10.1111/1365-2656.13583)
66. Coni EO, Booth DJ, Ferreira CM, Nagelkerken I. 2022 Behavioural generalism could facilitate coexistence of tropical and temperate fishes under climate change. *J. Anim. Ecol.* **91**, 86–100. (doi:10.1111/1365-2656.13599)
67. Morris JR, Allhoff KT, Valdovinos FS. 2021 Strange invaders increase disturbance and promote generalists in an evolving food web. *Sci. Rep.* **11**, 1–12. (doi:10.1038/s41598-020-79139-8)
68. Andrzejaczek S *et al.* 2022 Diving into the vertical dimension of elasmobranch movement ecology. *Sci. Adv.* **8**, eabo1754. (doi:10.1126/sciadv.abo1754)
69. Chapman DD, Pikitch EK, Babcock EA, Shivji MS. 2007 Deep-diving and diel changes in vertical habitat use by Caribbean reef sharks Carcharhinus perezi. *Mar. Ecol. Prog. Ser.* **344**, 271–275. (doi:10.3354/meps06941)
70. Andrzejaczek S, Gleiss AC, Jordan LK, Pattiaratchi CB, Howey LA, Brooks EJ, Meekan MG. 2018 Temperature and the vertical movements of oceanic whitetip sharks, *Carcharhinus longimanus*. *Scientific Reports* **8**, 8351.
71. Joyce TW, Durban JW, Claridge DE, Dunn CA, Fearnbach H, Parsons KM, Andrews RD, Ballance LT. 2017 Physiological, morphological, and ecological tradeoffs influence vertical habitat use of deep-diving toothed-whales in the Bahamas. *PLoS ONE* **12**, e0185113. (doi:10.1371/journal.pone.0185113)
72. Graham F, Rynne P, Estevanez M, Luo J, Ault JS, Hammerschlag N. 2016 Use of marine protected areas and exclusive economic zones in the subtropical western North Atlantic Ocean by large highly mobile sharks. *Diversity and Distributions* **22**, 534–546. (doi:10.1111/ddi.12425)
73. Brunnschweiler JM, Queiroz N, Sims DW. 2010 Oceans apart? Short-term movements and behaviour of adult bull sharks Carcharhinus leucas in Atlantic and Pacific Oceans determined from pop-off satellite archival tagging. *J. Fish Biol.* **77**, 1343–1358. (doi:10.1111/j.1095-8649.2010.02757.x)
74. Claridge D, Dunn C, Ylitalo G, Herman D, Durban J, Parsons K. 2015 *Behavioral ecology of deep-diving odontocetes in The Bahamas. (draft final report RC-2114)*. Marsh Harbor, Abaco, The Bahamas: Bahamas Marine Mammal Organization, p. 132.
75. Lübcker N, Whiteman JP, Millar RP, De Bruyn PJ, Newsome SD. 2020 Fasting affects amino acid nitrogen isotope values: a new tool for identifying nitrogen balance of free-ranging mammals. *Oecologia* **193**, 53–65. (doi:10.1007/s00442-020-04645-5)
76. Laxson CJ, Condon NE, Drazen JC, Yancey PH. 2011 Decreasing urea∶ trimethylamine N-oxide ratios with depth in chondrichthyes: a physiological depth limit? *Physiol. Biochem. Zool.* **84**, 494–505. (doi:10.1086/661774)
77. Shipley ON, Olin JA, Whiteman JP, Bethea DM, Newsome SD. 2022 Bulk and amino acid nitrogen isotopes suggest shifting nitrogen balance of pregnant sharks across gestation. *Oecologia* **199**, 313–328.
78. Rooney N, McCann K, Gellner G, Moore JC. 2006 Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–269.
79. Rooney N, McCann KS. 2012 Integrating food web diversity, structure and stability. *Trends Ecol. Evol.* **27**, 40–46.
80. Smith JA, Mazumder D, Suthers IM, Taylor MD. 2013 To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. *Methods Ecol. Evol.* **4**, 612–618.
81. Matich P, Shipley ON, Weideli OC. 2021 Quantifying spatial variation in isotopic baselines reveals size-based feeding in a model estuarine predator: implications for trophic studies in dynamic ecotones. *Mar. Biol.* **168**, 1–12. (doi:10.1007/s00227-021-03920-0)
82. Guttridge TL *et al.* 2017 Philopatry and regional connectivity of the great hammerhead shark, Sphyrna mokarran in the US and Bahamas. *Front. Mar. Sci.* **4**, 3. (doi:10.3389/fmars.2017.00003)
83. Ward-Paige CA, Mora C, Lotze HK, Pattengill-Semmens C, McClenachan L, Arias-Castro E, Myers RA. 2010 Large-scale absence of sharks on reefs in the greater-Caribbean: a footprint of human pressures. *PloS one* **5**, e11968. (doi:10.1371/journal.pone.0011968)
84. Taylor MA, Stephenson TS, Chen AA, Stephenson KA. 2012 Climate change and the Caribbean: Review and response. *Caribbean studies* **40**, 169–200. (doi:10.1353/crb.2012.0020)
85. McCauley DJ, Pinsky ML, Palumbi SR, Estes JA, Joyce FH, Warner RR. 2015 Marine defaunation: animal loss in the global ocean. *Science* **347**, 1255641. (doi:10.1126/science.1255641)
86. Roff G, Brown CJ, Priest MA, Mumby PJ. 2018 Decline of coastal apex shark populations over the past half century. *Communications Biology* **1**, 223.
87. Shipley ON *et al.* 2023 Energetic connectivity of diverse elasmobranch populations – implications for ecological resilience. Figshare. (doi:10.6084/m9.figshare.c.6471283)