



Energetic consequences of resource use diversity in a marine carnivore

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Abstract

Understanding how intraspecific variation in the use of prey resources impacts energy metabolism has strong implications for predicting long-term fitness and is critical for predicting population-to-community level responses to environmental change. Here, we examine the energetic consequences of variable prey resource use in a widely distributed marine carnivore, juvenile sand tiger sharks (*Carcharias taurus*). We used carbon and nitrogen isotope analysis to identify three primary prey resource pools—demersal omnivores, pelagic forage, and benthic detritivores and estimated the proportional assimilation of each resource using Bayesian mixing models. We then quantified how the utilization of these resource pools impacted the concentrations of six plasma lipids and how this varied by ontogeny. Sharks exhibited variable reliance on two of three predominant prey resource pools: demersal omnivores and pelagic forage. Resource use variation was a strong predictor of energetic condition, whereby individuals more reliant upon pelagic forage exhibited higher blood plasma concentrations of very low-density lipoproteins, cholesterol, and triglycerides. These findings underscore how intraspecific variation in resource use may impact the energy metabolism of animals, and more broadly, that natural and anthropogenically driven fluctuations in prey resources could have longer term energetic consequences.

Keywords Ecophysiology · Stable isotope analysis · Bayesian mixing model · Nutritional condition · Elasmobranch

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Introduction

Intraspecific variation in dietary resource use is a central theme in ecology due to its role in modulating population dynamics, community assembly, and ecosystem-level processes like food-web coupling and stabilization (Devictor et al. 2010; Costa-Pereira et al. 2018; Manlick and Newsome 2021). Foraging at the individual-level can dictate these processes most proximately through energetic condition that leads to diet-mediated variation in fitness at the population-level (Long et al. 2014; Costa-Pereira et al. 2018). This variation is thought to underpin selection and adaptation required for long-term persistence of species and their ecological function(s), such that a diversity of foraging strategies can buffer populations from environmental stochasticity (i.e., portfolio effects; Watanuki 1992; Woo et al. 2008). Given the rapid rate at which many ecosystems are changing due to human development and global climate change (Perry et al. 2005; Prober et al. 2019), quantifying mechanistic links between diet variation, energetic condition, and fitness is key to predicting how individuals and populations may respond

to fluctuations in the availability of prey resources (Bastille-Rousseau et al. 2018; Manlick et al. 2021).

Ecologists have long recognized that individuals exhibit significant differences in diets (Bolnick et al. 2011), and adaptive foraging theory predicts that animals adjust foraging strategies relative to conspecifics to maximize fitness (Pyke 1984; Layman et al. 2007; Loeuille 2010; Beckerman et al. 2010). For example, individual foraging specialization is often presumed to be an adaptive, fitness maximizing foraging strategy, and early theory predicted that energetic status, and therefore fitness, is maximized when consumers specialize on the most abundant or nutritious prey (Stephens and Krebs 1986; Holbrook and Schmidt 1992; Valera et al. 2005; Gremillet et al. 2008). In aquatic ecosystems, a consumer's available prey resource pool may be supported by energy originating from several, distinct, prey resource pools or 'energy channels' (e.g., C_3 , C_4 , or detrital; McCauley et al. 2012), which can promote fitness diversity among prey and higher consumers. The energetic consequences of resource use diversity have been previously observed in cape gannets (*Morus capensis*) where a greater consumption of pelagic forage fishes relative to fisheries offal promoted greater chick survival (Gremillet et al. 2008). Further, utilization of diverse prey resource pools has also been linked to long-term persistence of several skate species (Barbini et al. 2020). Although there are clear linkages between dietary resource use variation, energetic condition, and fitness, patterns in marine fishes remain largely unexplored, in part due to the challenges of measuring fine-scale ecological processes in marine taxa that often traverse great expanses of ocean.

Approaches based on biochemical tracers have revolutionized our understanding of both dietary and energetic patterns in animals that are otherwise challenging to study in-situ (Newsome et al. 2007, 2012; Fleming et al. 2018; Shipley and Matich 2020). Stable isotope analysis has become particularly effective for studying the ecology of individuals (e.g., Newsome et al. 2012; Reum et al. 2020; Manlick et al. 2021; Matich et al. 2021), where quantitative measures of intraspecific diet variation can be determined by measuring tissues with different isotopic incorporation rates (e.g., Maldonado et al. 2017) or identifying the geometric position of individuals relative to each other in a dietary mixing space (Newsome et al. 2012). The analysis of physiological tracers in consumer tissues can also be used to quantify energetic condition. For example, free-circulating plasma lipid concentrations, such as triglycerides (TAGs), cholesterol (CHOL), free fatty acids (FFAs), and associated lipoprotein fractions (Kaduce and Folk 2002; Gallagher et al. 2014, 2017) can provide an effective, non-lethal assessment of energetic condition. Such evaluations have been applied to fishes (Gallagher et al. 2017; Hammerschlag et al. 2018),

marine mammals (Kaduce and Folk 2002; Whiteman et al. 2013), and birds (Jenni-Eiermann and Jenni 1994).

The interpretation of plasma lipid concentrations is highly complex, often taxon-specific, and may vary with various environmental and biological characteristics. For some taxa, elevated concentrations may reflect individuals of better nutritional condition, as is typically seen in sharks (e.g., Gallagher et al. 2017) and teleost fishes (Eldøy et al. 2021). For example, strong relationships between TAG, morphometric body condition, and reproductive status were observed in tiger sharks (*Galeocerdo cuvier*, Gallagher et al. 2014; Hammerschlag et al. 2018), while several plasma lipids were found to respond to life-history stage, sex, and season in several species of coastal shark (Gallagher et al. 2017; Moorhead et al. 2021). Conversely, elevated plasma lipid concentrations indicate poorer nutritional condition in animals like mammals or birds that exhibit tissue catabolism during energetically demanding events like migration (Jenni-Eiermann and Jenni 1994) or fasting (Kaduce and Folk 2002). Although plasma lipid concentrations are useful for tracing the energetic conditions of animals (e.g., Rangel et al. 2021), a marriage of isotope and blood lipid analyses is lacking, despite clear potential for providing mechanistic links between diet variation and energetic condition.

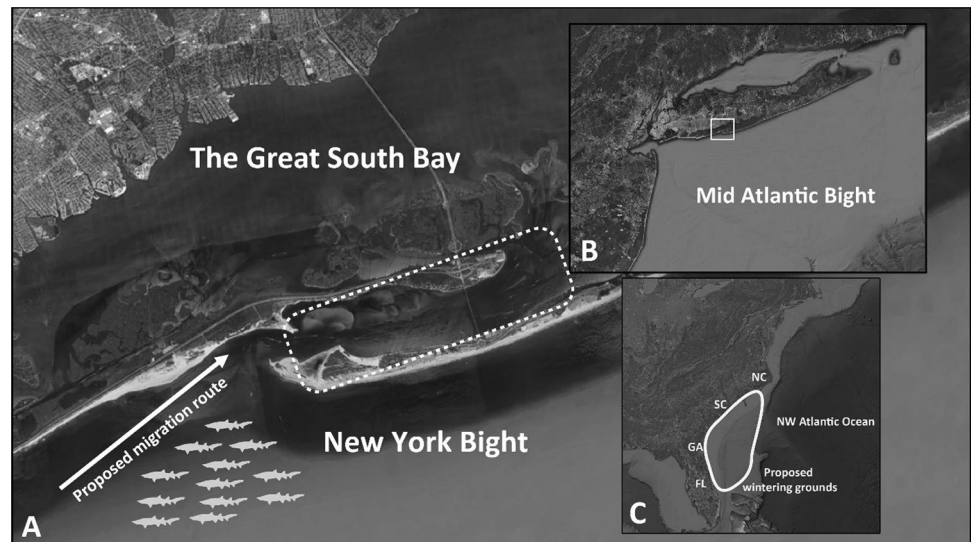
Here, we combine carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis with measurement of lipid concentrations (TAGs, CHOL, and lipoprotein fractions) in blood plasma to explore the energetic consequences of dietary resource use variation in a widely distributed marine carnivore, the sand tiger shark (*Carcharias taurus*). During summer residency periods in temperate estuaries, we identified three primary prey resource pools for sand tiger sharks—demersal omnivores, pelagic forage, and benthic detritivores. We predicted that energetic status may respond to the differential utilization of prey resource pools given known differences in energy densities of potential prey species throughout northwestern Atlantic (Lawson et al. 1998; Lamb et al. 2017). Considering natural and human-driven fluctuations in prey resources (Hillborn et al. 2017; Bartley et al. 2019), evaluating the energetic consequences of diet variation is critical to predicting how organisms may respond to ongoing environmental change.

Methods

Animal sampling

Research was undertaken in the Great South Bay (GSB), New York, USA (Fig. 1). Juvenile sand tiger sharks were captured using static rod and reel angling. Upon capture, individuals were secured alongside the research vessel

Fig. 1 A Sampling location (white dashed box) of juvenile sand tiger sharks in the Great South Bay, New York, relative to **B** the Mid-Atlantic Bight and **C** proposed southern winter grounds (adapted from Shipley et al. 2021a, b). Source: The Great South Bay and NE US Seaboard, Google Earth, Accessed 1/18/21



and morphometric measurements and sex were recorded. Approximately, 6 mL of whole blood was drawn from the caudal vein and centrifuged immediately to isolate blood plasma. Some samples ($n = 7$) were stored in a vacutainer lined with lithium heparin anticoagulant on ice for up to 6 h before centrifugation. This was assumed to elicit no impact on blood chemistry panels of isotopic analysis based on recommended best practices (Lemons et al. 2012; Weideli et al. 2019). Upon return to the laboratory blood was centrifuged for 10 min at 3000g to separate constituents (red blood cells, white blood cells and blood plasma/serum). Blood plasma samples were stored in 1.0 ml aliquots, at -80°C .

Potential prey species for juvenile sand tiger sharks (e.g., finfish and mobile invertebrates) were collected during an otter trawl survey conducted in 2015 (see Olin et al. 2020; Shipley et al. 2021a, b for specific methodologies). Upon collection, all fishes and mobile invertebrates were measured; total length for fishes and penaeids and disk width for rays and decapods (to the nearest mm). All individuals were stored on ice in the field and then stored frozen upon return to the laboratory (-20°C) until further preparation for stable isotope analysis. We acknowledge moderate sample sizes for some prey groups and that opportunistic sampling may not account for the total prey resources utilized by sharks in the study system.

Stable isotope analysis

For sand tiger sharks, approximately 2 mL of blood plasma was oven dried at 60°C for 72 h and ground to a fine powder using a mortar and pestle. Following recommendations of Kim and Koch (2012), we did not undertake any chemical extraction techniques on shark blood plasma because very few evaluations have been performed. Approximately 0.35–0.45 mg of ground tissue was weighed into

4×6 mm tin capsules. The relative abundance of carbon and nitrogen stable isotope ratios were determined using a Delta V Plus isotope ratio mass spectrometer coupled to a Flash elemental analyzer (EA-IRMS, Thermo Scientific). Ratios were normalized to standard reference materials of Vienna Pee Dee Belemnite (V-PDB) for Carbon and AIR for Nitrogen. Analytical precision based on certified reference materials (IU L-Glutamic Acid, USGS65, and IAEA-600) did not exceed 0.09‰ and 0.17‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Blood plasma samples from an initial candidate dataset of $n = 64$ individuals were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

For prey, muscle tissue was sub-sampled (~ 1.0 g), oven dried at 60°C for 48 h, and ground into a fine powder using a mortar and pestle. Lipids were removed from all samples prior to isotopic analysis using a modified method outlined by Bligh and Dyer (1959): twice vortexing the pulverized tissue in 2 ml of 2:1 chloroform:methanol solution for 24 h and decanting the solvent. The remaining solvent was evaporated under a fume hood for 24 h. Relative abundances of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) isotopes were determined on ~ 0.5 mg sub-samples sealed in tin capsules on a Thermo Finnigan Delta V Plus mass-spectrometer (Thermo Finnigan, San Jose, California, USA) coupled with an elemental analyzer (Costech, Valencia, California, USA). Analytical precision based on the standard deviation of replicate analyses of four standards [NIST 1577c; internal standard; USGS 40; Urea ($n = 27$ for all)], measured $\leq 0.13\text{‰}$ for $\delta^{15}\text{N}$ and $\leq 0.18\text{‰}$ for $\delta^{13}\text{C}$ for all the standards. Instrumentation accuracy checked throughout the period that these samples were analyzed was based on NIST standards 8573, 8547 and 8574 for $\delta^{15}\text{N}$ and 8542, 8573, 8574 for $\delta^{13}\text{C}$ ($n = 10$ for all). The mean difference from the certified values were -0.09 , 0.14 , 0.03‰ for $\delta^{15}\text{N}$ and 0.14 , -0.03 and -0.09‰ for $\delta^{13}\text{C}$, respectively.

Analysis of blood plasma lipids

Shark blood plasma was also analyzed for a subset of individuals ($n=35$) for concentrations of six plasma lipids used as indices for nutritional condition in fish: triglycerides (TAG); cholesterol (CHOL); high, low, and very low-density lipoproteins (HDL, LDL, VLDL); and lipoprotein-a (LP-a). Cholesterol and triglyceride levels were determined using a Vitros 250 analyzer (Ortho, Rochester, NY). Cholesterol electrophoresis was performed using the Helena SPIFE 3000 system utilizing the Vis cholesterol profile kit (Helena Laboratories Inc., Beaumont, TX). The procedure provided by the electrophoresis analysis system and cholesterol profile kit were followed. Samples were separated on an agarose gel using 4-nitro blue tetrazolium staining. Results were produced following gel scanning and analysis by manufacturer software. Four fractions were delimited (fractions 1–4) and correspond with similar mammalian fractions: Fraction 1—high-density lipoprotein (HDL), Fraction 2—lipoprotein(a) [LP(a)], Fraction 3—very low-density lipoprotein (VLDL), and Fraction 4—low-density lipoprotein (LDL). Manufacturer software determined percentages for each fraction and absolute values (mg/dL) were determined by multiplying the percentage by the cholesterol concentration. Both analyzers were maintained, and quality control samples were used per manufacturer recommendations.

Statistical analyses

All statistical analyses were conducted in R (v 4.0.0, R Core Team 2020) and statistical significance assigned at $\alpha=0.05$; isotope data supporting these analyses are found in Shipley et al. (2021a).

Stable isotope clocks to define time-since-estuarine-arrival

Recent work has illustrated that juvenile sand tiger sharks migrate from southern wintering grounds off Florida and the Carolinas (Kneebone et al. 2014) into the New York estuaries during the early summer, and at the time of sampling may not have reached isotopic steady state with the local prey resource base (Shipley et al. 2021a). We therefore adopted a nitrogen isotopic clock approach based on Shipley et al. (2021a) to characterize whether individuals were likely to have reached isotopic steady state with the local prey resource base and remove individuals violating the steady state assumption. Nitrogen isotopes were selected, because discrimination of carbon isotopes between the NW Atlantic shelf and GSB estuary is less distinct due to the diverse array of primary producers that support both benthic and pelagic food-web across estuarine-to-marine gradients

(e.g., mix of phytoplankton and submarine grasses) (Shipley et al. 2021a).

The isotopic clock was defined by:

$$t_i = \frac{\ln\left(\frac{\delta_{0i} - \delta_{fi}}{\delta_i - \delta_{fi}}\right)}{\lambda_i} \quad (1)$$

where t = the time-since-estuarine-arrival, δ_0 and δ_f represent the isotope ratios of juvenile sand tiger sharks at steady state with the prior (southern wintering grounds) and new location (GSB estuary), λ is the rate of isotopic incorporation for the analyzed tissue (average rate change per day), and i represents 1000 resampling iterations from the mean

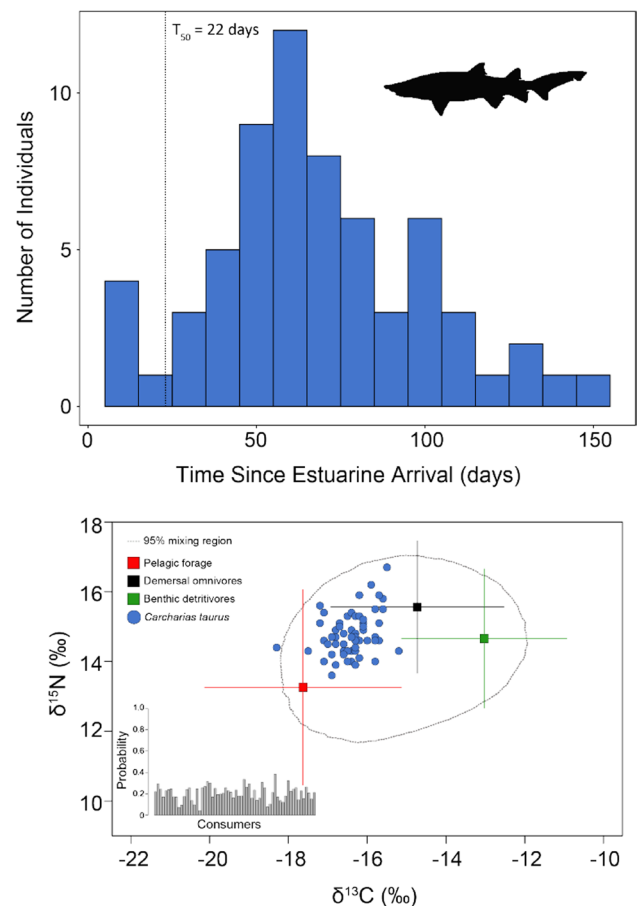


Fig. 2 Top panel: histogram of time-since-estuarine arrival estimates (t_i) derived from nitrogen stable isotope clocks. Note that one steady state individual for which isotope clock measurements could not be computed is not shown (where $\delta_i > \delta_f$). Vertical line highlights the cut-off point where individuals were unlikely to be at isotopic steady state with the estuarine prey base based on estimates of T_{50} (<22 days). Bottom Panel: sand tiger shark stable isotope values in relation to the three prey groups. Gray line represents 95% confidence region for the mixing polygon based on 10,000 model iterations. Inset highlights the individual level probability of falling within the mixing space, sharks with probabilities <0.05 were removed from subsequent analyses ($n=1$)

and standard deviation assuming a Gaussian distribution. We parameterized nitrogen isotopic clocks to calculate single-point time-since-estuarine arrival estimates (median values) for juvenile sand tiger sharks following the previously validated model of Shipley et al. (2021a). All individuals that were predicted to have been resident for less than T_{50} ($T_{50} = \text{LN}(2)/\lambda$) were removed from further analyses (Fig. 2).

To estimate δ_0 , we used the isotopic composition of blacktip sharks (*Carcharhinus limbatus*, $\delta^{15}\text{N} = 12.7 \pm 1.0\text{‰}$), a functionally equivalent species with similar dietary preferences found within the known wintering grounds of juvenile sand tiger sharks (Cortés 1999; Morgan et al. 2020). Estimation of δ_f is based on addition of published diet tissue discrimination factors to $\delta^{15}\text{N}$ values of potential prey [winter flounder (*Pseudopleuronectes americanus*), weakfish (*Cynoscion regalis*), and summer flounder (*Paralichthys dentatus*)] sampled from the GSB ($\delta^{15}\text{N} = 13.4 \pm 1.0\text{‰}$). The assigned trophic discrimination factors (TDFs) were literature derived values of 2.2‰ based on the weighted mean of TDFs published for shark blood plasma (Table 1). This differed from the primary model of Shipley et al. (2021a), given that lower TDFs generally provided a more conservative estimate of residency. This resulted in a δ_f value of $15.6 \pm 1.0\text{‰}$, representing the isotopic composition of juvenile sand tiger sharks at isotopic steady state with the GSB estuary. The isotopic incorporation rate constant (λ) was $0.0165 \pm 0.003 \text{ day}^{-1}$ based on values published from an experimental study of leopard sharks (*Triakis semifasciata*, Kim et al. 2012a).

Following a diet/habitat shift, the most significant isotopic changes occur within the isotopic half-life T_{50} of the measured tissue (Martinez del Rio et al. 2012; Thomas et al. 2015; Vander Zanden et al. 2015). Therefore, we calculated

the range of T_{50} estimates from λ values ($T_{50} = \text{LN}(2)/\lambda$) reported from individual leopard sharks in Kim et al. (2012a), which ranged from ~22 to ~87 days. All individuals that had been resident in the GSB for <22 days were removed from subsequent analyses; this provided a conservative cut off point to ensure all remaining sharks were likely at, or close to, isotopic steady state with the GSB prey base. For one individual with a $\delta^{15}\text{N}$ value of 16.7‰, isotopic clocks could not be computed, because this individual fell beyond the isotopic mixing space (i.e., $\delta_t > \delta_f$), thus it was assumed that this individual was at isotopic steady state with the GSB. Several individuals were recaptured across subsequent years, but these were treated as independent fish for isotopic clock purposes, because of interannual variation in the timing of migrations, and expected ontogenetic shifts in diets.

The isotopic clock model revealed that four individuals were recent migrants into the GSB (i.e., $t_i = 7\text{--}14$ days), which fell below the lower estimates of T_{50} for shark blood plasma (~22 days); these individuals were subsequently removed from all further analyses (Fig. 2).

Analysis of blood plasma lipids

We used Pearson's correlation to examine the relationships between the concentrations of different types of plasma lipids, to gain insight into their mechanistic functions, and assess shark nutritional condition (see full justification in Table 2). We assumed that higher levels of blood plasma lipids (e.g., TAG and CHOL) were indicative of individuals in better nutritional condition, given previous validation in elasmobranchs (Gallagher et al. 2017) and teleosts (Congleton and Wagner 2006; Eldøy et al. 2021, Table 2).

Table 1 Trophic discrimination factors (TDFs) from elasmobranch captive feeding studies

		Fin ^{4,5,7} (‰)	Muscle ^{1–5,7} (‰)	Red blood cells ^{2,3,5} (‰)	Whole blood ^{5,6} (‰)	Plasma ^{2,3,5,6} (‰)	Liver ^{1,4} (‰)
$\Delta^{13}\text{C}$	Mean _w	3.64	2.48	1.88	2.58	3.05	2.06
	Min	1.06	0.52	1.22	1.70	2.14	– 1.00
	Max	5.41	4.28	2.80	3.30	3.70	2.40
	Mean _{Adj}	5.28	1.96	2.63	NA	3.17	0.22
$\Delta^{15}\text{N}$	Mean _w	0.43	1.98	2.44	2.11	2.16	1.42
	Min	– 1.95	– 1.81	0.70	1.80	0.42	0.96
	Max	2.89	5.50	4.60	2.50	4.20	2.04
	Mean _{Adj}	2.57	3.28	3.87	NA	3.08	1.50

Values include weighted means (Mean_w) based on study-specific sample sizes, minimum and maximum reported TDFs, and adjusted weighted means based on sample sizes for studies at least 365 days in duration. NA no published DTDF studies were conducted for ≥ 365 days

1—Hussey et al. (2010), 2, 3—Kim et al. (2012a, b), 4—Malpica-Cruz et al. (2012), 5—Caut et al. (2013), 6—Galvan et al. (2016a, b), 7—Wyatt et al. (2019)

Table 2 Definitions and justification for inclusion of plasma lipids as predictor variables in Bayesian stable isotope mixing models to examine the nutritional consequences of individual level diet variation

Predictor	Definition and justification	Supporting literature
Triglycerides (TAG)	Main source of metabolic fuel in fishes, where higher concentrations have been found to indicate <i>better</i> nutritional condition in sharks (Gallagher et al. 2017). TAG concentrations were validated as a nutritional proxy in shortbelly rockfish (<i>Sebastes jordani</i>), rainbow trout (<i>Oncorhynchus mykiss</i>), brown trout (<i>Salmo trutta</i>), and chinook salmon (<i>Oncorhynchus tshawytscha</i>)	Ballantyne (1997), Norton et al. (2001), Congleton and Wagner (2006), Gallagher et al. (2017), Eldøy et al. (2021)
Cholesterol (CHOL)	Structural lipid and critical component of cell membranes. Some studies associate high cholesterol concentrations with good nutritional condition in sharks and poor nutritional condition in mammals and birds, reflecting tissue catabolism (i.e., breakdown of structural lipids in the absence of TAG)	Carballo et al. (2005), Congleton and Wagner (2006), Gallagher et al. (2017)
TAG:CHOL	Indicates the ratio of free circulating relative to structural lipids. In fishes, higher TAG:CHOL is typically associated with individuals of better nutritional condition	Amara and Galois (2004), Gallagher et al. (2017)
High density lipoproteins (HDL)	Transporter of excess cholesterol back to the liver, where it is catabolized and then excreted. High concentrations signify animals in better nutritional condition	
Lipoprotein-a (LP)	Cholesterol-rich and resemble LDLs. Higher concentrations may represent excess cholesterol signifying animals in better nutritional condition	
Low density lipoproteins (LDL); very low-density lipoproteins (VLDL)	Generally found at high concentrations in elasmobranch plasma and represent major constituent of blood plasma proteins. Sharks use LDLs and VLDLs to transport free fatty acids, predominantly lipoprotein fraction Palmitic acid (LCFA). High concentrations of LDLs and VLDLs may indicate greater transport of fatty acids in sharks of better nutritional condition, especially if LDLs and VLDLs correlate with TAG concentrations	Tartu et al. (2017), Speers-Roesche et al. (2010)

Note that we assume higher levels of plasma lipids are associated with stronger nutritional condition in juvenile sand tiger sharks, as individuals are unlikely to be in a catabolic state (i.e., fasting)

Bayesian mixing models

We used an isotopic endmember approach (McCauley et al. 2012; Phillips et al. 2014) to categorize prey into three, broad resource functional groups associated with different energy pathways (pelagic versus benthic): pelagic forage ($n = 17$), demersal omnivores ($n = 160$), and benthic detritivores ($n = 11$; Table 3). Prey resource pools were defined by life-history, feeding modes, and their isotope ratios. Pelagic forage included species reliant upon planktonic primary producers (e.g., butterfish [*Peprilus triacanthus*], ribbed mussels [*Geukensia* spp.]; Table 3). Demersal omnivores included species using both planktonic and benthic resource pools (e.g., summer flounder [*Paralichthys dentatus*], squid [*Loligo* spp.]; Table 3). Benthic species included those that forage exclusively on benthic resources, such as seagrasses and associated detrital components (e.g., caridean shrimp [*Crangon* spp.]; Table 3). We simulated prey mixing polygons (Smith et al. 2013) based on 10,000 resampling iterations from the mean and SD of all three prey groups to evaluate their appropriateness for characterizing the dietary space of juvenile sand tiger sharks. For individuals assumed to be approaching or have reached isotopic steady state with the GSB, a single individual was $> 95\%$ likely to fall beyond the prey mixing space and was subsequently removed from the remaining analyses (Fig. 2). Therefore, a total of $n = 34$ individuals were carried forward into Bayesian mixing models.

Simulated mixing polygons (Smith et al. 2013) revealed that juvenile sand tiger sharks clustered between pelagic forage and demersal omnivore resource pools (Fig. 2); therefore, we removed benthic detritivores and assumed

a two-endmember mixing scenario. Bayesian stable isotope mixing models were implemented using the R package ‘MixSIAR’ (Stock et al. 2018) to quantify potential relationships between intraspecific diet variability (i.e., an individual’s reliance upon the two prey resource pools) and nutritional condition. Despite correlations between many of the nutritional assays (Fig. 3), all were included as individual candidate predictors because MixSIAR uses a leave-one-out cross validation (LOOic) and Akaike weights to quantify the strongest predictor/s of resource use variability (Stock et al. 2018). Nine candidate models were run, which were compared to a null model (i.e., no predictors). Because teleosts and elasmobranchs (sharks, skates, and rays) are known to exhibit diet shifts as they grow (Jennings et al. 2002; Galvan et al. 2010; Matich et al. 2021; Shipley et al. 2019), the models included a categorical, fixed effect of size class. Here, we calculated the median fork length of sampled individuals (median = 121.5 cm) and categorized those < 121.5 cm as ‘small’ and those > 121.5 cm as ‘large’. The remaining models included the fixed effect of size class, in addition to each nutritional assay as a single continuous predictor. We also included a single model including the fixed effect of sampling year, to account for potential annual variation in shark stable isotope values.

Mixing models incorporated both process*residual error and 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 using Gelman diagnostics, where parameters should equal ~ 1.0 (Stock et al. 2018), and generally not exceed 1.05. Trophic discrimination factors for sand tiger sharks were assigned as 2.2‰ and 3.05‰ for

Fig. 3 **A** Box and whisker plots for seven nutritional markers measured in the blood plasma of juvenile sand tiger ($n = 34$): TAG Triglycerides, CHOL Cholesterol, HDL High density lipoproteins, LP Lipoprotein-a, LDL Low density lipoproteins, VLDL very low-density lipoproteins. Solid horizontal line is the median, boxes are 25th and 75th percentiles, and whiskers are $1.5 \times \text{IQR}$, open circles are outliers. **B** Pearson correlation coefficients between each nutritional assay, circles are only shown for significant correlations at $\alpha = 0.05$, circle size is scaled to the correlation coefficient and color represents the direction (i.e., positive or negative) of the correlation coefficient

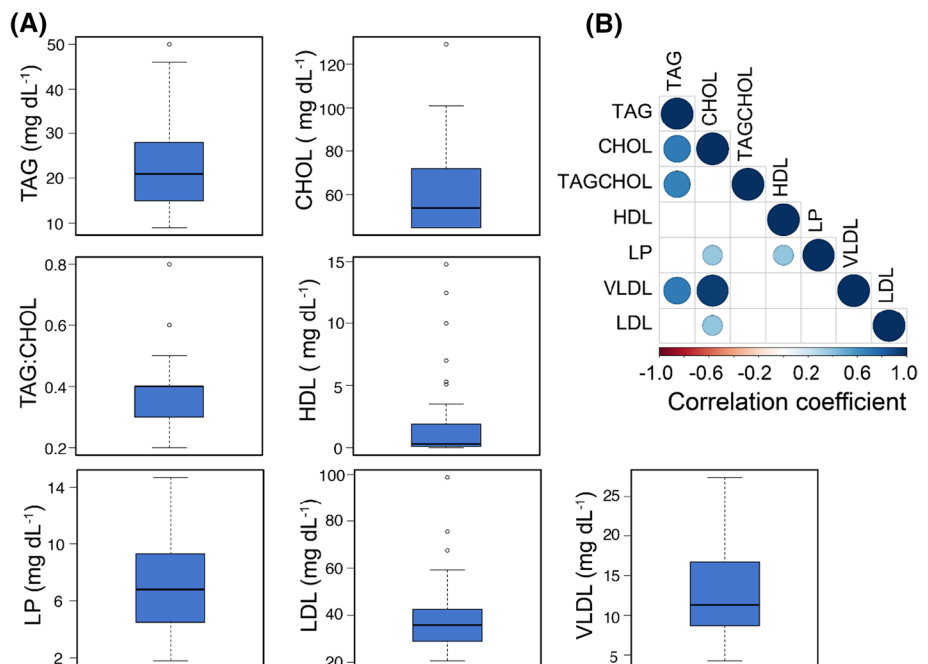


Table 3 Summary of carbon and nitrogen stable isotope values (mean \pm 1 SD) measured in common prey items sampled in the Great South Bay, New York, USA

Group	Common name	Scientific name	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Pelagic forage	Atlantic menhaden	<i>Brevoortia tyrannus</i>	1	−20.8	9.5
	Butterfish	<i>Peprilus triacanthus</i>	7	−19.7 (0.8)	12.2 (1.7)
	Scup	<i>Stenotomus chrysops</i>	2	−19.7 (0.8)	12.6 (0.2)
	Ribbed mussel	<i>Geukensia</i> spp.	7	−22.2 (1.2)	9.7 (0.3)
		Group mean (\pm SD)	17	−20.8 (1.5)	11.1 (1.8)
Demersal omnivores	Summer flounder	<i>Paralichthys dentatus</i>	42	−17.2 (1.0)	13.6 (13.6)
	Squid	<i>Loligo</i> spp.	22	−18.5 (0.8)	13.8 (0.5)
	Winter flounder	<i>Pseudopleuronectes americanus</i>	37	−17.8 (1.3)	12.8 (0.9)
	Bluefish	<i>Pomatomus saltatrix</i>	12	−18.4 (0.7)	13.9 (0.9)
	Striped sea robin	<i>Prionotus evolans</i>	15	−17.6 (0.5)	13.2 (0.7)
	Weakfish	<i>Cynoscion regalis</i>	25	−18.4 (0.8)	13.5 (0.9)
	Tautog	<i>Tautoga onitis</i>	7	−18.1 (2.1)	13.7 (1.0)
		Group Mean (\pm SD)	160	−17.9 (1.2)	13.4 (0.9)
Benthic detritivores	Crangon	<i>Crangon</i> spp.	7	−16.4 (1.4)	13.1 (0.6)
	Northern puffer	<i>Sphoeroides maculatus</i>	2	−15.8 (1.8)	12.4 (0.4)
	Pipefish	<i>Syngnathus fuscus</i>	2	−15.9 (1.4)	12.4 (1.4)
	Gastropod	<i>Tritia</i> spp.	3	−16.3 (0.1)	11.1 (0.1)
		Group mean (\pm SD)	14	−16.2 (1.1)	12.5 (1.0)

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively; these estimates were based on weighted means calculated from published TDFs for shark blood plasma from the scientific literature (Table 1). Each TDF was assigned a standard deviation of $\pm 1.0\text{‰}$, given their high uncertainty for elasmobranchs (e.g., Hussey et al. 2010; Kim et al. 2012b; Olin et al. 2013) and more generally, across the animal kingdom (Caut et al. 2009; Shipley and Matich 2020).

To contextualize Bayesian mixing model results in terms of energetic dynamics, we reviewed the literature to summarize reported values of prey energy densities for potential prey items of juvenile sand tiger sharks. Studies

were restricted to the northwest Atlantic and are reported in kJ g^{-1} WW.

Results

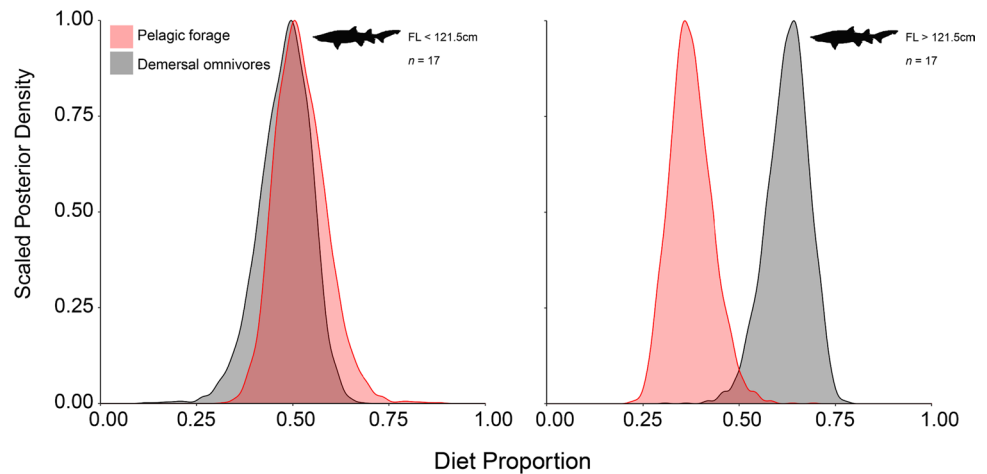
Time-since-estuarine arrival estimates ranged from (median = 23 \rightarrow 149 days, Fig. 2). These individuals were assumed to be approaching or have reached full isotopic steady state with the GSB prey ecosystem, supporting their inclusion in Bayesian stable isotope mixing models (see below).

Table 4 Summary statistics comparing six candidate Bayesian stable isotope mixing models to evaluate the nutritional implications of diet variation in juvenile sand tiger sharks

Model	LOOic	SE (LOOic)	ΔLOOic	SE (ΔLOOic)	<i>w</i>	ξ_{C}	ξ_{N}
Size class + VLDL	42.6	14.7	0	—	0.736	0.1	0.2
Size class + CHOL	45.6	14.3	3.0	2.5	0.164	0.1	0.2
Size class + TAG	47.5	14.3	4.9	3.4	0.064	0.1	0.2
Size class	50.5	15.5	7.9	6.6	0.014	0.1	0.2
Size class + LP	52.0	15.0	9.4	6.1	0.007	0.1	0.2
Size class + TAG:CHOL	52.5	15.7	9.9	6.1	0.005	0.1	0.2
Size class + HDL	52.6	15.2	10.0	6.4	0.005	0.1	0.2
Size class + LDL	52.7	15.6	10.1	7.0	0.005	0.1	0.2
Null	60.8	16.1	18.5	8.6	0.000	0.2	0.2
Sampling year	61.9	16.8	19.3	7.7	0.000	0.2	0.2

Models are ordered based on LOOic scores and associated Akaike weights (*w*). Table also highlights LOOic standard error (SE), the difference in LOOic between subsequent models (ΔLOOic), and the associated standard error. ξ_j represent multiplicative error terms for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, where lower values imply a high proportion of variance is explained by predictor variables (Stock et al. 2018)

Fig. 4 Posterior density distributions for juvenile sand tiger sharks across small and large size classes illustrating reliance upon pelagic forage and demersal omnivore resource pools. Posterior density distributions are for the two individuals with the median VLDL concentrations (most likely model based on LOOic criteria and Akaike weights) from each size class and are synonymous to a ‘population level’ estimate of resource use



Plasma lipids concentrations of juvenile sand tiger sharks ($n = 34$) assumed to be close to, or at isotopic steady state with the GSB estuary were: TAG ($\mu = 22.4 \pm 10.4$ mg dL⁻¹), CHOL ($\mu = 60.5 \pm 19.3$ mg dL⁻¹), TAG:CHOL ($\mu = 0.4 \pm 0.1$), HDL ($\mu = 2.0 \pm 3.8$ mg dL⁻¹), LP ($\mu = 7.0 \pm 3.2$ mg dL⁻¹), VLDL ($\mu = 38.8 \pm 16.1$ mg dL⁻¹), and LDL ($\mu = 12.6 \pm 5.6$ mg dL⁻¹) (Fig. 3A). We found several statistically significant, positive correlations between plasma lipids (Fig. 3B). Statistically significant correlations were observed between TAG and CHOL ($r = 0.705$, $p < 0.001$), TAG:CHOL ($r = 0.678$, $p < 0.001$), and VLDLs ($r = 0.706$, $p < 0.001$). Positive correlations were also observed between CHOL and LP-a ($r = 0.381$, $p = 0.026$), LDL ($r = 0.391$, $p = 0.022$), and VLDL ($r = 0.950$, $p < 0.001$) (Fig. 3B). Finally, LP-a was positively correlated with HDL ($r = 0.393$, $p = 0.022$) (Fig. 3B).

Mixing models revealed that juvenile sand tiger sharks relied upon varying degrees of demersal omnivores and pelagic forage prey pools (Fig. 4). The top model carried 74% of the weight and showed that individuals consuming higher proportions of pelagic forage had higher concentrations of blood plasma VLDLs, and this relationship was consistent across both size classes (Table 4, Fig. 5). Models including size class + CHOL and size class + TAG carried 15% and 8% of the weights, respectively (Table 4, Fig. 5). Like VLDLs, both CHOL and TAG concentrations were higher in sharks that exhibited greater reliance upon pelagic forage compared to demersal omnivores. These trends were slightly more prominent in the smaller, relative to the larger size class (Fig. 5).

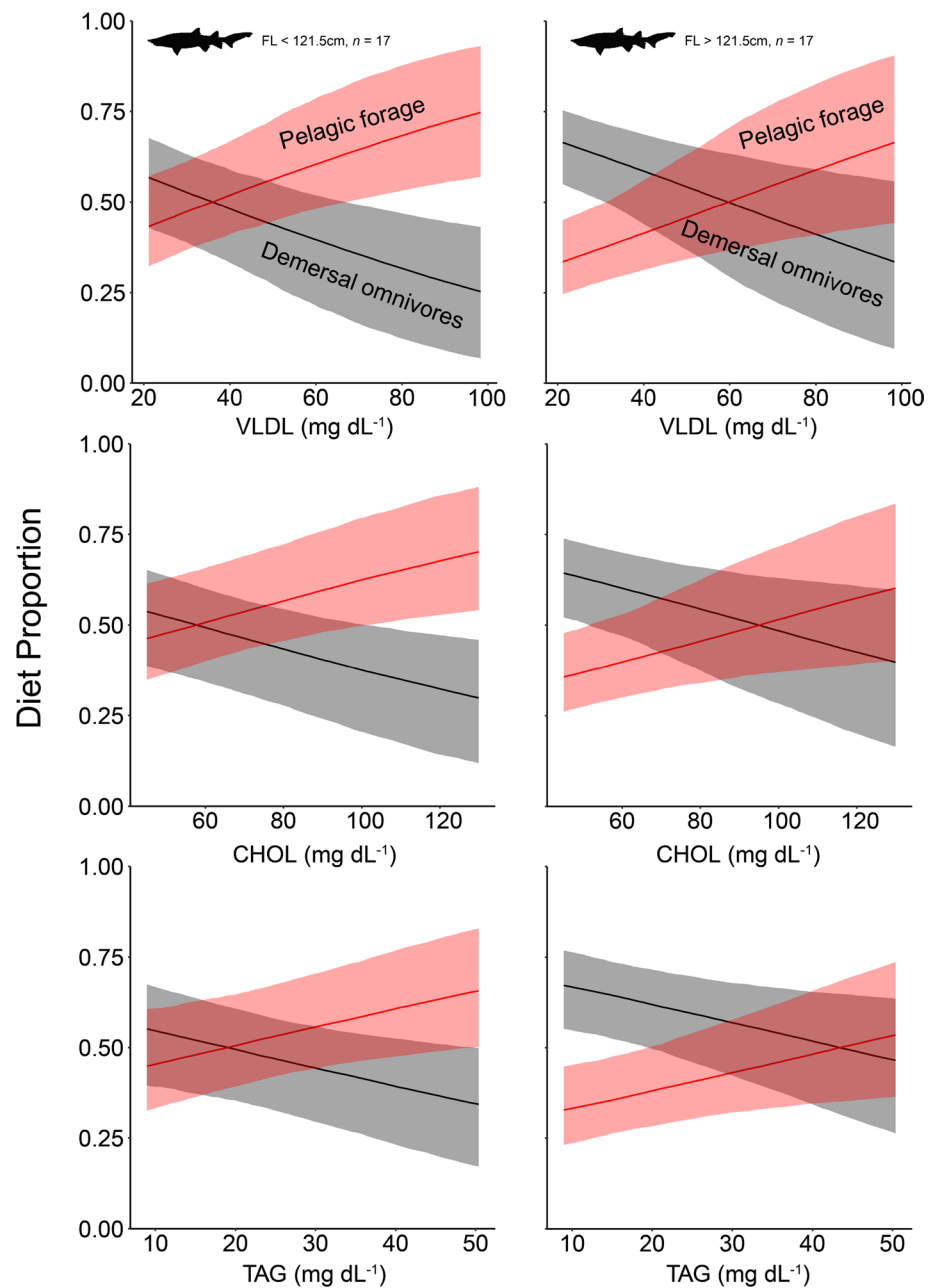
Literature-derived estimates of energy densities for potential sand tiger shark prey were highly variable. However, on average, pelagic forage prey resources exhibited the highest energy densities (5.4 ± 1.7 kJ g⁻¹), followed by demersal omnivores (4.6 ± 0.9 kJ g⁻¹) and benthic detritivores (4.2 ± 0.5 kJ g⁻¹) (Table 5).

Discussion

Intraspecific dietary variation may have profound effects on energetic status, potentially leading to fitness variation in wild populations. Therefore, assessing the energetic consequences of different foraging strategies may enhance our understanding of how populations may respond to changes in food webs resultant from climate change and human disturbance (Toft 1999; Bolnick et al. 2003; Costa-Pereira et al. 2018, 2019; Manlick et al. 2021). Here, we found that juvenile sand tiger sharks exhibiting a greater reliance upon pelagic forage resources had higher concentrations of blood VLDVs, CHOL, and TAG relative to those more reliant upon demersal omnivores or a mix of the two prey resource pools. These findings suggest that differential utilization of available prey resource pools may have energetic consequences that promote nutritional diversity between conspecifics, with potential implications for longevity and fitness.

As predicted, the energetic status of juvenile sand tiger sharks responded strongly to the differential use of available prey resource pools between conspecifics, and we hypothesize that variation in energetic condition may result from differences in energy densities between specific prey items (see Table 5). For example, quintessential pelagic forage fishes, such as Atlantic mackerel, menhaden, and herring are often associated with higher energy densities relative to more omnivorous prey such as cod and croaker (Elliott and Gaston 2008; Spitz and Jouma 2013; Lamb et al. 2017). It is therefore plausible that utilization of prey with greater energy density on average may drive higher concentrations of plasma lipids in juvenile sand tiger sharks. Though we acknowledge that a suite of environmental and biological factors may drive variation in plasma lipid concentrations of vertebrates, we hypothesize that higher concentrations in juvenile sand tiger sharks may indicate higher energetic status for several reasons. First, there is little evidence to

Fig. 5 Relationship between individual diet variability and plasma lipid concentrations in small and larger size classes of juvenile sand tiger sharks ($n = 34$). Results illustrate the most three likely models that included the effects of size class and VLDL (LOOic = 42.6, $w = 0.735$), CHOL (LOOic = 45.8, $w = 0.148$), and TAG (LOOic = 47.0, $w = 0.081$), respectively (see Table 4)



suggest that juvenile sharks undergo periods of fasting and/or starvation, which was found to drive higher TAG concentrations in larger vertebrates such as polar bears (Kaduce and Folk 2002). Second, though lipid metabolite concentrations have been linked to reproductive status in sharks (Hammerschlag et al. 2018; Rangel et al. 2021), all of the individuals sampled in this study were juveniles, suggesting that reproductive status was unlikely to impact the energetic condition of individuals. Finally, there are a growing number of studies that have validated the use of plasma lipid concentrations as a proxy for condition in sharks (Gallagher et al. 2014, 2017; Hammerschlag et al. 2018) and teleosts (Ballantyne 1997; Norton et al. 2001; Congleton and Wagner 2006; Eldøy et al.

2021, see Table 1). While the drivers of plasma lipid concentrations should certainly be further explored, data presented here suggests that diet variation may elicit, at the very least, a first order control on the energetic status of juvenile sand tiger sharks.

The differential utilization of prey resource pools with different energy densities, could potentially drive fitness variation between individuals if the implications for energetic status are significant. For example, the decision to migrate, and the timing of migrations, has been linked to nutritional condition in anadromous brown trout (*Salmo trutta*), where individuals exhibiting lower concentrations of TAGs, indicative of poorer energetic condition, spent more time at sea

Table 5 Summary of prey energy density values for northwest Atlantic species reported in the scientific literature

Species	<i>n</i>	Resource pool	Location	ED	References
Brown shrimp	2	Benthic detritivores	Northern Gulf of Mexico	3.9 (0.3)	Lamb et al. (2017)
Pink shrimp	4	Benthic detritivores	Northern Gulf of Mexico	4.2 (0.6)	Lamb et al. (2017)
Spot	9	Benthic detritivores	Northern Gulf of Mexico	4.8 (1.7)	Lamb et al. (2017)
Striped mullet	7	Benthic detritivores	Northern Gulf of Mexico	3.9 (0.6)	Lamb et al. (2017)
Northern shrimp	33	Benthic detritivores	North Atlantic	4.8 (0.5)	Lawson et al. (1998)
Decapods	2	Benthic detritivores	Canadian Arctic	3.5 (0.5)	Elliott and Gaston (2008)
Average				4.2 (0.5)	
Atlantic Croaker	47	Demersal omnivorous fish and squid	Northern Gulf of Mexico	4.0 (0.8)	Lamb et al. (2017)
Pinfish	21	Demersal omnivorous fish and squid	Northern Gulf of Mexico	4.6 (0.7)	Lamb et al. (2017)
Red Drum	1	Demersal omnivorous fish and squid	Northern Gulf of Mexico	4.5	Lamb et al. (2017)
Ribbonfish	12	Demersal omnivorous fish and squid	Northern Gulf of Mexico	5.0 (0.7)	Lamb et al. (2017)
Sand seatrout	9	Demersal omnivorous fish and squid	Northern Gulf of Mexico	3.5 (0.2)	Lamb et al. (2017)
Blue whiting	74	Demersal omnivorous fish and squid	Bay of Biscay	4.9 (0.8)	Spitz and Jouma (2013)
Atlantic cod	106	Demersal omnivorous fish and squid	North Atlantic	4.2 (0.6)	Lawson et al. (1998)
American plaice	37	Demersal omnivorous fish and squid	North Atlantic	4.3 (0.5)	Lawson et al. (1998)
Arctic cod	79	Demersal omnivorous fish and squid	North Atlantic	4.4 (0.8)	Lawson et al. (1998)
Redfish	54	Demersal omnivorous fish and squid	North Atlantic	5.4 (0.8)	Lawson et al. (1998)
Greenland halibut	48	Demersal omnivorous fish and squid	North Atlantic	5.5 (1.1)	Lawson et al. (1998)
Daubed shanny	16	Demersal omnivorous fish and squid	North Atlantic	5.9 (1.4)	Lawson et al. (1998)
Squid Illex	32	Demersal omnivorous fish and squid	North Atlantic	5.9 (0.6)	Lawson et al. (1998)
Squid Gonatus	47	Demersal omnivorous fish and squid	North Atlantic	6.9 (1.8)	Lawson et al. (1998)
Daubed shanny	6	Demersal omnivorous fish and squid	Canadian Arctic	5.0 (0.2)	Elliott and Gaston (2008)
Gymnelus spp.	7	Demersal omnivorous fish and squid	Canadian Arctic	4.1 (0.2)	Elliott and Gaston (2008)
Fourline snakeblenny	3	Demersal omnivorous fish and squid	Canadian Arctic	3.2 (0.4)	Elliott and Gaston (2008)
Arctic cod	16	Demersal omnivorous fish and squid	Canadian Arctic	4.7 (0.2)	Elliott and Gaston (2008)
Sculpin	16	Demersal omnivorous fish and squid	Canadian Arctic	4.3 (0.2)	Elliott and Gaston (2008)
Atlantic poacher	5	Demersal omnivorous fish and squid	Canadian Arctic	3.5 (0.3)	Elliott and Gaston (2008)
Gonatus squid	2	Demersal omnivorous fish and squid	Canadian Arctic	3.5 (1.5)	Elliott and Gaston (2008)
Average				4.6 (0.9)	
Atlantic Menhaden	67	Pelagic forage	Northern Gulf of Mexico	4.5 (1.2)	Lamb et al. (2017)
Bay anchovy	20	Pelagic forage	Northern Gulf of Mexico	4.1 (0.2)	Lamb et al. (2017)
Dusky anchovy	1	Pelagic forage	Northern Gulf of Mexico	4.4	Lamb et al. (2017)
Scaled sardine	2	Pelagic forage	Northern Gulf of Mexico	5.2 (0.4)	Lamb et al. (2017)
Striped anchovy	9	Pelagic forage	Northern Gulf of Mexico	4.9 (0.4)	Lamb et al. (2017)
Thread herring	8	Pelagic forage	Northern Gulf of Mexico	4.9 (0.7)	Lamb et al. (2017)
Atlantic mackerel	49	Pelagic forage	Bay of Biscay	7.5 (1.5)	Spitz and Jouma (2013)
Sand lance	44	Pelagic forage	North Atlantic	4.4 (0.8)	Lawson et al. (1998)
Capelin	84	Pelagic forage	North Atlantic	8.4 (3.3)	Lawson et al. (1998)
Altantic herring	40	Pelagic forage	North Atlantic	9.4 (1.4)	Lawson et al. (1998)
Arctic shanny	5	Pelagic forage	Canadian Arctic	4.1 (0.1)	Elliott and Gaston (2008)
Capelin	17	Pelagic forage	Canadian Arctic	4.9 (0.2)	Elliott and Gaston (2008)
Sand Lance	8	Pelagic forage	Canadian Arctic	5.1 (0.1)	Elliott and Gaston (2008)
Atlantic menhaden	200	Pelagic forage	Chesapeake Bay	3.9 (0.9)	Rippeto (1993)
Average				5.4 (1.7)	

Energy densities are reported in kJ g⁻¹ WW and average represent mean of means

and migrated further offshore to sustain the energetic condition necessary for seasonal reproduction (Eldøy et al. 2021). Understanding how resource use and subsequent nutritional

condition influences the performance and timing of important ecological events therefore presents a critical focus for future work, especially in slow growing species where

survival to adulthood is a strong determinant of population growth (Otway et al. 2004; Frisk et al. 2005; Taborsky 2006; Pardo et al. 2016).

Diet-mediated behavior and fitness have broader implications for predicting how consumers will respond to natural and anthropogenically driven changes in prey abundance and nutritional quality. Recent projections suggest continued fisheries exploitation and climate change will drive significant shifts in the distribution and abundance of pelagic forage species (Hilborn et al. 2017), with the potential for disrupting energy transfer across marine food webs (Rosen and Trites 2000; Essington et al. 2006; von Biela et al. 2019). For example, population declines due to a deteriorating nutritional condition in Alaskan Steller sea lions (*Eumetopias jubatus*) was attributed to climate and fisheries-induced reduction of pelagic forage diversity in sea lion diets (Merrick et al. 1997; Rosen and Trites 2000). These dynamics have the capacity to magnify given recent climate projections (e.g., Arimitsu et al. 2021, IPCC 2021), but the approaches outlined herein can illuminate the mechanistic links between diet and energetic status, and potentially fitness consequences required to predict how populations may respond to ongoing global change.

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Author contribution statement ONS, PJM, ALN, SDN, and JAO conceived project. ONS, JAO, ALN, JL, HW, and MC conducted fieldwork. ONS, JAO, AN, and GAH conducted laboratory analyses. ONS and PM analyzed the data. MGF, JAO, JAN, and RMC provided project funding. ONS wrote the paper with significant input from PJM, SDN, and JAO. All authors provided additional comments and approved the final version of the manuscript.

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Availability of data and materials All materials are available from the corresponding author upon request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval All research was conducted under state permits acquired by the Wildlife Conservation Society and Stony Brook University from the New York State Department for Environmental Conservation (NYDEC) License to Collect or Possess: Scientific, permits nos. 1036; 1409; 1145; 1110, and 2305.

Consent to participate Not applicable.

Consent for publication Not applicable.

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