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A global perspective on the trophic geography of sharks

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Supplementary Information Guide

Supplementary Figure 1: Simulated effect of trophic attenuation: The black points show two 12-month cycles of $\delta^{13}C$ values of phytoplankton production simulated by the Magozzi, et al. [1] NEMO MEDUSA isotopic extension for the North East Atlantic around the coast of west Ireland, a region characterised by a strong seasonal plankton bloom. Note the pronounced enrichment in $\delta^{13}C$ values associated with bloom conditions in May-July. Dashed black line indicates the biomass-weighted annual average $\delta^{13}C$ POM value, the relatively positive average $\delta^{13}C$ value indicating that the bulk of all production occurs during bloom conditions. Animals feeding at successive trophic levels are simulated assuming constant feeding levels through the year and a trophic fractionation factor of 1 per mille. For trophic level (TL) 2 (red), an isotopic incorporation rate of 2 months was assumed, for TL 3 (blue) the incorporation rate is 4 months and for TL 4 (green) it is 6 months. Note that by TL 4 even the pronounced seasonal fluctuations in $\delta^{13}C$ POM values of >3 per mille are essentially attenuated to less than 0.5 per mille through successive temporal smoothing, and the biomass weighted annual average is a reasonable approximation. In reality attenuation is likely to be more pronounced as feeding is not constant through the year but weighted to times of year with greater production.

Supplementary Figure 2: Latitudinal trends in mean $\delta^{13}C$ values (with standard deviation bars) for shelf shark species (and one oceanic species: *C. longimanus*) that have the potential to migrate over multiple habitats (i.e either shelf and deep-sea habitats or shelf and oceanic habitats). Each point represents mean values for a population within an individual study with each colour corresponding to a different species. The latitudinal $\delta^{13}C$ regression observed for oceanic shark muscle is also provided (dashed blue). 500 Monte Carlo iterations of the latitudinal trends in $\delta^{13}C_P$ observed in shelf sharks, considering the variance within each Longhurst Biogeographic Province (dark grey solid lines), and the latitudinal trends predicted for $\delta^{13}C_S$ with a trophic offset of 4.6 per mille (red solid lines - see Methods section and Figure 2).

Supplementary Figure 3: a): Boxes represent extent of environmental chlorophyll *a* (Chl *a*) and sea surface temperature (SST) data used to calculate latitudinal trends for each ha. Blue points represent locations of oceanic shark samples. Chl *a* **(b)** and SST **(c)** for median sampling year, 2009, within oceanic waters. Bold vertical line represents median value for

that latitudinal bin, box represents 50% spread of the data and horizontal lines are the 95% confidence intervals. Latitude where abrupt shift in environmental data occurs shown with dashed grey line.

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Linking the $\delta^{13}C$ values of sharks to simulated $\delta^{13}C$ values of phytoplankton

The stable isotopic composition of a consumer's tissue reflects a time-integrated average of the composition of primary production fuelling the base of the food web, modified by isotopic fractionation during metabolism (i.e. preferential excretion of light isotopes and resulting enrichment of heavy isotopes in assimilated body proteins). We therefore consider four variables when predicting carbon stable isotopic compositions in shark tissues:
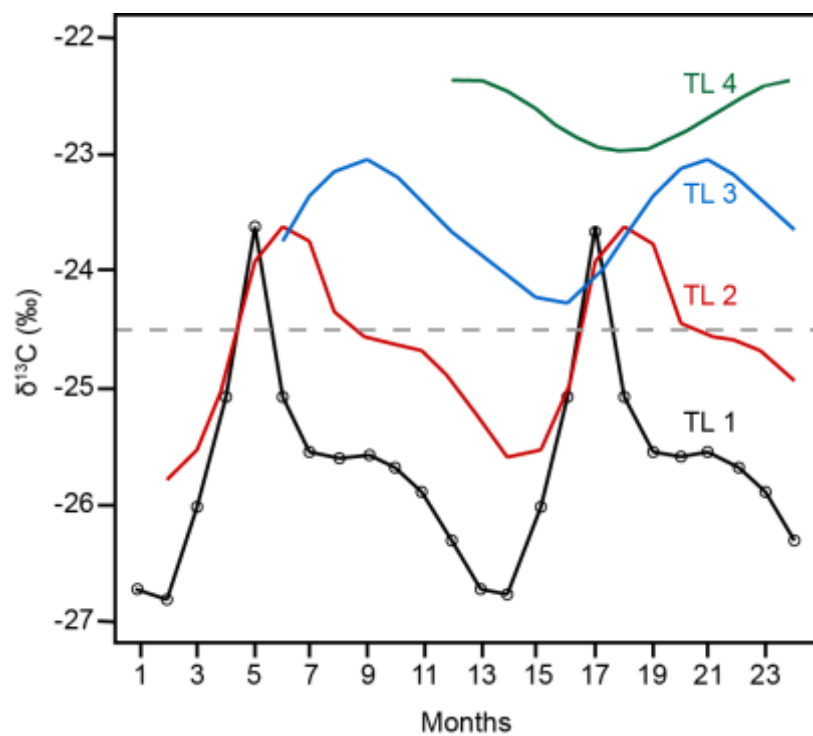
1. Variation in the isotopic composition of primary production between Longhurst Biogeographic Provinces.
2. Spatio-temporal variation of primary production within Longhurst Biogeographic Provinces.
3. Trophic fractionation between sharks and primary production.
4. Turnover rate of shark tissues, and implications for stable isotopes.

To determine the variation in the stable isotopic composition of carbon in primary production between Longhurst Biogeographic Provinces, we took biomass-weighted annual average predictions of $\delta^{13}C$ values at one-degree intervals, and calculated the median of the annually averaged $\delta^{13}C$ values within each biogeographic province. The biomass-weighted annual average simply weights the stable isotopic composition of diatoms and non-diatoms predicted at monthly intervals by the proportion of total annual production produced in that month [1]. Thus in temperate latitudes with seasonal plankton blooms, the biomass weighted average is closer to the isotopic composition of plankton grown under bloom conditions.

The use of annual (biomass weighted) average $\delta^{13}C_P$ values could in theory complicate spatial interpretations, however seasonal short-term variations in primary production $\delta^{13}C$ values are attenuated through food chains, as the isotopic incorporation (turnover) rate increases with body size, and thus trophic level in size structured marine ecosystems. As an illustration, we simulate temporal fluctuations in the stable isotopic compositions of successive trophic levels sustained by phytoplankton in temperate latitudes characterised by extreme seasonal variations in $\delta^{13}C_P$ values (Supplementary Figure 1). We simulate the $\delta^{13}C$ values in tissues of consumers at sequential trophic levels with isotopic equilibration rates of two, four, and six months respectively. By trophic level three (with an isotopic equilibration rate of six months, which is lower than predicted for most sharks), the amplitude of seasonal fluctuations in $\delta^{13}C$ values is reduced from >6 per mille in phytoplankton to less than 2 per mille. Seasonal

fluctuations in $\delta^{13}C_P$ values are therefore effectively smoothed through trophic attenuation, justifying the use of a constant biomass-weighted annual average reference value.

We considered the effect of spatial variability in $\delta^{13}C_P$ values within Longhurst Provinces by calculating the standard deviation and maximum range of $\delta^{13}C$ values within each province. We estimated uncertainty around latitudinal trends in $\delta^{13}C_P$ values characterising Longhurst Provinces with a Monte Carlo simulation where we sampled $\delta^{13}C_P$ values randomly from a Gaussian distribution taking the $\delta^{13}C$ value in the latitudinal mid-point of the province as the mean and using the measured standard deviation.

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The rate of isotopic turnover (the rate at which new atoms of carbon are assimilated from diet into tissues through growth and tissue turnover) varies between taxa and under differing conditions. We use as a first approximation scaling relationships between body size and turnover rate [2] to estimate likely rates of turnover. Sharks with body masses between 10^4g and 10^5g are predicted to exhibit isotopic half-lives on the order of 100-200 days, with temperature influencing rates so that turnover will be greater at higher temperatures. Thus, a 10kg shark moving between feeding sites separated by 10 degrees of latitude (reflecting 1.2 per mille difference in baseline δ^{13}C values on average) would need to forage for 100 days in the new environment to express an isotopic shift in excess of 0.5 per mille. Isotopic turnover rate does, of course, limit the sensitivity to movement across isotopic gradients: animals foraging across isotopic gradients at timescales significantly shorter than isotopic turnover rates will form tissues with isotopic compositions reflecting a weighted average of the ingested food sources over the timescale of equilibration. If populations are comprised of individuals switching feeding between two isotopically-distinct resources, the median composition of the population will trend towards a value between the two sources, and the isotopic variance within the population will reduce as the rate at which the individuals switch resources (e.g. move between habitats) increases. Thus if individuals forage across a latitudinal range, the slope of the isotopic gradient reflected in the population mean of tissue isotopic compositions will reduce, the extent of any reduction depending on the relative proportion of tissues assimilated outside of the catch location during the period of isotopic equilibration, and the mean geographic distance between assimilation site and capture location.

Shelf sharks display population mean latitudinal slopes that are similar to that of local phytoplankton (Figure 2), implying little attenuation of isotopic gradients due to latitudinal mixing. Oceanic sharks, however, show shallow isotopic gradients that could, in theory, reflect either derivation of the majority of nutrients from restricted latitude, or foraging across large latitudinal gradients. In both cases derivation of nutrients with lower δ^{13}C values (i.e. from higher latitudes) is needed to explain the shallow latitudinal gradients seen. Nutrients assimilated from regions characterised by primary production with higher δ^{13}C (i.e. low latitude areas) must therefore be balanced by nutrients assimilated from isotopically depleted (high latitude) regions. Oceanic sharks are not commonly found in latitudes greater than c.50°N or S, limiting the potential to balance isotopically positive dietary sources, and we therefore infer that the majority of nutrients assimilated had a similar and relatively ^{13}C-depleted isotopic composition, consistent with derivation from intermediate latitudes between

c.30-50 degrees from the equator. The $\delta^{13}C$ values of oceanic shark tissues captured at 10 degrees average around 17.5 per mille. A simple two component mass balance considering diet $\delta^{13}C$ end member values estimated from phytoplankton models implies that between c.65-100% of all nutrients must be derived from latitudes between 30 and 50 degrees.

Interpretation of shelf variation

Shelf dwelling shark populations display greater ranges in $\delta^{13}C$ values than slope or pelagic dwelling sharks. This variation could be caused by increased spatial variation in regional phytoplankton baselines in coastal systems, or through increasing use of food webs supported by isotopically distinct sources.

Variations in $\delta^{13}C$ values within Longhurst Biogeographic Provinces increase towards high latitudes that are characterised by steep latitudinal temperature gradients (Figure 2). Isotopic variation in shelf shark populations, however, is greater in tropical latitudes indicating that isotopic variability is not primarily controlled by spatial variation within the local biogeographic province.

Sharks are typically viewed as generalist consumers, however generalism may occur through individuals foraging across a wide range of resources or through populations comprised of individuals specialising on locally abundant, discrete sources. Individual generalism would tend to produce relatively low between-individual isotopic variability; therefore the high variance seen within populations of shelf sharks implies individual-level food web specialisation within the timescale of isotopic incorporation. Median $\delta^{13}C$ values in shelf sharks populations are indistinguishable from those predicted for sharks feeding on local phytoplankton-dominated food webs. The null hypothesis that shelf sharks derive all carbon from local food webs supported by phytoplankton is therefore partially supported as latitudinal trends in $\delta^{13}C$ values are indistinguishable from those predicted for phytoplankton, but the range in $\delta^{13}C$ values observed in shelf sharks strongly implies additional utilisation of food webs characterised by high $\delta^{13}C$ values.

The $\delta^{13}C$ of shelf shark muscle muscles are relatively high compared to local phytoplankton at both low and high latitude ranges, likely as a consequence of a greater proportion of individual shelf sharks feeding on prey supported by primary production with higher $\delta^{13}C$, or at a higher trophic level than currently prescribed. The very high $\delta^{13}C$ values seen in some individual sharks (i.e. 5 per mille heavier than predicted) cannot realistically be explained

through increased trophic level, and thus strongly imply derivation of a substantial proportion of their nutrients from more coastal food webs characterised by higher $\delta^{13}C$, such as seagrasses, macrophytes, coral reefs, and/or terrestrially supported food webs [3].

It is quite possible that individual or species-level differences in the consumption and routing of lipid-derived carbon into muscle protein contribute to the variance observed in $\delta^{13}C$ values at all latitudes and in all shark groups. However, we know of no ecological or physiological reason to suspect either major differences in the degree and style of carbon routing between shelf and oceanic sharks or differential latitudinal effects of fasting or carbon routing between shelf and oceanic sharks.

Moving forward, the data compiled here will form the "Chondrichthyan Stable Isotope Data Project" and we invite the utilisation of these data and addition of new data to help build on the global geographic trends observed here.

Supplementary Figure 2: Latitudinal trends in mean $\delta^{13}C$ values (with standard deviation bars) for shelf shark species (and one oceanic species: *C. longimanus*) that have the potential to migrate over multiple habitats (i.e either shelf and deep-sea habitats or shelf and oceanic habitats). Each point represents mean values for a population within an individual study with each colour corresponding to a different species. The latitudinal $\delta^{13}C$ regression observed for oceanic shark muscle is also provided (dashed blue). 500 Monte Carlo iterations of the latitudinal trends in $\delta^{13}C_P$ observed in shelf sharks, considering the variance within each Longhurst Biogeographic Province (dark grey solid lines), and the latitudinal trends predicted for $\delta^{13}C_S$ with a trophic offset of 4.6 per mille (red solid lines - see Methods section and Figure 2).

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Supplementary Table 1 (Please see attached Supplementary_Tables.xlsx): Primary habitat assignment for each shark species sampled within this study with corresponding paper provided. Asterisks denote species that are likely to migrate over multiple habitats and appear in Supplementary Figure 2.

Supplementary Table 2: List of trophic discrimination factors used to calculate trophic offset values for shark samples.

Species	$\Delta^{13}C$ (SD), ‰	Reference
Scyliorhinus canicula	0.80 (0.10)	59
Carcharias taurus & *Negaprion brevirostris*	0.84 (0.23)	60
Triakis semifasciata	1.00	61
Triakis semifasciata	1.70 (0.50)	62
Mean	1.10	

Supplementary Table 3: Results from the most parsimonious generalised additive models (GAMs). Particulate organic carbon (POC) models describe POC $\delta^{13}C$ as a function of distance from equator (DistEq). $\delta^{13}C$ shark models describe $\delta^{13}C$ trends in shark muscle as a function of DistEq, log total length (logTL) and depth (only for deep-sea sharks) where all measurements were available. SE is standard error, edf is estimated degrees of freedom and DE% is the deviance explained by the explanatory variables. Difference is the difference between POC and shark models for the independent variables.

Habitat	Smooth Term	Parametric Coefficients				Significance of smooth terms				n	DE%	AIC
		Estimate	S.E	t	Pr(>|t|)	edf	Ref.df	F	p value			
Shelf	POC ~ DistEq	-20.89	0.02	-1008	<0.001	2.00	2.00	2969.00	<0.001	3029	**66.3**	9397
	DistEq	-16.17	0.03	-523	<0.001	2.00	2.00	1098.00	<0.001	3029	42.0	11824
	logTL	-16.17	0.04	-404	<0.001	1.91	1.99	45.66	<0.001	3029	3.1	13381
	DistEq x logTL	-16.17	0.03	-545	<0.001				<0.001	3029	**46.7**	11570
	DistEq					2.00	2.00	1248.30	<0.001			
	logTL					1.00	1.00	267.50	<0.001	DIFF		
											19.6	
Oceanic	POC ~ DistEq	-20.24	0.02	-811	<0.001	2.00	2.00	1918.00	<0.001	651	**85.6**	1264
	DistEq	-17.22	0.03	-495	<0.001	1.83	1.97	79.37	<0.001	651	20.2	1697
	logTL	-17.22	0.04	-453	<0.001	1.97	2.00	15.51	<0.001	651	4.8	1813
	DistEq x logTL	-17.22	0.03	-499	<0.001					651	**21.7**	1689
	DistEq					1.87	1.98	68.24	<0.001			
	logTL					1.83	1.97	5.18	0.004			
										DIFF	**63.9**	
Bathyal	POC ~ DistEq	-21.75	0.03	-838	<0.001	1.98	2.00	1604.00	<0.001	1452	**68.8**	4091
	DistEq	-17.42	0.03	-598	<0.001	1.98	2.00	22.89	<0.001	1452	3.1	4431
	logTL	-17.42	0.03	-681	<0.001	1.97	2.00	248.00	<0.001	1452	25.3	4052
	Depth	17.42	0.03	-598	<0.001	1.97	2.00	138.00	<0.001	1452	17.6	3764
	DistEq x logTL	-17.42	0.03	-695	<0.001					1452	**28.5**	3994
	DistEq					1.99	2.00	31.61	<0.001			
	logTL					1.99	2.00	255.40	<0.001			
										DIFF	**40.3**	
	DistEq x logTL x Depth	-17.42	0.03	-667	<0.001					1452	**34.0**	3994
	DistEq					1.97	2.00	10.23	<0.001			
	logTl					1.96	2.00	121.23	<2E-16			
	Depth					1.81	1.96	38.82	<2E-16			
										DIFF	**34.8**	

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