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A global perspective on the trophic geography of sharks

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Sharks are a diverse group of mobile predators that forage across varied spatial scales and have the potential to influence food web dynamics. The ecological consequences of recent declines in shark biomass may extend across broader geographic ranges if shark taxa display common behavioural traits. By tracking the original site of photosynthetic fixation of carbon atoms that were ultimately assimilated into muscle tissues of 5,394 sharks from 114 species, we identify globally consistent biogeographic traits in trophic interactions between sharks found in different habitats. We show that populations of shelf-dwelling sharks derive a substantial proportion of their carbon from regional pelagic sources, but contain individuals that forage within additional isotopically diverse local food webs, such as those supported by terrestrial plant sources, benthic production and macrophytes. In contrast, oceanic sharks seem to use carbon derived from between 30° and 50° of latitude. Global-scale compilations of stable isotope data combined with biogeochemical modelling generate hypotheses regarding animal behaviours that can be tested with other methodological approaches.

Sharks are one of the most speciose groups of predators on the planet and can be found over a broad range of habitats in every ocean[1]. Globally, population declines have been reported in many species of sharks, largely due to fishing pressures and habitat degradation over the last century[2–4]. However, the impacts of these declines on broader ecosystem structure and function remain uncertain[5–11]. Global-scale ecological consequences from declining shark numbers are likely and may be apparent if shark taxa perform broadly similar functions across different regions and habitat types, such that local effects scale across wide geographic regions. In marine systems, the impact of an individual on the wider ecosystem is strongly influenced by trophic interactions[12]. Thus, the composition and spatial origin of diet plays an important part in shaping the ecological roles of individuals, species and functional groups. Here, we use the term 'trophic geography' to refer to spatial aspects of feeding and nutrition. Broadly quantifying the trophic geography of marine consumers is particularly challenging because the spatial and temporal scales over which individuals forage can extend for thousands of kilometres and over months to years. Nevertheless, trophic geography provides critical information on how food webs are structured and the biological connectivity of ecosystems.

Extensive use of stable isotope analysis in localized studies of marine food webs has provided a wealth of published information on trophic ecology across broad geographic regions, and numerous ecosystems within those regions. Of particular utility, the stable isotopic composition of carbon ($\delta^{13}C$) in marine food webs provides spatial and trophic information on nutrient and biomass residence and translocation because of the predictable variation in $\delta^{13}C$ values with latitude and among different primary production types, such as phytoplankton (−24‰ to −18‰), macrophytes (−27‰ to −8‰) and seagrasses (−15‰ to −3‰)[13–15]. The stable isotope composition of carbon in primary producers is directly assimilated by

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consumers through feeding, and provides a biochemical tracer linking a consumer to the basal source of carbon and/or latitudinal origin of the food webs that support tissue growth[16]. The extent of fractionation of stable isotopes of carbon during photosynthesis by algal phytoplankton varies strongly with latitude, and to a lesser extent with dissolved nutrient contents, due to temperature and latitude-dependent variation in factors such as cell size, growth rates and the concentration and isotopic composition of dissolved CO_2[14,17]. The stable isotope composition of carbon in algal phytoplankton has been simulated using isotope-enabled biogeochemical models[17], providing global-scale predictions of latitude-dependent variation in $\delta^{13}C$ values. Stable isotope data can thus be used as an indicator of the latitudinal origin of carbon assimilated by mobile marine consumers, providing insight into cross-ecosystem foraging without the need to directly track the movements of individual animals[13,16]. Sharks assimilating food fuelled by primary production source(s) in one region but captured in an isotopically distinct second region should have isotopic compositions that differ from those of primary producers in the capture location. Here, we compare latitudinal trends in $\delta^{13}C$ values observed in the muscle tissues of sharks found on continental shelf, open ocean and deep-sea habitats, with those predicted for phytoplankton from the known capture locations to establish global patterns of trophic geography in sharks.

We compile a global-scale database of $\delta^{13}C$ values of white muscle tissue from 5,394 individual sharks from 114 species associated with continental shelves (neritic waters <200 m in depth), oceanic (open-ocean waters but mainly occurring <200 m) and deep-sea (continental slopes and seamounts ≥200 m) habitats (Supplementary Table 1, Fig. 1). We compare observed shark $\delta^{13}C$ values ($\delta^{13}C_S$) with the biomass-weighted annual average $\delta^{13}C$ values predicted for phytoplankton ($\delta^{13}C_P$) within biogeographically distinct ecological regions (Longhurst biogeographic provinces) that correspond to shark capture locations (Fig. 2). We test the null hypothesis that sharks feed exclusively within the phytoplankton-derived food webs of their capture locations by comparing the observed and predicted latitudinal trends in $\delta^{13}C$ values. Capture location $\delta^{13}C_P$ values are calculated from a carbon-isotope-enabled global ocean ecosystem model[17] (Fig. 1). Global-scale isoscapes are not available for sources of marine production other than phytoplankton, thus we cannot discount the possibility that all sources of production show consistent latitudinal gradients in $\delta^{13}C$ values. However, the isotopic offset between phytoplankton, seagrass, macrophytes and benthic production varies substantially between sites[16]. Furthermore, variables such as cell size, growth rates and dissolved CO_2 concentrations have less influence on the $\delta^{13}C$ values of alternative marine production sources[14]. We therefore expect that the $\delta^{13}C$ values of alternative primary production sources will vary more at the local level, and differing contributions from production sources within shark food webs will predominantly influence the variance seen in shark $\delta^{13}C$ values. A detailed description of the considerations and rationale behind the isotopic comparisons are given in the Supplementary Information.

Results

The isotopic compositions of carbon in shark muscle ($\delta^{13}C_S$) covary negatively with latitude for oceanic and shelf sharks, but the relationship between latitude and $\delta^{13}C_S$ values differs among habitats (Fig. 2). In continental shelf waters, latitudinal trends observed in shark muscle were similar to those estimated from biochemical models. The observed rate of change in $\delta^{13}C$ values per 1° of latitude was −0.11 for sharks and −0.13 for plankton, although these rates were statistically distinguishable (ANCOVA $F_{11.864}$, $P = 0.0006$).

The average isotopic offset between plankton and shelf sharks (the difference in intercept values between the best fit linear regressions) is 4.6‰, close to the expected trophic offset of 4.5‰, given that the median trophic level for sharks is estimated at 4.1[18] and the mean isotopic difference between sharks and their prey (that is, the trophic discrimination factor for $\delta^{13}C$) is 1.1‰ (Supplementary Table 2). Best-fit generalized additive models (GAMs) indicate that the largest amount of deviance in $\delta^{13}C_S$ in shelf sharks is explained by latitude (42.0%), with shark size having very little effect (3.1%) and a combined explanatory deviance of 46.7% (Supplementary Table 3). Across all latitudes, the range of $\delta^{13}C_S$ values within a given single-species population of shelf sharks is higher than that of oceanic or deep-sea sharks (Fig. 2).

Although oceanic and shelf sharks were sampled from a similar latitudinal range, the observed latitudinal trends in $\delta^{13}C_S$ values from oceanic sharks are less steep than those predicted for phytoplankton from the corresponding Longhurst biogeographic province (ANCOVA: $F_{205.63}$, $P < 0.001$; Fig. 2). Irrespective of capture latitude, the observed range of $\delta^{13}C_S$ values in oceanic sharks was small (-17.22 ± 0.99‰) across the sampling range. The lack of covariance of $\delta^{13}C_S$ with latitude suggests oceanic sharks assimilate the majority of their carbon from a relatively restricted latitudinal range, although temporal differences in habitat use and $\delta^{13}C$ values of prey coupled with relatively slow isotopic turnover rates of muscle in elasmobranchs could potentially mask variability driven by latitude (discussed further in Supplementary Information). Best-fit GAM models indicate that only 20.2% and 4.8% of the deviance in oceanic shark muscle isotope values is explained by latitude and shark size, respectively (Supplementary Table 3).

Despite the concentration of deep-sea samples from the North Atlantic, latitudinal trends in $\delta^{13}C_S$ for deep-sea sharks do not covary with latitude ($R^2 = < 0.001$, $P = 0.314$) or with $\delta^{13}C_P$ (ANCOVA: $F_{1581.9}$, $P < 0.001$; Fig. 2), displaying patterns similar to those seen in oceanic sharks. Body size explained 25.3% and depth of capture 17.6% of the deviance in carbon isotope compositions of deep-sea sharks (Supplementary Table 3), which implies that their trophic ecology is strongly depth and size-structured, consistent with other fishes from continental slopes[19].

Discussion

Stable carbon isotope compositions measured in shelf sharks express similar latitudinal trends to modelled carbon isotope compositions in phytoplankton and are consistent with our null hypothesis that shelf shark populations are supported primarily by phytoplanktonic production close to their capture location. Shelf sharks display relatively high intraspecific variability in stable carbon isotope compositions compared with oceanic and deep-sea populations (Fig. 2). Thus although the median isotopic compositions of populations imply that the bulk of food assimilated by shelf sharks is supported by phytoplankton production, it seems that individuals within populations assimilate nutrients from a range of isotopically distinct sources. Shelf, and particularly coastal, ecosystems contain a wider diversity of ecological and isotopic niches than oceanic ecosystems, including food webs that are supported by seagrasses, benthic production, macroalgae and coral[13,20]. In most shelf habitats, pelagic phytoplankton yields more negative $\delta^{13}C$ values than alternative carbon sources[13]. Foraging across coastal food webs will tend to produce more varied and less negative $\delta^{13}C$ values than foraging solely in food webs supported by local phytoplankton. We infer that at the population level, shelf sharks act as generalist predators, but populations of at least some of those species are composed of specialist individuals that forage within distinct food webs during the timescale of isotopic turnover (probably 1–2 years[21]). The range of $\delta^{13}C_S$ values observed within populations of shelf sharks is greater in latitudes lower than around 40° (Fig. 2), potentially indicating a greater reliance on food webs that are supported by a range of non-phytoplankton-based resources such as seagrasses and coral reefs in less productive tropical settings. These hypotheses related to the range of primary production sources fuelling shark populations could be further tested using essential amino acid carbon isotope fingerprinting[22].

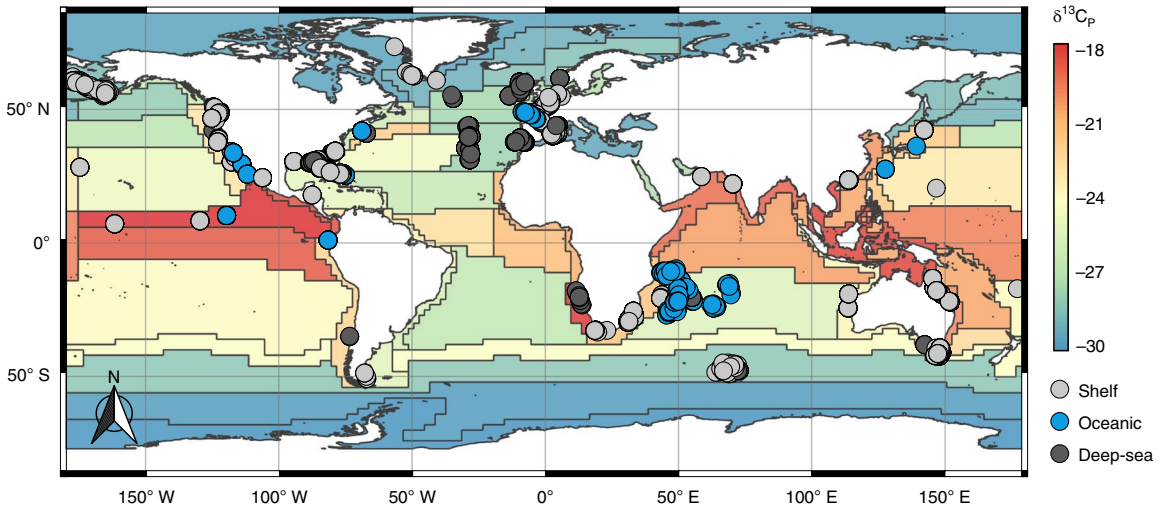

Fig. 1 | Distribution of compiled shark data overlaid on a spatial model of annual average biomass weighted $\delta^{13}C_P$ within Longhurst biogeographic provinces from the median sampling year (2009). The coloured points signify the habitat classification of those samples. Most studies provided one location for multiple samples.

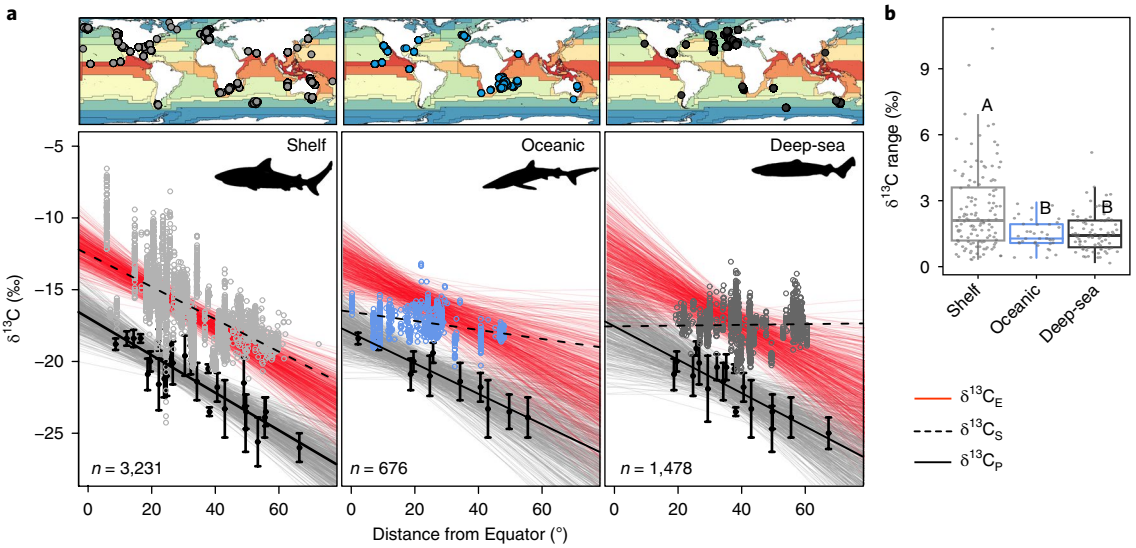

Fig. 2 | Carbon isotope data. a, The relationship between $\delta^{13}C_P$ from Longhurst biogeographic provinces associated with shark capture locations (solid black line) and $\delta^{13}C_S$ values (dashed black line and open circles) and latitude (bottom row). The confidence envelopes reflect 500 Monte Carlo iterations considering the variance in $\delta^{13}C_P$ values within each Longhurst biogeographic province (grey lines) and the same latitudinal trends predicted for $\delta^{13}C_S$ with an offset of 4.6‰ added corresponding to the mean offset between $\delta^{13}C_P$ and $\delta^{13}C_S$ (red lines) and to the trophic effects on $\delta^{13}C$ values. The maps provide the individual shark sample locations overlaid with the $\delta^{13}C_P$ isoscape from Fig. 1. **b**, Distribution of the observed $\delta^{13}C_S$ ranges of species-specific shark populations in each habitat. The horizontal line is the mean $\delta^{13}C_S$ range across shark populations within that habitat. Boxes contain 50% of the data and lines correspond to the 95% confidence interval. The letters signify analysis of variance, Tukey HSD results for significant difference, with the same letters representing mean values that are not significantly different from each other.

Pairing stable isotope analysis with more traditional habitat-use methodologies could improve our understanding of shark behaviour on continental shelves. Tracking studies demonstrate that while spatial residency and/or repeated return-migrations (philopatry) are common traits among sharks that use continental shelves, some species are capable of undertaking large oceanic migrations (for example, white and tiger sharks) and philopatry is still under investigation[23]. Some species, identified a priori here as shelf sharks (such as tiger, white and bull sharks), use multiple habitats and can undertake offshore migrations in excess of 1,000 km[24]. The isotopic compositions of sharks classified as mixed-habitat species diverge in latitudes lower than 35° (Supplementary Fig. 2). Among studies of species that are capable of utilizing multiple habitats, the majority of populations surveyed displayed $\delta^{13}C$ values that are more consistent with obligate shelf sharks than oceanic sharks (Supplementary Fig. 2). This suggests that while some shelf shark species may be highly migratory, the carbon supporting tissue growth is largely assimilated from foraging within shelf areas.

In contrast to shelf sharks, the stable isotope compositions of carbon in oceanic sharks and local phytoplankton do not co-vary, and oceanic shark populations sampled within these studies show similar carbon isotope compositions across all reported capture

Table 1 | Regression coefficients for modelled $\delta^{13}C_P$ and observed $\delta^{13}C_S$ values

$\delta^{13}C_P$				$\delta^{13}C_S$			
Intercept	**Slope**	R^2	P	**Intercept**	**Slope**	R^2	P
−16.87	−0.13	0.61	<0.001	−12.54	−0.11	0.37	<0.001
−17.75	−0.11	0.80	<0.001	−16.55	−0.03	0.17	<0.001
−16.74	−0.12	0.67	<0.001	−17.55	<−0.01	<0.001	0.314

latitudes (Fig. 2). The limited isotopic variability seen in oceanic sharks could reflect either derivation of the majority of nutrients from a restricted latitudinal range, or extensive foraging across large latitudinal gradients to produce a consistent average value. In both cases the consumption of carbon with relatively low $\delta^{13}C$ values (that is, from higher latitudes) is needed to explain the relatively ^{13}C-depleted values seen in sharks caught at low latitudes. Oceanic sharks are not commonly found in latitudes greater than approximately 50° N or S[25], limiting the potential to balance diet sources with higher $\delta^{13}C$ values. We therefore infer that the majority of the carbon assimilated was relatively depleted in ^{13}C and is consistent with phytoplankton-based food webs (including mesopelagic food webs) from intermediate latitudes between approximately 30–50° from the Equator. The uncertainty surrounding the predictions of baseline $\delta^{13}C_P$, capture locations and isotopic turnover rates limit our ability to identify preferential foraging latitudes. Oceanic sharks could also potentially be intercepting migratory prey that originated from a restricted latitudinal range, such as squid[26]. Regardless of the mechanism(s), our data imply that intermediate latitude areas may provide globally important sources of energy and nutrients for the oceanic shark populations sampled in these studies.

Our inferences of regionally restricted foraging areas are consistent with latitudinal trends in oceanic productivity and satellite telemetry studies of several oceanic shark species[27,28]. Pelagic ecosystems at intermediate latitudes are typically characterized by strong thermal gradients that act to concentrate ocean productivity in frontal and eddy systems (Supplementary Fig. 3) which subsequently attract and support oceanic consumers including cetaceans, fishes, seabirds and marine turtles[27,29,30]. Tracking data from some oceanic shark species show high residency within intermediate latitudes[28,30,31], and our interpretation of the stable isotope data supports these predictions of centralized foraging locations. Migrations away from productive foraging grounds may provide optimal habitats for behaviours such as breeding, pupping and avoiding intraspecific competition and harassment[28,32]. Oceanic sharks have distributional ranges spanning ocean basins[33], therefore, recognizing that most of the carbon assimilated into their muscle tissues is derived from photosynthesis occurring in a relatively limited latitudinal region highlights the global importance of regional food webs. More observations of oceanic sharks and/or potentially migratory prey from tropical waters are required to test our hypotheses of centralized foraging.

Similar latitudinal isotopic gradients are observed between oceanic and deep-sea sharks, which may imply a shared nutrient resource supporting sharks in both habitats (Supplementary Fig. 4). Deep-sea sharks rely on the vertical flux of nutrients derived mainly from surface phytoplanktonic production[19], and may therefore be expected to closely track the stable isotope composition of surface production. However, the concentration of deep-sea shark samples from the North Atlantic Ocean (74%) makes it difficult to determine the tropho-spatial dynamics of this group, because the ameliorating effects of the Gulf Stream suppresses latitudinal variation in $\delta^{13}C_P$ (Fig. 1). Latitudinal trends are further complicated by the strong effect of body size and depth (Supplementary Table 3), whereby some species of deep-sea shark express bathymetric segregations by size[34]. Although movement data for most deep-sea shark species is limited, some larger species undertake long-distance migrations that are possibly linked to ontogeny, but may also undertake diel vertical migrations linked with foraging[35,36]. More research is needed to fully understand the trophic geography of deep-sea sharks and their functional roles in deep-sea ecosystems.

Concluding remarks

Nearly a quarter of all chondrichthyan species are evaluated as threatened on the International Union for Conservation of Nature *Red List of Threatened Species*, raising concerns on the future of many populations and the resulting effects such declines may have on ecosystem function[2,4,7,37]. Concurrent declines in species with shared trophic geographies help identify common risks associated with fishing or climate change. While it is beyond the scope of this study, and these data, to predict the effects of further removal of sharks from the oceans, we suggest areas that warrant further investigation, specifically: (1) many shark species foraging in shelf environments are typically classed as generalist consumers, but our data suggest that populations are commonly composed of individuals that forage in distinct food webs that are supported by a range of different carbon sources. Such behavioural specialization within generalist populations could in theory reduce within-species competition by partitioning resources and habitats, but the role of individual specialization in regulating shark population densities is unclear. (2) Oceanic sharks seem to predominantly forage on carbon resources from a restricted latitudinal range in sub-tropical regions that are characterized by relatively high productivity. We hypothesize that sharks migrate away from highly productive regions into warmer waters to engage in alternative behaviours such as reproduction, but the mechanisms and drivers underpinning latitude-restricted foraging in oceanic sharks remain unknown. Global patterns of trophic geography in other large mobile marine predators are generally unknown, but may reveal the role mobile animals play in distributing nutrients and connecting ecosystems across the global ocean, and help to predict population responses to changes in local productivity. We have provided evidence that suggests that on a global scale sharks typically forage within spatially restricted, regional seascapes. Conservation of shelf marine environments is increasingly being addressed through the creation of marine protected areas (MPAs)[38]. MPAs may be effective measures for protecting locally resident shelf shark species, providing they encompass the range of adjacent habitats and core areas utilized by these shark populations[39,40]. Although the distributional ranges for most oceanic sharks are expansive, core intermediate latitudes seem to be important for the provision of nutrients and energy. Productive intermediate latitudes are also targeted by pelagic fisheries, which increases the susceptibility of oceanic sharks to exploitation[28]. Establishing management and protective strategies that encompass all critical habitats utilized by a species is complex. However, our results suggest that oceanic sharks may benefit from global strategies that mitigate negative impacts on intermediate-latitude food webs and from fishing practices that minimize shark mortality in these areas[27,28].

Electronic tagging has revolutionized shark spatial ecology, providing detailed records of the movement of individual animals[23,30]. Tracking the movement of nutrients can complement information

on individual animal movements by providing a link between the presence of an animal in an area and the importance of that area for provisioning, enhancing our knowledge of the extent and scale of connectivity between oceanic habitats. Locating ecologically relevant provisioning areas may also assist in the effective design and placement of MPAs, particularly in open ocean and deep-water habitats.

Methods

Raw stable carbon isotope data (bulk tissue $\delta^{13}C$ values) were compiled from 54 publications and 7 unpublished datasets yielding measurements from 5,602 individual sharks of 116 species. Where possible, information such as location, body size, sample size, lipid extraction method and date were reported. The majority of studies were only able to provide a general area of capture and the mapped locational assignment was taken as the median of the latitudinal and longitudinal ranges of these areas. Likewise, some studies sampled landing docks so were only able to provide the area of that landing dock. The locations provided by these studies were of the landing docks and it was assumed that fishers were catching sharks in waters in the vicinity of the landing port. Species habitat preferences were categorized using published information from their prospective papers (Supplementary Table 1) and on the advice of the corresponding authors. Species that had multiple habitat descriptions were classified as shelf sharks. Examples of this are *Hexanchus* spp., which are classified here as shelf sharks ($n=198$). Although typically treated as deep-sea sharks, all species in this study occur consistently over the shelf so were not considered as obligate deep-sea shark species.

Samples from two plankivorous species (*Rhinocodon typus*, $n=26$[41,42]; *Megachasma pelagios*, $n=2$; A. S. J. Wyatt, unpublished observations), from ecotourism provisioning sites (*Carcharhinus perezii*, $n=23$[43]), and from a riverine study (*Carcharhinus leucas*, $n=125$[44]) were excluded as the study focuses on marine predators under natural conditions. Within the studies that comprise the dataset, five chemical treatments were used (no treatment, $n=2{,}386$; water washed, $n=1{,}407$; 2:1 chloromethanol, $n=748$; cyclohexane, $n=696$; and petroleum ether, $n=157$). Tests for lipid extraction effects were not significant and it is assumed that any effect associated with chemical pre-treatment methods are spatially averaged across the data. Samples with a C:N ratio greater than 10 were removed as it is highly unlikely that the $\delta^{13}C$ value of these samples represents muscle protein. A further 314 samples with C:N ratios ranging between 4–10 were subjected to mathematical correction for lipid influences on $\delta^{13}C$ values[45]. All other values were used under the assumption that published values were representations of true isotopic composition of muscle protein. The data compiled will form the Chondrichthyan Stable Isotope Data Project and we invite the utilization of these data and addition of new data to help build on the global geographic trends observed here.

For each major ocean, annual mean sea surface temperature (SST) and chlorophyll *a* concentrations (Chl *a*) were derived from the moderate-resolution imaging spectroradiometer (MODIS) 9 km AQUA night-time SST and 9 km MODIS AQUA Chl *a* concentration data (NASA Oceancolor) for the median sampling year for the shark data, 2009 (Supplementary Fig. 3). Environmental data extraction was constrained to oceanic waters within areas highlighted on the map (Supplementary Fig. 3).

$\delta^{13}C$ baseline predictions. A mechanistic model predicting the spatio-temporal distribution of global $\delta^{13}C$ values of particulate organic matter ($\delta^{13}C_P$) was used to interpret shark isotope data[17]. Briefly, the model estimates $\delta^{13}C$ values in phytoplankton from ocean carbon chemistry, phytoplankton composition and phytoplankton growth rate variables output from the NEMO-MEDUSA biogeochemical model system at 1° and monthly resolutions. Biomass weighted annual average phytoplankton $\delta^{13}C$ values together with associated spatial and temporal standard deviations were averaged across each Longhurst biogeochemical province (Fig. 1). Model-predicted baseline $\delta^{13}C$ values were then inferred for the capture location for each individual shark data point.

Mathematical models. The relationship between latitude and stable carbon isotope composition (both $\delta^{13}C_P$ and $\delta^{13}C_S$) was modelled using linear regression (Fig. 2, Table 1). For phytoplankton, we recovered the median and standard deviation of annual average $\delta^{13}C_P$ values simulated within each Longhurst biogeographic province with a corresponding shark sample. We then ran 500 repeated (Monte Carlo) linear regressions to account for the spatial variation in predicted $\delta^{13}C_P$ values within each biogeographic province. We predicted null hypothesis shark isotope compositions by adding 4.6‰ (reflecting 4.1‰ as the median trophic level of sharks and using published experimental studies of trophic discrimination factors for $\delta^{13}C$ values in elasmobranch tissues of 1.1‰ (Supplementary Table 2) to the intercept of each of the 500 simulated regression models. ANCOVA analyses were run to compare the slopes of regressions within a given habitat and between comparable variables between habitats ($\delta^{13}C_S$, $\delta^{13}C_P$). ANOVA with post-hoc Tukey HSD were used to test for significant differences between population carbon ranges among habitats.

GAMs were developed to describe latitudinal trends in $\delta^{13}C_S$. Specific habitat models were used to determine the amount of deviance that could be explained by single and multiple explanatory variables, including distance from the Equator and predicted $\delta^{13}C_P$ (Supplementary Table 3). A depth parameter was also added to the deep-sea shark models. $\delta^{13}C_P$ values were modelled separately from corresponding capture locations as a function of distance from the Equator. By comparing the amount of deviance explained within both the $\delta^{13}C_S$ and $\delta^{13}C_P$ models, it was possible to determine how much of the predicted $\delta^{13}C_P$ patterns were captured within $\delta^{13}C_S$ values. All models were limited to two smoothing knots to make models comparable and interpretable. Model comparisons were drawn using Akaike's information criterion to determine the most parsimonious model. Final models were visually inspected using standard residual Q–Q plots to assess model suitability. All data analysis was performed in R-cran (https://cran.r-project.org) and mapping visualizations were performed in QGIS (http://www.qgis.org).

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Data availability. All data used in these analyses are archived via Dryad (https://doi.org/10.5061/dryad.d1f0d). This project is an output of the Chondrichthyan Stable Isotope Data Project (a collection of stable isotope data on sharks, rays and chimaeras); further details are provided on the project's GitHub page (https://github.com/Shark-Isotopes/CSIDP).

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Author contributions

C.S.B. and C.N.T. contributed the concept and design. C.S.B., C.N.T. and A.V. led the project. C.S.B. and C.N.T. wrote the manuscript. C.S.B., C.N.T., S.M. and A.Y analysed and interpreted the data. C.S.B., C.N.T., A.V., K.G.A., A.A., H.A.-R., A.B., D.M.B., G.B., A.B., M. Bouchoucha, M. Boyle, E.J.B., J.B., P.B., A.C., D.C., J. Ciancio, J. Claes, A.C., D.C., P.C., R.D., L.d.N., T.E., I.F., A.J.F., J.H.H., M.H., N.E.H., J.I., F.J., M.J.K., J.J.K., D.K., R.L., Y.L., S.A.K., A.L., D.M., A.M., L.M.-C., P.M., M.M., F.M., G.M.M., S.M., M.N., Y.P., H.P., J.D.P., C.P.-S., K.Q.-D., V.R., J.R., Y.E.T.-R., D.S.S., O.N.S., C.W.S., M.S., A. Teffer, A. Tilley, M.V., J.J.V., T-C.W., R.J.D.W. and A.S.J.W. provided data and/or samples. All authors have read, provided comments and approved the final manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

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