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A Global Perspective on the Trophic Geography of Sharks

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A global perspective on the trophic geography of sharks

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Abstract

Sharks are a diverse group of mobile predators that forage across varied spatial scales and have the potential to influence food web dynamics. 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 ultimately assimilated into muscle tissues of 5394 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 appear to use carbon derived from between 30 and 50 degrees of latitude. Global-scale compilations of stable isotope data combined with biogeochemical modelling generate hypotheses regarding animal behaviours that can be tested with additional methodological approaches.

Introduction

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 localised studies of marine food webs has provided a wealth of published information on trophic ecology across broad geographic

220 regions, and numerous ecosystems within those regions. Of particular utility, the stable
221 isotopic composition of carbon ($\delta^{13}C$) in marine food webs provides spatial and trophic
222 information on nutrient and biomass residence and translocation, because of the
223 predictable variation in $\delta^{13}C$ values with latitude and among different primary production
224 types, such as phytoplankton (-24‰ to -18‰), macrophytes (-27‰ to -8‰), and
225 seagrasses (-15‰ to -3‰) [13-15]. The carbon stable isotope composition of primary
226 producers is directly assimilated by consumers through feeding, and provides a
227 biochemical tracer linking a consumer to the basal source of carbon and/or latitudinal
228 origin of the food webs that support tissue growth [16]. The extent of fractionation of carbon
229 stable isotopes during photosynthesis by algal phytoplankton varies strongly with latitude,
230 and to a lesser extent with dissolved nutrient contents, due to temperature and latitude-
231 dependent variation in variables such as cell size, growth rates and the concentration and
232 isotopic composition of dissolved CO_2 [14,17]. The stable isotopic composition of algal
233 phytoplankton has been simulated using isotope-enabled biogeochemical models [17],
234 providing global-scale predictions of latitude-dependent variation in $\delta^{13}C$ values. Stable
235 isotope data can thus be used as an indicator of the latitudinal origin of carbon assimilated
236 by mobile marine consumers, providing insight into cross-ecosystem foraging without the
237 need to directly track movements of individual animals [13,16]. Sharks assimilating food
238 fuelled by primary production source(s) in one region but captured in an isotopically
239 distinct second region should exhibit anomalous isotopic compositions compared to
240 primary producers in the capture location. Here, we compare latitudinal trends in $\delta^{13}C$
241 values observed in muscle tissues of sharks found on continental shelves, open oceans, and
242 deep-sea habitats, with those predicted for phytoplankton in the known capture locations to
243 establish global patterns of trophic geography in sharks.
244
245 We compile a global-scale database of $\delta^{13}C$ values of white muscle tissue from 5394
246 individual sharks from 114 species associated with continental shelves (neritic waters
247 <200m in depth), oceanic (open-ocean waters but mainly occurring <200m) and deep-sea
248 (continental slopes and seamounts ≥200m) habitats (Supplementary Table 1, Figure 1). We
249 compare observed shark $\delta^{13}C$ values ($\delta^{13}C_S$) to biomass-weighted annual average $\delta^{13}C$
250 values predicted for phytoplankton ($\delta^{13}C_P$) within biogeographically distinct ecological
251 regions (Longhurst Biogeographical Provinces) corresponding to shark capture locations
252 (Figure 2). We test the null hypothesis that sharks feed exclusively within the
253 phytoplankton-derived food webs of their capture locations by comparing the observed
254 and predicted latitudinal trends in $\delta^{13}C$ values. Capture location $\delta^{13}C_P$ values are calculated
255 from a carbon-isotope-enabled global ocean-ecosystem model ([17], Figure 1). Global-scale

256 isoscapes are not available for sources of marine production other than phytoplankton, thus
257 we cannot discount the possibility that all sources of production show consistent latitudinal
258 gradients in $\delta^{13}C$ values. However, the isotopic offset between phytoplankton, seagrass,
259 macrophytes and benthic production varies substantially between sites [16]. Furthermore,
260 variables such as cell size, growth rates and dissolved CO_2 concentrations, have less
261 influence on the $\delta^{13}C$ values of alternative marine production sources [14]. We therefore
262 expect that $\delta^{13}C$ values of alternative primary production sources will vary more at the
263 local level, and varying contributions of different production sources within shark food
264 webs will predominantly influence the variance seen in shark $\delta^{13}C$ values. A detailed
265 description of the considerations and rationale behind the isotopic comparisons are given
266 in the supplementary material.
267
268 **Results**
269 Carbon isotope values of shark muscle ($\delta^{13}C_S$) co-vary negatively with latitude for oceanic
270 and shelf sharks, but the relationship between latitude and $\delta^{13}C_S$ values differs among
271 habitats (Figure 2). In continental shelf waters, latitudinal trends observed in shark muscle
272 were similar to those estimated from biochemical models. The observed rate of change in
273 $\delta^{13}C$ values per degree of latitude was -0.11 for sharks and -0.13 for plankton, although
274 these rates were statistically distinguishable (ANCOVA $F_{11.864}$, $p=0.0006$).
275
276 The average isotopic offset between plankton and shelf sharks (the difference in intercept
277 values between the best fit linear regressions) is 4.6‰, close to the expected trophic offset
278 of 4.5‰, given that the median trophic level for sharks is estimated at 4.1 [18], and the mean
279 isotopic difference between sharks and their prey, i.e. trophic discrimination factor for
280 $\delta^{13}C$, is 1.1‰ (Supplementary Table 2). Best-fit generalised additive models (GAMs)
281 indicate that the largest amount of deviance in $\delta^{13}C_S$ in shelf sharks is explained by latitude
282 (42.0%), with very little effect of shark size (3.1%), and a combined explanatory deviance
283 of 46.7% (Supplementary Table 3). Regional biogeography among continental shelf sharks
284 are not ubiquitous though, and across all latitudes, the range of $\delta^{13}C_S$ values within a given
285 single-species population of shelf sharks is higher than that of oceanic or deep-sea sharks
286 (Figure 2).
287
288 Conversely, while oceanic and shelf sharks were sampled from a similar latitudinal range,
289 the observed latitudinal trends in $\delta^{13}C_S$ values from oceanic sharks are less steep than those
290 predicted for phytoplankton from the corresponding Longhurst Biogeographic Province
291 (ANCOVA: $F_{205.63}$, $p<0.001$; Figure 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 methods). 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 co-vary with latitude (R^2 = <0.001, p = 0.314) or with $\delta^{13}C_P$ (ANCOVA: $F_{1581.9}$, p<0.001; Figure 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

Carbon stable isotope compositions estimated from phytoplankton and those measured in shelf sharks ($\delta^{13}C_S$) express similar latitudinal trends. The observed similarity in latitudinal isotopic trends between phytoplankton and sharks is 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 carbon stable isotope compositions compared to oceanic and deep-sea populations (Figure 2). Thus while population median isotopic compositions imply that the bulk of food assimilated by shelf sharks is supported by phytoplankton production, it appears that individuals within populations assimilate nutrients from a range of isotopically-distinct sources. Shelf, and particularly coastal, ecosystems provide access to a wider diversity of ecological and isotopic niches than oceanic ecosystems, including food webs 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 within alternative, more isotopically positive, coastal food webs will tend to produce less negative $\delta^{13}C$ values than predicted based on 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 (likely 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 degrees (Figure 2), potentially indicating greater reliance on food webs 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].

Pairing stable isotope analysis with more traditional habitat use methodologies could improve the resolution 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 (e.g. white and tiger sharks), and philopatry is still under investigation [23]. Some species, identified *a priori* here as shelf sharks (i.e. tiger, white, bull sharks etc.), use multiple habitats and undertake offshore migrations in excess of 1000 km [24]. The isotopic compositions of sharks classified as mixed habitat species diverge in latitudes lower than 35° (Figure 2). Among studies of species capable of utilising multiple habitats, the majority of populations surveyed displayed $\delta^{13}C$ values more consistent with obligate shelf sharks than oceanic sharks (Supplementary Figure 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, stable carbon isotope compositions of oceanic sharks and local phytoplankton do not co-vary, and oceanic shark populations sampled within these studies show similar carbon isotope values across all reported capture latitudes (Figure 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 consumption of carbon with relatively low $\delta^{13}C$ values (i.e. 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 *c.*50° N or S [25], limiting the potential to balance diet sources with more positive $\delta^{13}C$ values. We therefore infer that the majority of carbon assimilated was relatively ^{13}C depleted and is consistent with phytoplankton-based food webs (including mesopelagic food webs) from intermediate latitudes between *c.*30-50 degrees from the equator. The uncertainty surrounding the predictions of baseline $\delta^{13}C_P$,

364 capture locations, and isotopic turnover rates limit our ability to identify preferential
365 foraging latitudes. Oceanic sharks could also potentially be intercepting migratory prey
366 that has originated from a restricted latitudinal range, such as squid [26]. Regardless of the
367 mechanism(s), our data imply that intermediate latitude areas may provide globally
368 important sources of energy and nutrients for the oceanic shark populations sampled in
369 these studies.
370
371 Our inferences of regionally-restricted foraging areas are consistent with latitudinal trends
372 in oceanic productivity and satellite telemetry studies of several oceanic shark species [27,28].
373 Pelagic ecosystems at intermediate latitudes are typically characterized by strong thermal
374 gradients that act to concentrate ocean productivity in frontal and eddy systems
375 (Supplementary Figure 3) which subsequently attract and support oceanic consumers
376 including cetaceans, fishes, seabirds and marine turtles [27,29,30]. Tracking data from some
377 oceanic shark species show high residency within intermediate latitudes [28,30,31], and our
378 interpretation of the stable isotope data supports these predictions of centralised foraging
379 locations. Migrations away from productive foraging grounds may provide optimal habitat
380 for behaviours such as breeding, pupping, and avoiding intraspecific competition and
381 harassment [28,32]. Oceanic sharks have distributional ranges spanning ocean basins [33].
382 Therefore, recognising that most of the carbon assimilated into their muscle tissues is
383 derived from photosynthesis occurring in a relatively limited latitudinal region highlights
384 the global importance of regional food webs. More observations of oceanic sharks and/or
385 potentially migratory prey from tropical waters are required to test our hypotheses of
386 centralised foraging.
387
388 Similar latitudinal isotopic gradients are observed between oceanic and deep-sea sharks,
389 which may imply a shared nutrient resource supporting sharks in both habitats
390 (Supplementary Figure 4). Deep-sea sharks rely on the vertical flux of nutrients derived
391 mainly from surface phytoplanktonic production [19], and may therefore be expected to
392 closely track the stable isotopic composition of surface production. However, the
393 concentration of deep-sea shark samples from the North Atlantic Ocean (74%) make it
394 difficult to determine the tropho-spatial dynamics of this group, because the ameliorating
395 effects of the Gulf Stream suppresses latitudinal variation in $\delta^{13}C_P$ (Figure 1). Latitudinal
396 trends are further complicated by the strong effect of body size and depth (Supplementary
397 Table 3), whereby some species of deep-sea shark express bathymetric segregations by
398 size [34]. While movement data for most deep-sea shark species is limited, some larger
399 species undertake long-distance migrations possibly linked to ontogeny, but may also
400 undertake diel vertical migrations linked with foraging [35,36]. More research is needed to

401 fully understand the trophic geography of deep-sea sharks and their functional roles in
402 deep-sea ecosystems.
403

404 **Concluding Remarks**

405 Nearly a quarter of all chondrichthyan species are evaluated as threatened on the IUCN
406 Red List of Threatened Species, raising concerns on the future of many populations and
407 the resulting effects such declines may have on ecosystem function [2,4,7,37]. Concurrent
408 declines in species with shared trophic geographies help identify common risks associated
409 with fishing or climate change. While it is beyond the scope of this study, and these data,
410 to predict the effects of further removal of sharks from the oceans, we generate questions
411 that warrant further investigation, specifically (1) many shark species foraging in shelf
412 environments are typically classed as generalist consumers, but our data suggest that
413 populations are commonly comprised of individuals that forage in distinct food webs
414 supported by a range of different carbon sources. Such behavioural specialisation within
415 generalist populations could in theory reduce within-species competition by partitioning
416 resources and habitats, but the role of individual specialisation in regulating shark
417 population densities is unclear. (2) Oceanic sharks appear to predominantly forage on
418 carbon resources from a restricted latitudinal range in sub-tropical regions characterised by
419 relatively high productivity. We hypothesise that sharks migrate away from highly
420 productive regions into warmer waters to engage in alternative behavioural strategies such
421 as reproduction, but the mechanisms and drivers underpinning latitude-restricted foraging
422 in oceanic sharks remain unknown. Global patterns of trophic geography in other large
423 mobile marine predators are generally unknown, but may reveal the role mobile animals
424 play in distributing nutrients and connecting ecosystems across the global ocean, and help
425 to predict population responses to changes in local productivity.
426

427 We have provided evidence suggesting that on a global scale, sharks typically forage
428 within spatially restricted, regional seascapes. Conservation of shelf marine environments
429 is increasingly addressed through the creation of marine protected areas (MPAs) [38]. MPAs
430 may be effective measures for protecting locally-resident shelf shark species, providing
431 they encompass the range of adjacent habitats and core areas utilized by these shark
432 populations [39,40]. Although the distributional ranges for most oceanic sharks are expansive,
433 core intermediate latitudes appear to be important for the provision of nutrients and
434 energy. Productive intermediate latitudes are also targeted by pelagic fisheries, which
435 increase the susceptibility of oceanic sharks to exploitation [28]. Establishing management
436 and protective strategies that encompass all critical habitats utilised by a species is

complex. However, our results suggest that oceanic sharks may benefit from global strategies that mitigate deleterious impacts on intermediate-latitude food webs and from fishing practices that minimise 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 compliment 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 effective design and placement of marine protected areas, particularly in open ocean and deep-water habitats.

Methods

Raw carbon stable isotope data (bulk tissue $\delta^{13}C$ values) were compiled from 54 publications and 7 unpublished datasets yielding measurements from 5602 individual sharks of 117 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 categorised 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 quoted 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; Wyatt unpublished*), from ecotourism provisioning sites (*Carcharhinus perezii*; n = 23; [43]), and from a riverine study (*Carcharrhinus leucas*; n = 125; [44]) were excluded as the study focuses on marine predators under natural conditions. Within the studies comprising the dataset, five chemical treatments were used (none: *n* = 2386; water washed: 1407; 2:1 chloromethanol: 748; cyclohexane: 696; and petroleum ether: 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 utilisation 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) 9km AQUA night time sea surface temperatures and 9km MODIS AQUA CHL-a concentration data (NASA Oceancolor) for the median sampling year for the shark data, 2009 (Supplementary Figure 3). Environmental data extraction was constrained to oceanic waters within areas highlighted on the map (Supplementary Figure 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 degree and monthly resolution. Biomass weighted annual average phytoplankton $\delta^{13}C$ values together with associated spatial and temporal standard deviations were averaged across Longhurst Biogeochemical Provinces (Figure 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 carbon stable isotope composition for both phytoplankton ($\delta^{13}C_P$) and shark muscle ($\delta^{13}C_S$) was modelled using linear regression (Figure 2, Table 1). For phytoplankton, we recovered the median and standard deviation of annual average $\delta^{13}C_P$ values simulated within each Longhurst 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 per mille

(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 per mille (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.

Generalised additive models (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 in order to make models comparable and interpretable. Model comparisons were drawn using Akaike's information criterion (AIC) to determine the most parsimonious model. Final models were visually inspected using standard residual q-q plots to assess model suitability. All data analysis were performed in R-cran (https://cran.r-project.org) and mapping visualisations in QGIS (http://www.qgis.org).

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Data Availability: All data used in these analyses are archived via Dryad (submitted – awaiting DOI). This project is an output of the 'Chondrichthyan Stable Isotope Data Project' – a collection of stable isotope data on sharks, rays and chimaera - further details are provided on the project's GitHub page (https://github.com/Shark-Isotopes/CSIDP)

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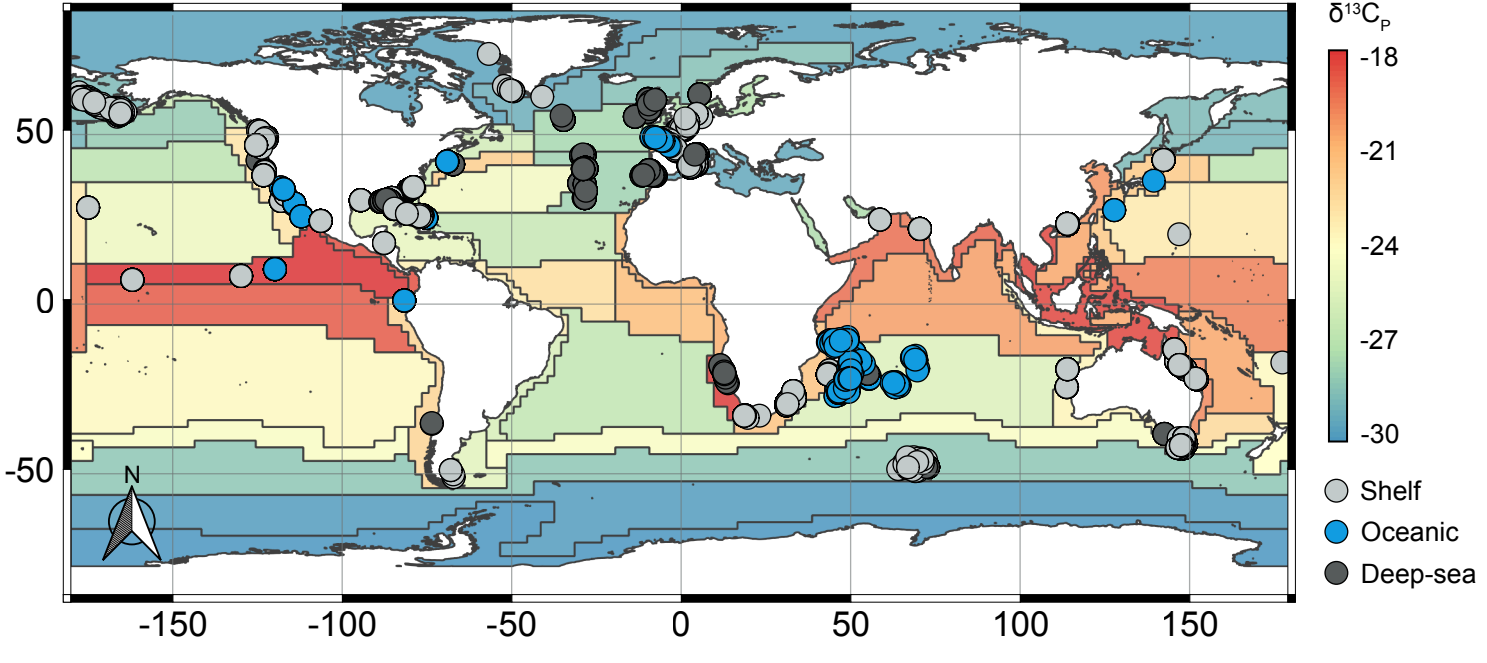
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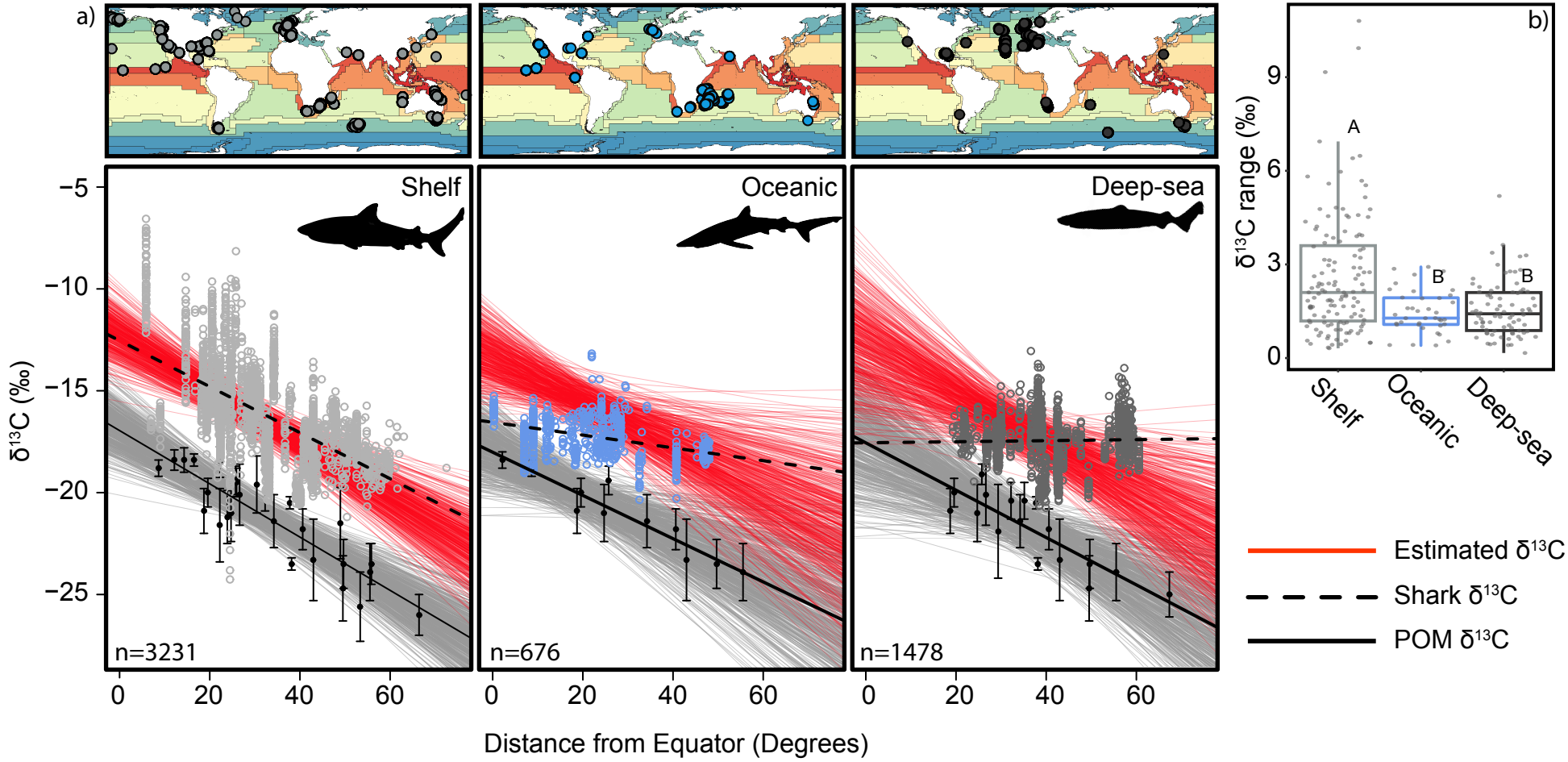
Figure 1: Distribution of compiled shark data overlaid on a spatial model of annual average biomass weighted $\delta^{13}C$ values in particulate organic matter ($\delta^{13}C_P$) [17] within Longhurst biogeographical provinces from the median sampling year, 2009. Coloured points signify habitat classification of those samples. Most studies provided one location for multiple samples.

Figure 2: a) The relationship between carbon isotope compositions of modelled particulate organic carbon $\delta^{13}C$ ($\delta^{13}C_P$) from Longhurst Biogeographic Provinces associated with shark capture locations (solid black line), and shark muscle stable carbon isotope ($\delta^{13}C_S$) values (dashed black line & open circles) and latitude. Confidence envelopes around linear regression lines (grey solid lines) reflect 500 Monte Carlo iterations considering variance in $\delta^{13}C_P$ values within each Longhurst Biogeographic Provinces, and in red the same latitudinal trends predicted for $\delta^{13}C_S$ with an offset of 4.6 per mille added corresponding to the mean offset between $\delta^{13}C_P$ and $\delta^{13}C_S$, and corresponding to likely trophic effects on $\delta^{13}C$ values. Maps provide individual shark sample locations overlaid with the $\delta^{13}C_P$ isoscape from Figure 1. **b)** Distribution of the observed $\delta^{13}C_S$ ranges of shark populations in each habitat. 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 95% confidence interval. 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.

Table 1: Regression coefficients for modelled particulate organic matter (POM) $\delta^{13}C$ ($\delta^{13}C_P$), estimated $\delta^{13}C$ ($\delta^{13}C_E$) and observed $\delta^{13}C$ shark muscle ($\delta^{13}C_S$) values from Figure 2. Lettered figures are statistically similar as determined from an ANCOVA.

$\delta^{13}C_P$ - soild				$\delta^{13}C_S$ - dashed			
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


δ13CP
-18
-21
-24
-27
-30
Shelf
Oceanic
Deep-sea
N
50
0
-50
-150
-100
-50
0
50
100
150


a)
Shelf
Oceanic
Deep-sea
n=3231
n=676
n=1478
δ13C (‰)
−5
−10
−15
−20
−25
0
20
40
60
Distance from Equator (Degrees)
b)
δ13C range (‰)
0
3
6
9
A
B
B
Shelf
Oceanic
Deep-sea
Estimated δ13C
Shark δ13C
POM δ13C