

## 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. 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.

199

200 **Introduction**

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

217

218 Extensive use of stable isotope analysis in localised studies of marine food webs has  
219 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 ( $\delta^{13}\text{C}$ ) in marine food webs provides spatial and trophic  
222 information on nutrient and biomass residence and translocation, because of the  
223 predictable variation in  $\delta^{13}\text{C}$  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‰) <sup>13-15</sup>. 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 <sup>16</sup>. 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  $\text{CO}_2$  <sup>14,17</sup>. The stable isotopic composition of algal  
233 phytoplankton has been simulated using isotope-enabled biogeochemical models <sup>17</sup>,  
234 providing global-scale predictions of latitude-dependent variation in  $\delta^{13}\text{C}$  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 <sup>13,16</sup>. 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  $\delta^{13}\text{C}$   
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  $\delta^{13}\text{C}$  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  $\geq 200\text{m}$ ) habitats (Supplementary Table 1, Figure 1). We  
249 compare observed shark  $\delta^{13}\text{C}$  values ( $\delta^{13}\text{C}_\text{S}$ ) to biomass-weighted annual average  $\delta^{13}\text{C}$   
250 values predicted for phytoplankton ( $\delta^{13}\text{C}_\text{P}$ ) 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  $\delta^{13}\text{C}$  values. Capture location  $\delta^{13}\text{C}_\text{P}$  values are calculated  
255 from a carbon-isotope-enabled global ocean-ecosystem model (<sup>17</sup>, 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  $\delta^{13}\text{C}$  values. However, the isotopic offset between phytoplankton, seagrass,  
259 macrophytes and benthic production varies substantially between sites <sup>16</sup>. Furthermore,  
260 variables such as cell size, growth rates and dissolved  $\text{CO}_2$  concentrations, have less  
261 influence on the  $\delta^{13}\text{C}$  values of alternative marine production sources <sup>14</sup>. We therefore  
262 expect that  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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 ( $\delta^{13}\text{C}_\text{S}$ ) co-vary negatively with latitude for oceanic  
270 and shelf sharks, but the relationship between latitude and  $\delta^{13}\text{C}_\text{S}$  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  $\delta^{13}\text{C}$  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 <sup>18</sup>, and the mean  
279 isotopic difference between sharks and their prey, i.e. trophic discrimination factor for  
280  $\delta^{13}\text{C}$ , is 1.1‰ (Supplementary Table 2). Best-fit generalised additive models (GAMs)  
281 indicate that the largest amount of deviance in  $\delta^{13}\text{C}_\text{S}$  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  $\delta^{13}\text{C}_\text{S}$  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  $\delta^{13}\text{C}_\text{S}$  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

292 of  $\delta^{13}\text{C}_\text{S}$  values in oceanic sharks was small ( $-17.22 \pm 0.99\%$ ) across the sampling range.  
293 The lack of covariance of  $\delta^{13}\text{C}_\text{S}$  with latitude suggests oceanic sharks assimilate the  
294 majority of their carbon from a relatively restricted latitudinal range, although temporal  
295 differences in habitat use and  $\delta^{13}\text{C}$  values of prey coupled with relatively slow isotopic  
296 turnover rates of muscle in elasmobranchs could potentially mask variability driven by  
297 latitude (discussed further in supplementary methods). Best-fit GAM models indicate that  
298 only 20.2% and 4.8% of the deviance in oceanic shark muscle isotope values is explained  
299 by latitude and shark size, respectively (Supplementary Table 3).

300

301 Despite the concentration of deep-sea samples from the North Atlantic, latitudinal trends  
302 in  $\delta^{13}\text{C}_\text{S}$  for deep-sea sharks do not co-vary with latitude ( $R^2 = <0.001$ ,  $p = 0.314$ ) or with  
303  $\delta^{13}\text{C}_\text{P}$  (ANCOVA:  $F_{1581,9}$ ,  $p < 0.001$ ; Figure 2), displaying patterns similar to those seen in  
304 oceanic sharks. Body size explained 25.3% and depth of capture 17.6% of the deviance in  
305 carbon isotope compositions of deep-sea sharks (Supplementary Table 3), which implies  
306 that their trophic ecology is strongly depth and size-structured, consistent with other fishes  
307 from continental slopes<sup>19</sup>.

308

### 309 **Discussion**

310 Carbon stable isotope compositions estimated from phytoplankton and those measured in  
311 shelf sharks ( $\delta^{13}\text{C}_\text{S}$ ) express similar latitudinal trends. The observed similarity in latitudinal  
312 isotopic trends between phytoplankton and sharks is consistent with our null hypothesis  
313 that shelf shark populations are supported primarily by phytoplanktonic production close  
314 to their capture location.

315

316 Shelf sharks display relatively high intraspecific variability in carbon stable isotope  
317 compositions compared to oceanic and deep-sea populations (Figure 2). Thus while  
318 population median isotopic compositions imply that the bulk of food assimilated by shelf  
319 sharks is supported by phytoplankton production, it appears that individuals within  
320 populations assimilate nutrients from a range of isotopically-distinct sources. Shelf, and  
321 particularly coastal, ecosystems provide access to a wider diversity of ecological and  
322 isotopic niches than oceanic ecosystems, including food webs supported by seagrasses,  
323 benthic production, macroalgae and coral<sup>13,20</sup>. In most shelf habitats, pelagic  
324 phytoplankton yields more negative  $\delta^{13}\text{C}$  values than alternative carbon sources<sup>13</sup>.  
325 Foraging within alternative, more isotopically positive, coastal food webs will tend to  
326 produce less negative  $\delta^{13}\text{C}$  values than predicted based on local phytoplankton. We infer  
327 that at the population level, shelf sharks act as generalist predators, but populations of at

328 least some of those species are composed of specialist individuals that forage within  
329 distinct food webs during the timescale of isotopic turnover (likely 1-2 years <sup>21</sup>). The  
330 range of  $\delta^{13}\text{C}_s$  values observed within populations of shelf sharks is greater in latitudes  
331 lower than around 40 degrees (Figure 2), potentially indicating greater reliance on food  
332 webs supported by a range of non-phytoplankton based resources such as seagrasses and  
333 coral reefs in less productive tropical settings. These hypotheses related to the range of  
334 primary production sources fuelling shark populations could be further tested using  
335 essential amino acid carbon isotope fingerprinting <sup>22</sup>.

336

337 Pairing stable isotope analysis with more traditional habitat use methodologies could  
338 improve the resolution of shark behaviour on continental shelves. Tracking studies  
339 demonstrate that while spatial residency and/or repeated return-migrations (philopatry) are  
340 common traits among sharks that use continental shelves, some species are capable of  
341 undertaking large oceanic migrations (e.g. white and tiger sharks), and philopatry is still  
342 under investigation <sup>23</sup>. Some species, identified *a priori* here as shelf sharks (i.e. tiger,  
343 white, bull sharks etc.), use multiple habitats and undertake offshore migrations in excess  
344 of 1000 km <sup>24</sup>. The isotopic compositions of sharks classified as mixed habitat species  
345 diverge in latitudes lower than 35° (Figure 2). Among studies of species capable of  
346 utilising multiple habitats, the majority of populations surveyed displayed  $\delta^{13}\text{C}$  values  
347 more consistent with obligate shelf sharks than oceanic sharks (Supplementary Figure 2).  
348 This suggests that while some shelf shark species may be highly migratory, the carbon  
349 supporting tissue growth is largely assimilated from foraging within shelf areas.

350

351 In contrast to shelf sharks, stable carbon isotope compositions of oceanic sharks and local  
352 phytoplankton do not co-vary, and oceanic shark populations sampled within these studies  
353 show similar carbon isotope values across all reported capture latitudes (Figure 2). The  
354 limited isotopic variability seen in oceanic sharks could reflect either derivation of the  
355 majority of nutrients from a restricted latitudinal range, or extensive foraging across large  
356 latitudinal gradients to produce a consistent average value. In both cases consumption of  
357 carbon with relatively low  $\delta^{13}\text{C}$  values (i.e. from higher latitudes) is needed to explain the  
358 relatively <sup>13</sup>C depleted values seen in sharks caught at low latitudes. Oceanic sharks are not  
359 commonly found in latitudes greater than c.50° N or S <sup>25</sup>, limiting the potential to balance  
360 diet sources with more positive  $\delta^{13}\text{C}$  values. We therefore infer that the majority of carbon  
361 assimilated was relatively <sup>13</sup>C depleted and is consistent with phytoplankton-based food  
362 webs (including mesopelagic food webs) from intermediate latitudes between c.30-50  
363 degrees from the equator. The uncertainty surrounding the predictions of baseline  $\delta^{13}\text{C}_p$ ,

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 <sup>26</sup>. 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 <sup>27,28</sup>.  
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 <sup>27,29,30</sup>. Tracking data from some  
377 oceanic shark species show high residency within intermediate latitudes <sup>28,30,31</sup>, 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 <sup>28,32</sup>. Oceanic sharks have distributional ranges spanning ocean basins <sup>33</sup>.  
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 <sup>19</sup>, 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  $\delta^{13}\text{C}_p$  (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 <sup>34</sup>. 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 <sup>35,36</sup>. 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 <sup>2,4,7,37</sup>. 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) <sup>38</sup>. 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 <sup>39,40</sup>. 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 <sup>28</sup>. Establishing management  
436 and protective strategies that encompass all critical habitats utilised by a species is

437 complex. However, our results suggest that oceanic sharks may benefit from global  
438 strategies that mitigate deleterious impacts on intermediate-latitude food webs and from  
439 fishing practices that minimise shark mortality in these areas<sup>27,28</sup>.

440

441 Electronic tagging has revolutionized shark spatial ecology, providing detailed records of  
442 the movement of individual animals<sup>23,30</sup>. Tracking the movement of nutrients can  
443 compliment information on individual animal movements by providing a link between the  
444 presence of an animal in an area and the importance of that area for provisioning,  
445 enhancing our knowledge of the extent and scale of connectivity between oceanic habitats.  
446 Locating ecologically-relevant provisioning areas may also assist effective design and  
447 placement of marine protected areas, particularly in open ocean and deep-water habitats.

448

#### 449 **Methods**

450 Raw carbon stable isotope data (bulk tissue  $\delta^{13}\text{C}$  values) were compiled from 54  
451 publications and 7 unpublished datasets yielding measurements from 5602 individual  
452 sharks of 117 species. Where possible, information such as location, body size, sample  
453 size, lipid extraction method, and date were reported. The majority of studies were only  
454 able to provide a general area of capture and the mapped locational assignment was taken  
455 as the median of the latitudinal and longitudinal ranges of these areas. Likewise, some  
456 studies sampled landing docks so were only able to provide the area of that landing dock.  
457 The locations provided by these studies were of the landing docks and it was assumed that  
458 fishers were catching sharks in waters in the vicinity of the landing port. Species habitat  
459 preferences were categorised using published information from their prospective papers  
460 (Supplementary Table 1) and on the advice of the corresponding authors. Species that had  
461 multiple habitat descriptions were classified as shelf sharks. Examples of this are  
462 *Hexanchus* spp, which are classified here as shelf sharks (n=198). Although typically  
463 quoted as deep-sea sharks, all species in this study occur consistently over the shelf so  
464 were not considered as obligate deep-sea shark species.

465

466 Samples from two plankivorous species (*Rhinocodon typus*: n = 26;<sup>41,42</sup>, *Megachasma*  
467 *pelagios*: n=2; Wyatt unpublished), from ecotourism provisioning sites (*Carcharhinus*  
468 *perezii*; n = 23;<sup>43</sup>), and from a riverine study (*Carcharhinus leucas*; n = 125;<sup>44</sup>) were  
469 excluded as the study focuses on marine predators under natural conditions. Within the  
470 studies comprising the dataset, five chemical treatments were used (none: n = 2386; water  
471 washed: 1407; 2:1 chloromethanol: 748; cyclohexane: 696; and petroleum ether: 157).  
472 Tests for lipid extraction effects were not significant and it is assumed that any effect  
473 associated with chemical pre-treatment methods are spatially averaged across the data.

474 Samples with a C:N ratio greater than 10 were removed as it is highly unlikely that the  
475  $\delta^{13}\text{C}$  value of these samples represents muscle protein. A further 314 samples with C:N  
476 ratios ranging between 4-10 were subjected to mathematical correction for lipid influences  
477 on  $\delta^{13}\text{C}$  values<sup>45</sup>. All other values were used under the assumption that published values  
478 were representations of true isotopic composition of muscle protein. The data compiled  
479 will form the “Chondrichthyan Stable Isotope Data Project” and we invite the utilisation of  
480 these data and addition of new data to help build on the global geographic trends observed  
481 here.

482

483 For each major ocean, annual mean sea surface temperature (SST) and chlorophyll *a*  
484 concentrations (Chl *a*) were derived from the moderate-resolution imaging  
485 spectroradiometer (MODIS) 9km AQUA night time sea surface temperatures and 9km  
486 MODIS AQUA CHL-a concentration data (NASA OceanColor) for the median sampling  
487 year for the shark data, 2009 (Supplementary Figure 3). Environmental data extraction was  
488 constrained to oceanic waters within areas highlighted on the map (Supplementary Figure  
489 3).

490

#### 491 *$\delta^{13}\text{C}$ baseline predictions*

492 A mechanistic model predicting the spatio-temporal distribution of global  $\delta^{13}\text{C}$  values of  
493 particulate organic matter ( $\delta^{13}\text{C}_p$ ) was used to interpret shark isotope data<sup>17</sup>. Briefly, the  
494 model estimates  $\delta^{13}\text{C}$  values in phytoplankton from ocean carbon chemistry,  
495 phytoplankton composition and phytoplankton growth rate variables output from the  
496 NEMO-MEDUSA biogeochemical model system at 1 degree and monthly resolution.  
497 Biomass weighted annual average phytoplankton  $\delta^{13}\text{C}$  values together with associated  
498 spatial and temporal standard deviations were averaged across Longhurst Biogeochemical  
499 Provinces (Figure 1). Model-predicted baseline  $\delta^{13}\text{C}$  values were then inferred for the  
500 capture location for each individual shark data point.

501

#### 502 *Mathematical models*

503 The relationship between latitude and carbon stable isotope composition for both  
504 phytoplankton ( $\delta^{13}\text{C}_p$ ) and shark muscle ( $\delta^{13}\text{C}_s$ ) was modelled using linear regression  
505 (Figure 2, Table 1). For phytoplankton, we recovered the median and standard deviation of  
506 annual average  $\delta^{13}\text{C}_p$  values simulated within each Longhurst Province with a  
507 corresponding shark sample. We then ran 500 repeated (Monte Carlo) linear regressions to  
508 account for the spatial variation in predicted  $\delta^{13}\text{C}_p$  values within each biogeographic  
509 province. We predicted null hypothesis shark isotope compositions by adding 4.6 per mille

510 (reflecting 4.1 as the median trophic level of sharks and using published experimental  
511 studies of trophic discrimination factors for  $\delta^{13}\text{C}$  values in elasmobranch tissues of 1.1 per  
512 mille (Supplementary Table 2) to the intercept of each of the 500 simulated regression  
513 models. ANCOVA analyses were run to compare the slopes of regressions within a given  
514 habitat and between comparable variables between habitats ( $\delta^{13}\text{C}_S$ ,  $\delta^{13}\text{C}_P$ ). ANOVA with  
515 post-hoc Tukey HSD were used to test for significant differences between population  
516 carbon ranges among habitats.

517

518 Generalised additive models (GAMs) were developed to describe latitudinal trends in  
519  $\delta^{13}\text{C}_S$ . Specific habitat models were used to determine the amount of deviance that could  
520 be explained by single and multiple explanatory variables including distance from the  
521 equator and predicted  $\delta^{13}\text{C}_P$  (Supplementary Table 3). A depth parameter was also added  
522 to the deep-sea shark models.  $\delta^{13}\text{C}_P$  values were modelled separately from corresponding  
523 capture locations as a function of distance from the equator. By comparing the amount of  
524 deviance explained within both the  $\delta^{13}\text{C}_S$  and  $\delta^{13}\text{C}_P$  models, it was possible to determine  
525 how much of the predicted  $\delta^{13}\text{C}_P$  patterns were captured within  $\delta^{13}\text{C}_S$  values. All models  
526 were limited to two smoothing knots in order to make models comparable and  
527 interpretable. Model comparisons were drawn using Akaike's information criterion (AIC)  
528 to determine the most parsimonious model. Final models were visually inspected using  
529 standard residual q-q plots to assess model suitability. All data analysis were performed in  
530 R-cran (<https://cran.r-project.org>) and mapping visualisations in QGIS  
531 (<http://www.qgis.org>).

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687 **Data Availability:** All data used in these analyses are archived via Dryad (submitted –  
688 awaiting DOI). This project is an output of the ‘Chondrichthyan Stable Isotope Data  
689 Project’ – a collection of stable isotope data on sharks, rays and chimaera - further details  
690 are provided on the project’s GitHub page (<https://github.com/Shark-Isotopes/CSIDP>)  
691

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723 **List of Figures and Tables**

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726 **Figure 1:** Distribution of compiled shark data overlaid on a spatial model of  
727 annual average biomass weighted  $\delta^{13}\text{C}$  values in particulate organic matter ( $\delta^{13}\text{C}_\text{P}$ )  
728 <sup>17</sup> within Longhurst biogeographical provinces from the median sampling year,  
729 2009. Coloured points signify habitat classification of those samples. Most studies  
730 provided one location for multiple samples.

731

732 **Figure 2: a)** The relationship between carbon isotope compositions of modelled  
733 particulate organic carbon  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}_\text{P}$ ) from Longhurst Biogeographic Provinces  
734 associated with shark capture locations (solid black line), and shark muscle stable  
735 carbon isotope ( $\delta^{13}\text{C}_\text{S}$ ) values (dashed black line & open circles) and latitude.  
736 Confidence envelopes around linear regression lines (grey solid lines) reflect 500  
737 Monte Carlo iterations considering variance in  $\delta^{13}\text{C}_\text{P}$  values within each Longhurst  
738 Biogeographic Provinces, and in red the same latitudinal trends predicted for  $\delta^{13}\text{C}_\text{S}$   
739 with an offset of 4.6 per mille added corresponding to the mean offset between  
740  $\delta^{13}\text{C}_\text{P}$  and  $\delta^{13}\text{C}_\text{S}$ , and corresponding to likely trophic effects on  $\delta^{13}\text{C}$  values. Maps  
741 provide individual shark sample locations overlaid with the  $\delta^{13}\text{C}_\text{P}$  isoscape from  
742 Figure 1. **b)** Distribution of the observed  $\delta^{13}\text{C}_\text{S}$  ranges of shark populations in each  
743 habitat. Horizontal line is the mean  $\delta^{13}\text{C}_\text{S}$  range across shark populations within that  
744 habitat. Boxes contain 50% of the data and lines correspond to 95% confidence  
745 interval. Letters signify analysis of variance, Tukey HSD results for significant  
746 difference, with the same letters representing mean values that are not significantly  
747 different from each other.

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756 **Table 1:** Regression coefficients for modelled particulate organic matter (POM)  
 757  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}_P$ ), estimated  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}_E$ ) and observed  $\delta^{13}\text{C}$  shark muscle ( $\delta^{13}\text{C}_S$ )  
 758 values from Figure 2. Lettered figures are statistically similar as determined from  
 759 an ANCOVA.

760

$\delta^{13}\text{C}_P$ - soild				$\delta^{13}\text{C}_S$ - dashed			
intercept	slope	R <sup>2</sup>	p	intercept	slope	R <sup>2</sup>	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

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