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► **To cite this version:**

Christopher Bird, Ana Veríssimo, Sarah Magozzi, Kátya Abrantes, Alex Aguilar, et al.. A global perspective on the trophic geography of sharks. *Nature Ecology & Evolution*, 2018, 2 (2), pp.299-305. 10.1038/s41559-017-0432-z . hal-01697662

HAL Id: hal-01697662

<https://hal.science/hal-01697662v1>

Submitted on 19 Nov 2024

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1 **A global perspective on the trophic geography of sharks**

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183 **Abstract**

184 **Sharks are a diverse group of mobile predators that forage across varied spatial**
185 **scales and have the potential to influence food web dynamics. Ecological**
186 **consequences of recent declines in shark biomass may extend across broader**
187 **geographic ranges if shark taxa display common behavioural traits. By tracking the**
188 **original site of photosynthetic fixation of carbon atoms ultimately assimilated into**
189 **muscle tissues of 5394 sharks from 114 species, we identify globally consistent**
190 **biogeographic traits in trophic interactions between sharks found in different**
191 **habitats. We show that populations of shelf-dwelling sharks derive a substantial**
192 **proportion of their carbon from regional pelagic sources, but contain individuals that**
193 **forage within additional isotopically diverse local food webs, such as those supported**
194 **by terrestrial plant sources, benthic production and macrophytes. In contrast,**
195 **oceanic sharks appear to use carbon derived from between 30 and 50 degrees of**
196 **latitude. Global-scale compilations of stable isotope data combined with**
197 **biogeochemical modelling generate hypotheses regarding animal behaviours that can**
198 **be tested with additional 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 ¹. 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 ²⁻⁴. However, the impacts of these declines on broader ecosystem
205 structure and function remain uncertain ⁵⁻¹¹. 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 ¹². 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‰) 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 $\delta^{13}\text{C}$ 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 ^{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 $\delta^{13}\text{C}$
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 (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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values of alternative marine production sources ¹⁴. 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 ¹⁸, 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 slopes¹⁹.

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^{13,20}. In most shelf habitats, pelagic
324 phytoplankton yields more negative $\delta^{13}\text{C}$ values than alternative carbon sources¹³.
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 ²¹). 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 ²².

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 ²³. 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 ²⁴. 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 ¹³C 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 ²⁵, 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 ¹³C 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 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 $\delta^{13}\text{C}_p$ (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 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

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^{27,28}.

440

441 Electronic tagging has revolutionized shark spatial ecology, providing detailed records of
442 the movement of individual animals^{23,30}. 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;^{41,42}, *Megachasma*
467 *pelagios*: n=2; Wyatt unpublished), from ecotourism provisioning sites (*Carcharhinus*
468 *perezii*; n = 23;⁴³), and from a riverine study (*Carcharhinus leucas*; n = 125;⁴⁴) 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 $\delta^{13}\text{C}$ values⁴⁵. 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 data¹⁷. 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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545 References

- 546 1 Ebert, D. A., Fowler, S. L., Compagno, L. J. & Dando, M. *Sharks of the*
547 *world: A fully illustrated guide*. (Wild Nature Press, 2013).
- 548 2 Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R. & Lotze, H. K.
549 Patterns and ecosystem consequences of shark declines in the ocean.
550 *Ecology letters* **13**, 1055-1071 (2010).
- 551 3 Worm, B. *et al.* Global catches, exploitation rates, and rebuilding
552 options for sharks. *Marine Policy* **40** 194-204 (2013).
- 553 4 Dulvy, N. K. *et al.* Extinction risk and conservation of the world's sharks
554 and rays. *eLife* **3**, 1-34 (2014).
- 555 5 Kitchell, J. F., Essington, T. E., Boggs, C. H., Schindler, D. E. & Walters, C.
556 J. The role of sharks and longline fisheries in a pelagic ecosystem of the
557 central Pacific. *Ecosystems* **5**, 202-216 (2002).
- 558 6 Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P. & Peterson, C. H.
559 Cascading effects of the loss of apex predatory sharks from a coastal
560 ocean. *Science* **315**, 1846-1850 (2007).
- 561 7 Heithaus, M. R., Frid, A., Wirsing, A. J. & Worm, B. Predicting ecological
562 consequences of marine top predator declines. *Trends in Ecology &*
563 *Evolution* **23**, 202-210 (2008).
- 564 8 Heupel, M. R., Knip, D. M., Simpfendorfer, C. A. & Dulvy, N. K. Sizing up
565 the ecological role of sharks as predators. *Marine Ecology Progress*
566 *Series* **495**, 291-298 (2014).
- 567 9 Grubbs, R. D. *et al.* Critical assessment and ramifications of a purported
568 marine trophic cascade. *Scientific Reports* **6**, 20970 (2016).
- 569 10 Roff, G. *et al.* The ecological role of sharks on coral reefs. *Trends in*
570 *Ecology & Evolution* **31**, 395-407 (2016).
- 571 11 Ruppert, J. L., Fortin, M.-J. & Meekan, M. G. The ecological role of sharks
572 on coral reefs: Response to Roff *et al.* *Trends in Ecology & Evolution*, **8**,
573 586-587 (2016).
- 574 12 McCann, K., Hastings, A. & Huxel, G. R. Weak trophic interactions and
575 the balance of nature. *Nature* **395**, 794-798 (1998).
- 576 13 Fry, B. & Sherr, E. B. in *Stable Isotopes in Ecological Research* (eds P. W.
577 Rundel, J. R. Ehleringer, & K. A. Nagy) 196-229 (Springer New York,
578 1989).
- 579 14 Laws, E. A., Popp, B. N., Bidigare, R. R., Kennicutt, M. C. & Macko, S. A.
580 Dependence of phytoplankton carbon isotopic composition on growth
581 rate and [CO₂]_{aq}: Theoretical considerations and experimental results.
582 *Geochimica et Cosmochimica Acta* **59**, 1131-1138 (1995).
- 583 15 McMahan, K. W., Hamady, L. L. & Thorrold, S. R. A review of
584 ecogeochemistry approaches to estimating movements of marine
585 animals. *Limnology and Oceanography* **58**, 697-714 (2013).
- 586 16 Hobson, K. A. Tracing origins and migration of wildlife using stable
587 isotopes: A review. *Oecologia* **120**, 314-326 (1999).
- 588 17 Magozzi, S., Yool, A., Vander Zanden, H. B., Wunder, M. B. & Trueman, C.
589 N. Using ocean models to predict spatial and temporal variation in
590 marine carbon isotopes. *Ecosphere* **8**, e01763 (2017).
- 591 18 Cortés, E. Standardized diet compositions and trophic levels of sharks.
592 *ICES Journal of Marine Science: Journal du Conseil* **56**, 707-717 (1999).
- 593 19 Trueman, C. N., Johnston, G., O'Hea, B. & MacKenzie, K. M. Trophic

- 594 interactions of fish communities at midwater depths enhance long-
595 term carbon storage and benthic production on continental slopes.
596 *Proceedings of the Royal Society B: Biological Sciences* **281**, p. 20140669
597 (2014).
- 598 20 Briand, M. J., Bonnet, X., Guillou, G. & Letourneur, Y. Complex food webs
599 in highly diversified coral reefs: Insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable
600 isotopes. *Food Webs* **8**, 12-22 (2016).
- 601 21 Kim, S. L., del Rio, C. M., Casper, D. & Koch, P. L. Isotopic incorporation
602 rates for shark tissues from a long-term captive feeding study. *The*
603 *Journal of Experimental Biology* **215**, 2495-2500 (2012).
- 604 22 McMahan, K. W., Thorrold, S. R., Houghton, L. A. & Berumen, M. L.
605 Tracing carbon flow through coral reef food webs using a compound-
606 specific stable isotope approach. *Oecologia* **180**, 809-821 (2016).
- 607 23 Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. P. & Hueter, R. E.
608 There and back again: A review of residency and return migrations in
609 sharks, with implications for population structure and management.
610 *Annual Review of Marine Science* **7**, 547-570 (2015).
- 611 24 Lea, J. S. *et al.* Repeated, long-distance migrations by a philopatric
612 predator targeting highly contrasting ecosystems. *Scientific reports* **5**,
613 p11202 (2015).
- 614 25 Camhi, M. D., Pikitch, E. K. & Babcock, E. A. *Sharks of the open ocean:*
615 *biology, fisheries and conservation*. Vol. 15 (John Wiley & Sons, 2009).
- 616 26 Ichii, T., Mahapatra, K., Sakai, M. & Okada, Y. Life history of the neon
617 flying squid: Effect of the oceanographic regime in the North Pacific
618 Ocean. *Marine Ecology Progress Series* **378**, 1-11 (2009).
- 619 27 Scales, K. L. *et al.* On the front line: Frontal zones as priority at-sea
620 conservation areas for mobile marine vertebrates. *Journal of Applied*
621 *Ecology*, **51**, 1575-1583 (2014).
- 622 28 Queiroz, N. *et al.* Ocean-wide tracking of pelagic sharks reveals extent
623 of overlap with longline fishing hotspots. *Proceedings of the National*
624 *Academy of Sciences* **113**, 1582-1587 (2016).
- 625 29 Tittensor, D. P. *et al.* Global patterns and predictors of marine
626 biodiversity across taxa. *Nature* **466**, 1098-1101 (2010).
- 627 30 Block, B. A. *et al.* Tracking apex marine predator movements in a
628 dynamic ocean. *Nature* **475**, 86-90 (2011).
- 629 31 Hazen, E. L. *et al.* Predicted habitat shifts of Pacific top predators in a
630 changing climate. *Nature Clim. Change* **3**, 234-238 (2013).
- 631 32 Campana, S. E. *et al.* Migration pathways, behavioural thermoregulation
632 and overwintering grounds of blue sharks in the northwest Atlantic.
633 *PloS One* **6**, e16854 (2011).
- 634 33 Compagno, L. J. *Sharks of the world: An annotated and illustrated*
635 *catalogue of shark species known to date*. Vol. 2 (Food & Agriculture
636 Org., 2001).
- 637 34 Moura, T. *et al.* Large-scale distribution of three deep-water squaloid
638 sharks: Integrating data on sex, maturity and environment. *Fisheries*
639 *Research* **157**, 47-61 (2014).
- 640 35 Veríssimo, A., McDowell, J. R. & Graves, J. E. Population structure of a
641 deep-water squaloid shark, the Portuguese dogfish (*Centroscymnus*
642 *coelelepis*). *ICES Journal of Marine Science: Journal du Conseil* **68**, 555-

643 563 (2011).

644 36 Rodríguez-Cabello, C., González-Pola, C. & Sánchez, F. Migration and
645 diving behavior of *Centrophorus squamosus* in the NE Atlantic.
646 Combining electronic tagging and Argo hydrography to infer deep
647 ocean trajectories. *Deep Sea Research Part I: Oceanographic Research
648 Papers* **115**, 48-62 (2016).

649 37 Heupel, M. & Simpfendorfer, C. Importance of environmental and
650 biological drivers in the presence and space use of a reef-associated
651 shark. *Marine Ecology Progress Series* **496**, 47-57 (2014).

652 38 Edgar, G. J. *et al.* Global conservation outcomes depend on marine
653 protected areas with five key features. *Nature* **506**, 216-220 (2014).

654 39 Heupel, M. R. *et al.* Conservation challenges of sharks with continental
655 scale migrations. *Frontiers in Marine Science* **2**, 12 (2015).

656 40 White, T. D. *et al.* Assessing the effectiveness of a large marine
657 protected area for reef shark conservation. *Biological Conservation*
658 **207**, 64-71 (2017).

659 41 Borrell, A., Aguilar, A., Gazo, M., Kumarran, R. P. & Cardona, L. Stable
660 isotope profiles in whale shark (*Rhincodon typus*) suggest segregation
661 and dissimilarities in the diet depending on sex and size. *Environmental
662 Biology of Fishes* **92**, 559-567 (2011).

663 42 Hussey, N. E. *et al.* Expanded trophic complexity among large sharks.
664 *Food Webs* **4**, 1-7 (2015).

665 43 Maljković, A. & Côté, I. M. Effects of tourism-related provisioning on the
666 trophic signatures and movement patterns of an apex predator, the
667 Caribbean reef shark. *Biological Conservation* **144**, 859-865 (2011).

668 44 Matich, P., Heithaus, M. R. & Layman, C. A. Contrasting patterns of
669 individual specialization and trophic coupling in two marine apex
670 predators. *Journal of Animal Ecology* **80**, 294-305 (2011).

671 45 Kiljunen, M. *et al.* A revised model for lipid-normalizing $\delta^{13}\text{C}$ values
672 from aquatic organisms, with implications for isotope mixing models.
673 *Journal of Applied Ecology* **43**, 1213-1222(2006).

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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

692 **Acknowledgements:** This research was conducted as part of C.S.B.’s Ph.D dissertation,
693 which was funded by the University of Southampton and NERC (NE/L50161X/1), and
694 through a NERC ‘Grant-in-Kind’ from the Life Sciences Mass Spectrometry Facility
695 (LSMSF; EK267-03/16). Other funding bodies supporting collection of the compiled data
696 can be found in the respective papers. We thank Amanda Bates, David Sims, Francis Neat,
697 Rona McGill and Jason Newton for their analytical contributions and comments on the
698 manuscripts.
699

700 **Author Contributions:** C.S.B, C.N.T (concept and design); C.S.B, C.N.T, A.V (project
701 leaders); C.S.B, C.N.T (writers); C.S.B, C.N.T, S.M, A.Y (data analysis and
702 interpretation); 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.B,
703 M.B, J. B, P.B, A.C, D.C, J.C, J.C, A.C, D.C, P.C, R.D, L.N, T.E, I.F, A.J.F, J.H.H, M.H,
704 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,
705 F.M, G.M.M, S.M, M.N, Y.P, H.P, J.D.P, C.P-S, K.Q, V.R, J.R, Y.E.T-R, D.S.S, C.W.S,
706 M.S, A.T, A.T, M.V, J.J.V, T-K. W, R.J.D.W, A.S.J.W (data contribution and/or sample
707 provision); C.S.B, C.N.T (corresponding authors). All authors have read, provided
708 comments and approved the final manuscript.
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710 **Competing Financial Interests:** The authors declare no competing interests.
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723 **List of Figures and Tables**

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725

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 ¹⁷ 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 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

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