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 ($\delta^{13}C$) 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

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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

292   of $\delta^{13}C_S$ values in oceanic sharks was small (-17.22 ± 0.99‰) across the sampling range.

293   The lack of covariance of $\delta^{13}C_S$ 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 $\delta^{13}C$ 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 $\delta^{13}C_S$ for deep-sea sharks do not co-vary with latitude (R^2 = <0.001, p = 0.314) or with

303    $\delta^{13}C_P$ (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 [19].

308

309   **Discussion**

310   Carbon stable isotope compositions estimated from phytoplankton and those measured in

311   shelf sharks ($\delta^{13}C_S$) 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 $\delta^{13}C$ values than alternative carbon sources [13].

325   Foraging within alternative, more isotopically positive, coastal food webs will tend to

326   produce less negative $\delta^{13}C$ 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 $\delta^{13}C_S$ 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 $\delta^{13}C$ 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 $\delta^{13}C$ values (i.e. from higher latitudes) is needed to explain the
358 relatively ^{13}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 [25], limiting the potential to balance
360 diet sources with more positive $\delta^{13}C$ values. We therefore infer that the majority of carbon
361 assimilated was relatively ^{13}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 $\delta^{13}C_P$,

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.

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.

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

11

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 $\delta^{13}C$ 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 (*Carcharrhinus 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   δ^{13}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 δ^{13}C values [45]. 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   *δ^{13}C baseline predictions*

492   A mechanistic model predicting the spatio-temporal distribution of global δ^{13}C values of

493   particulate organic matter ($\delta^{13}C_P$) was used to interpret shark isotope data [17]. Briefly, the

494   model estimates δ^{13}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 δ^{13}C values together with associated

498   spatial and temporal standard deviations were averaged across Longhurst Biogeochemical

499   Provinces (Figure 1). Model-predicted baseline δ^{13}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 ($\delta^{13}C_P$) and shark muscle ($\delta^{13}C_S$) was modelled using linear regression

505   (Figure 2, Table 1). For phytoplankton, we recovered the median and standard deviation of

506   annual average $\delta^{13}C_P$ 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 $\delta^{13}C_P$ 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 $\delta^{13}C$ 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 ($\delta^{13}C_S$, $\delta^{13}C_P$). 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 $\delta^{13}C_S$. 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 $\delta^{13}C_P$ (Supplementary Table 3). A depth parameter was also added
522 to the deep-sea shark models. $\delta^{13}C_P$ 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 $\delta^{13}C_S$ and $\delta^{13}C_P$ models, it was possible to determine
525 how much of the predicted $\delta^{13}C_P$ patterns were captured within $\delta^{13}C_S$ 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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756   **Table 1:** Regression coefficients for modelled particulate organic matter (POM)
757    $\delta^{13}C$ ($\delta^{13}C_P$), estimated $\delta^{13}C$ ($\delta^{13}C_E$) and observed $\delta^{13}C$ shark muscle ($\delta^{13}C_S$)
758   values from Figure 2. Lettered figures are statistically similar as determined from
759   an ANCOVA.

760

$\delta^{13}C_P$ - 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

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767

a)

b)

Shelf

Oceanic

Deep-sea

n=3231

n=676

n=1478

δ¹³C (‰)

Distance from Equator (Degrees)

δ¹³C range (‰)

A

B

B

Shelf   Oceanic   Deep-sea

Estimated δ¹³C

Shark δ¹³C

POM δ¹³C