



Locations of marine animals revealed by carbon isotopes

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Received
3 March 2011

Accepted
31 May 2011

Published
23 June 2011

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Knowing the distribution of marine animals is central to understanding climatic and other environmental influences on population ecology. This information has proven difficult to gain through capture-based methods biased by capture location. Here we show that marine location can be inferred from animal tissues. As the carbon isotope composition of animal tissues varies with sea surface temperature, marine location can be identified by matching time series of carbon isotopes measured in tissues to sea surface temperature records. Applying this technique to populations of Atlantic salmon (*Salmo salar* L.) produces isotopically-derived maps of oceanic feeding grounds, consistent with the current understanding of salmon migrations, that additionally reveal geographic segregation in feeding grounds between individual philopatric populations and age-classes. Carbon isotope ratios can be used to identify the location of open ocean feeding grounds for any pelagic animals for which tissue archives and matching records of sea surface temperature are available.

Populations of most commercially exploited fish and their predators have declined significantly over the last century (e.g.^{1,2}). Effective management of marine ecosystems is reliant on accurate assessments of population identity, location and mixing, but this information is often lacking, particularly in highly migratory pelagic animals³. Conventionally, marine animals are studied by tag-recapture methods, where animals tagged in a known location are subsequently caught either in research or commercial fisheries elsewhere. In pelagic fish, high levels of mortality and low recapture rates mean that very large numbers must be tagged to provide statistically meaningful results, and recapture is frequently dependent on the location of commercial fisheries. Consequently, tag-recapture studies are inherently biased towards the numerically dominant species or populations occurring within capture areas, and are not ideally suited to studying rare species or mixed stock populations. Increasingly, electronic data storage tags (e.g.^{4,5}) and satellite tags (e.g.⁶) are deployed to investigate marine migrations, but data storage tags also rely on recapture, satellite tags are still too large to deploy on small or juvenile animals, and both are prohibitively expensive for large-scale studies. An urgent need remains for alternative methods to study spatial movements of pelagic animals on a population specific basis, independently of biases introduced by capture locations.

Stable isotopes have been used to identify population location in wide-ranging terrestrial species by relating the isotopic composition of animal tissues to known geographic variations in isotope distribution⁷, which are often termed 'isoscapes'. The reference isoscape is derived either from measures of tissues of the study organism in known locations⁷, from other non-migrant animals⁸, or from inorganic materials such as rainwater⁹ or geology¹⁰. This method assumes that the regional isoscape is constant over the time period of the study, and the accuracy and precision of any isoscape-based method depends on the quality of the underlying isoscape. Application of the isoscape method to marine environments is complicated by the relatively homogenous spatial distributions of oxygen, hydrogen and strontium isotope ratios in seawater¹¹. Latitudinal and offshore gradients in the isotopic composition of both carbon and nitrogen have previously been used to track movements of marine mammals^{12–14}. Short-term temporal and spatial variations in the isotopic compositions of C and N at the base of the marine food web, however, restrict the geographic resolution available from fixed isoscape approaches to broad basin-scale differences¹² or latitudinal effects¹⁴.

The isotopic composition of carbon (expressed here as $\delta^{13}\text{C}$ values) in tissues of pelagic animals is strongly dependent on fractionation of carbon isotopes during photosynthesis by the phytoplankton community at the

base of the marine food web¹⁵. The extent of fractionation of carbon isotopes during photosynthesis (E_p) varies inversely with the ratio of cell growth rate to dissolved carbonate concentration both in laboratory and natural ocean conditions (e.g.^{16–20}), and the nature of this relationship is further influenced by the degree of light and nutrient limitation^{20,21}. Both cell growth rates and dissolved carbonate concentrations are intrinsically related to temperature, and vary spatially and temporally across ocean basins (e.g.²²), leading to spatio-temporal variations in the $\delta^{13}\text{C}$ values of plankton in the North Atlantic in excess of 6‰^{14,23–25}. By contrast, fractionation of carbon isotopes associated with an increase in trophic level is on the order of 0–2‰ (e.g.^{26–28}). Thus, the carbon isotope composition of similarly sized pelagic predators varies largely according to feeding location (e.g.^{12–14,28–30}).

Sea surface temperature (SST) is a useful proxy for phytoplankton growth rates²², phytoplankton community structure³¹ and total global primary production^{32,33}, as it integrates many of the variables influencing phytoplankton growth. Dissolved carbonate concentrations also vary with SST; therefore, as all of the variables influencing E_p are either directly or indirectly associated with SST, SST should be a useful proxy for E_p and thus plankton $\delta^{13}\text{C}$ values, as seen in the strong latitudinal $\delta^{13}\text{C}$ gradients¹⁴. The algebraic relationship between SST and $\delta^{13}\text{C}$ values is complex (e.g.²¹), and varies spatially with climatic and oceanographic conditions. In any single area, however, temporal variations in SST will result in temporal fluctuations in E_p and therefore will be coincident with variations in $\delta^{13}\text{C}$ values of plankton. Thus the regions occupied by feeding animals are more likely to be regions where there is high co-variance between time series of tissue $\delta^{13}\text{C}$ values and SST than those regions showing little or no covariance^{34,35}. This approach assumes that animals return to the same area over the duration of the time series, but has advantages over the fixed isoscape approach in that no prior knowledge of baseline isotope values is needed, and the arithmetic relationship linking the controlling variable to the tissue isotope value is free to vary with location.

We illustrate the use of carbon isotope time series as a geolocation tool using the Atlantic salmon (*Salmo salar* L.) as a test species.

Atlantic salmon are economically, culturally and ecologically valuable anadromous fish, which return from the ocean to spawn in their natal rivers after spending either one winter at sea (1SW fish), or more than one winter at sea (MSW fish). Marine mortality in Atlantic salmon (*Salmo salar* L.) has increased from ~70% in the 1970s to over 90% by 2005³⁶, coincident with a major decline in the global population. The current understanding of marine location in salmon is derived largely from tagging fish in home waters and recovering tagged fish in the high seas fisheries^{37–41}. Almost 4 million fish have been tagged in English and Welsh rivers since the 1950s, but fewer than 3000 (<0.08%) have been recovered at sea, almost all from the two historic fishery areas west of Greenland and north of the Faroe Islands³⁹. Based on these data, European fish from rivers above 62°N are believed to migrate to feeding grounds off the Faroe Islands and in the Norwegian and Barents Seas, while fish originating in European rivers below 62°N are thought to feed further west with some MSW-returning fish feeding in the Labrador Sea west of Greenland^{35,42–47}. It is generally assumed that many river stocks and ages are mixed within marine feeding areas³⁹, but identifying feeding locations used by specific river stocks or regional populations is challenging³⁷, and stock-based management and conservation is hampered by a lack of information in the marine phase of life³⁹. Given the above information, and the availability of long-term tissue archives, Atlantic salmon are an ideal test species for isotope-based investigations of migration and distribution. We use the relationship between time series of SST and measured tissue isotopes to identify likely feeding grounds at a stock- and cohort-specific level.

Results

The effect of trophic level on carbon isotope values. The potential influence of trophic level on measured $\delta^{13}\text{C}$ values was tested by

comparison between carbon and nitrogen isotope compositions in scale tissue from salmon populations returning to the UK River Frome (RF) and North East Coast (NEC). The isotopic composition of carbon and nitrogen in fish tissues is controlled to different degrees by variations in isotopic composition at the base of the food web and by trophic discrimination. Nitrogen is more strongly fractionated than carbon during dietary assimilation, with a mean trophic increase of c.3‰ compared to c.1‰ in carbon^{26–28}. In our sampled scales, $\delta^{15}\text{N}$ values correlate positively with size (RF salmon: $n = 231$, $R^2 = 0.41$, $p < 0.001$; NEC salmon: $n = 162$, $R^2 = 0.17$, $p < 0.001$), reflecting changes in trophic level (Fig. 1). Fish returning after more than one winter at sea clearly fed at higher trophic levels than the smaller 1SW returning fish. $\delta^{13}\text{C}$ values also differ between 1SW and MSW returning fish, but show no positive relationship with either size (Fig. 1) or with $\delta^{15}\text{N}$ values (Fig. 2), indicating that differences in the carbon isotope composition of scales cannot be explained by mass or trophic level. This strongly indicates that the carbon isotope composition of salmon collagen is dominated by variations in photosynthesis-related fractionation at the base of the food chain, and that salmon feeding in a common marine area are expected to have similar $\delta^{13}\text{C}$ values⁴⁵.

Despite the large variation in plankton $\delta^{13}\text{C}$ values across the North Atlantic Ocean^{14,23,48}, salmon returning to the River Frome maintain consistently different $\delta^{13}\text{C}$ values to those returning to the NE Coast throughout the 18 year sampling period (ANOVA, with geographic origin as sole co-factor; $n = 523$, $df = 1$, $F = 116.9$, $p < 0.001$). In addition, year and sea age both significantly influence $\delta^{13}\text{C}$ values (Year, $n = 523$, $df = 17$, $F = 9.1$, $p < 0.001$; sea age $df = 1$, $F = 16$, $p < 0.001$), with a significant interaction between all factors. These data strongly suggest that, in each sampled year, returning salmon from different natal origins fed in distinct locations. Stable isotope evidence for stock separation in feeding grounds is further explored in the supplementary information.

Locating marine feeding grounds from stable isotope time series.

To determine the likely location of open ocean feeding areas for our test salmon populations, we assessed the temporal covariance between scale $\delta^{13}\text{C}$ values and SST in each one-degree grid square between 45–75°N latitude and 65°W–20°E longitude for the period

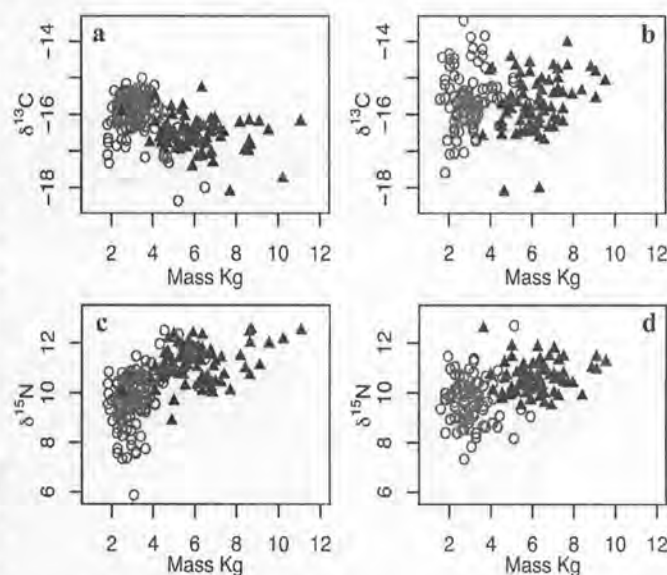


Figure 1 | Relationship between fish mass and stable isotope composition in salmon returning to natal rivers either as 1SW (circle symbols) or MSW (triangle symbols) fish. (a) River Frome $\delta^{13}\text{C}$ values, (b) North East Coast $\delta^{13}\text{C}$ values, (c) River Frome $\delta^{15}\text{N}$ values, (d) North East Coast $\delta^{15}\text{N}$ values.

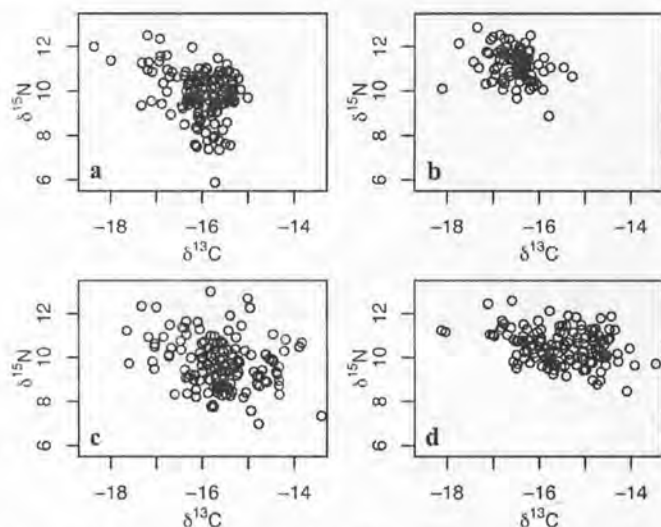


Figure 2 | Relationship between the stable isotope composition of carbon and nitrogen in salmon returning to natal rivers either as 1SW or MSW fish. (a) River Frome 1SW, (b) River Frome MSW, (c) North East Coast 1SW, (d) North East Coast MSW. Despite the large spread in $\delta^{15}\text{N}$ values, there is no positive covariance between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, indicating limited effects of trophic level on $\delta^{13}\text{C}$ values.

1985 to 2002^{49,50}. Time series of tissue isotopes and SST are autocorrelated, violating the assumptions of serial independence demanded by most classical inference tests⁵¹. Autocorrelated time series are frequently de-trended to remove underlying low-frequency variations, however we are primarily interested in low frequency variations that are common to both time series, thus de-trending would be counter-productive⁵¹. Instead, the influence of high frequency fluctuations in the time series was reduced by applying LOESS smoothing with a span of 0.5 and polynomial order 2 (Fig. 3). Low frequency variations in the smoothed time series were correlated, and the influence of autocorrelation on significance tests was accounted for by adjusting the effective degrees of freedom for each time series pair using the modified Chelton method⁵¹. Areas with the highest correspondence between

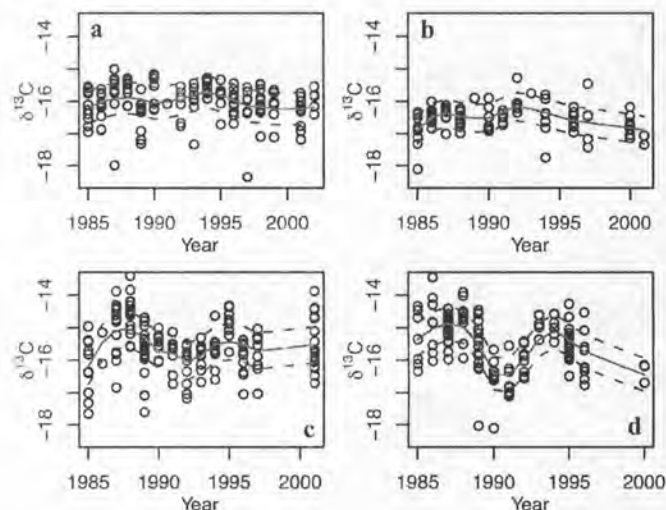


Figure 3 | Temporal trends in $\delta^{13}\text{C}$ values (‰) in salmon scale collagen. (a) River Frome 1SW, (b) River Frome MSW, (c) North East Coast 1SW, (d) North East Coast MSW. Temporal scale represents the last year of marine feeding. Solid (red) line is a first-order LOESS fit with a span width of 0.5; dashed (blue) lines show \pm standard error of the residuals of the

temporal variations in SST and measured $\delta^{13}\text{C}$ values are suggested as the most likely marine feeding areas during deposition of scale collagen (Fig. 4).

The correlation approach taken here is based on the LOESS smoothed fit, and is sensitive to within-year variance, i.e. the assumption that all fish sampled return from the same location at sea. We tested the effect of within-year variance in $\delta^{13}\text{C}$ values by removing all years where within-year $\delta^{13}\text{C}$ standard deviations exceeded 5% of the mean value for that year. Two years were removed from the River Frome 1SW data, one from the River Frome MSW data, four from the NE Coast 1SW data and three from the NE Coast MSW data. Removing years of high variance did not have a dramatic effect on the locations of the proposed feeding grounds, but increased the strength of correlations.

Correlations between time series of scale $\delta^{13}\text{C}$ values and SST vary spatially across the possible range for Atlantic salmon, reaching p values below 0.02 in MSW fish from both populations, with significant covariance (p values lower than 0.05) seen for all populations and sea ages. The spatial distribution of correlation coefficients is highly structured, and provides estimates of location that are consistent with known salmon feeding grounds and migration patterns^{35,38,47,52,53}. The largest contiguous areas of highest correlations, and thus most likely feeding areas, for both the 1SW and MSW components of the NE Coast mixed stock are found in the Norwegian Sea. Correlations for the 1SW component of the NE Coast stock are relatively low, perhaps reflecting a greater range of feeding locations within this population, but a region of high correlation is located within the suspected feeding ground north of the Faroe Islands. Two relatively small areas of high correlation are seen in the Grand Banks and Davis Strait areas. Based on information from tagging and likely swimming capabilities of 1SW returning fish^{41,52,53}, these can be identified as spurious correlations, and as with all such studies, the results of isotopic analyses should be viewed in the context of other available data to aid interpretation. Tissue isotope records for the MSW component of the NE Coast stock are strongly correlated with SST in the Norwegian Sea. These results are highly consistent with tag-recapture and return rate datasets^{35,41,47,52,53}, and suggest that salmon originating from the North East Coast of the UK generally follow the easterly branch of the North Atlantic current into the Norwegian Sea^{37,47}. Our results suggest that fish from the River Frome, in contrast, feed in more westerly regions, with 1SW returning fish occupying an area centred around the Faroe Islands and east Iceland (Fig. 4). The isotopic composition of MSW fish returning to the River Frome strongly implies marine feeding around the Icelandic shelf. Tagging databases show that southern European fish are caught more frequently in the west Greenland than the Faroese fisheries⁵³, and limited fishing surveys suggest a salmon feeding ground east of Greenland, possibly in the Irminger Sea^{46,53}, both indicating an overall westerly migration route for salmon originating from southern European rivers. Our results support this, suggesting that fish originating from the River Frome follow the western branch of the North Atlantic current. The confidence associated with any location identified through correlation analyses will depend on the length of the time series and the degree of variability in both SST and measured $\delta^{13}\text{C}$ values. The strong match between isotope derived feeding grounds, and known feeding areas strongly suggests that in this case the 18 year archive is sufficient to identify feeding areas at least to the same resolution as is possible through traditional tagging and capture fisheries.

Large multi-year variations in $\delta^{13}\text{C}$ scale values are seen in the NE Coast salmon (Fig. 3), suggesting that their feeding areas are subject to higher inter-annual variability in oceanic conditions than those of the River Frome fish. This implies that variations in ocean climate have greater potential to influence growth or return rates for the NE Coast origin fish than for the Frome stock. A significant negative

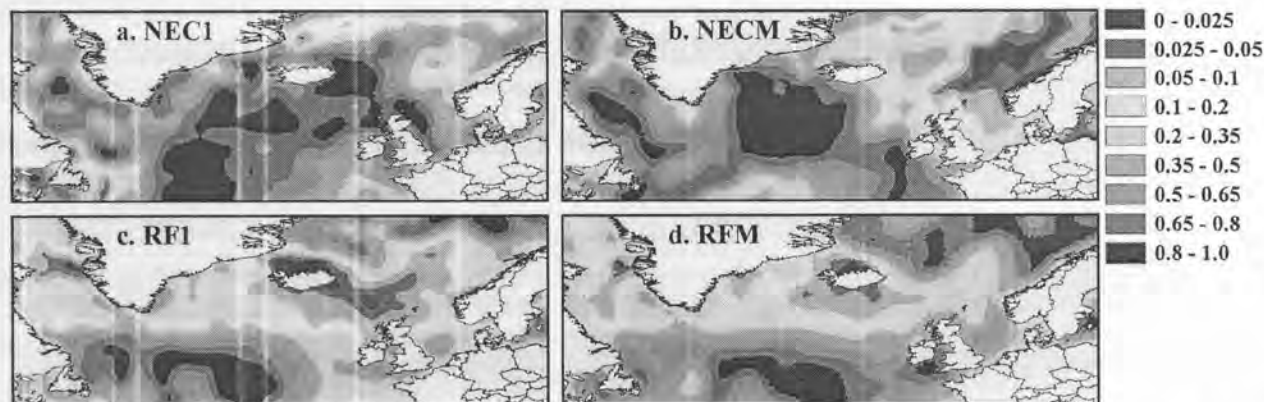


Figure 4 | Proposed feeding areas for two Atlantic salmon populations indicated by the strength of correlation between temporal records of sea surface temperature and scale collagen $\delta^{13}\text{C}$ values. Eight month summer SST (March to October) records were extracted from the HADISST dataset^{49,50} at the native one-degree grid square resolution between 45–75°N latitude and 65°W–20°E longitude for the period 1985 to 2002. Yearly median summer temperatures were calculated for each degree square throughout the period studied. Correlations are based on LOESS fits to temporal data (span = 0.5). Colours indicate the significance of the correlation (p value) after adjustment of effective degrees of freedom to account for autocorrelation in both time series⁵¹. Each map represents feeding areas for a specific population and cohort: (a) North East Coast 1SW, (b) North East Coast MSW, (c) River Frome 1SW, (d) River Frome MSW.

returning to rivers in north east Scotland and SST in the Norwegian Sea³⁵. Differences in marine feeding location may thus underpin the variation in relationships between growth indices, return rates and ocean climate indices observed between salmon populations^{35,38}.

Where autocorrelation adjusted correlations are significant at the 95% level, variations in SST explain between 43 and 97% of the observed variation in $\delta^{13}\text{C}$ scale values. The unexplained variation may be attributed to a combination of variations in the isotopic composition of salmon diet (e.g. variations in trophic level, trophic fractionation, and plankton community composition), violations of the assumption of site fidelity within and between years, and possible contributions of later-formed collagen. The spatially constrained nature of the areas of high correlation, however, demonstrates that unexplained sources of isotopic variation are relatively minor compared to the effect of SST.

Implications for models of salmon migration. Our hypotheses of feeding ground location proposed from isotopic data are consistent with previous salmon migration models. In both the North East Coast and River Frome populations, proposed feeding areas for fish successfully returning after one winter at sea are closer to the river of origin than those proposed for MSW fish, and logical migration routes following the prevailing currents connect the proposed 1SW and MSW fish feeding areas. Our interpretations are based exclusively on fish that returned successfully to the home waters, and therefore we cannot rule out the possibility that fish from individual river stocks feed in a wider range of regions, but with differential rates of return. Tagged fish of UK origin (including one fish originating in the River Frome) have been recovered in the west Greenland fishery, but our isotopic data suggest that this is either a rare occurrence, or that River Frome origin fish feeding off west Greenland are relatively unlikely to return successfully.

The similar temporal trends, and thus relatively close geographic association between feeding grounds for 1SW and MSW fish for both test populations imply that stocks are spatially differentiated during their early outward migration. Hypotheses regarding stock origin within marine feeding grounds may be tested by genetically identifying the natal river origin of salmon caught in these feeding areas. Our interpretations are not biased by historic fishery areas, and identify a high degree of spatial segregation in marine feeding areas between regional populations and potentially, individual river stocks. This is similar to the strong coherence in regional populations noted for Pacific salmonids³⁴, and supported by long term temporal records

of catch and return rates in Norwegian and Scottish salmon³⁸. Conservation of dwindling salmon stocks may require identification and management of open seas feeding grounds on a region- or river stock-specific basis, reflecting the different ocean conditions experienced by each stock.

Discussion

The isotopic composition of carbon varies significantly both spatially and temporally across ocean basins, especially in the temperate ocean, and these variations are transferred up food webs. Fractionation of carbon isotopes during photosynthesis varies with sea surface temperature, and consequently stable isotope analyses may be used to identify location in migratory marine animals by correlating coeval temporal records in tissue isotopes and SST over the possible spatial range of that species. This novel approach provides higher spatial resolution at a population-scale than is possible with traditional tag-recovery studies, and crucially is not restricted by historical fishing or tagging effort. Unlike the isoscape method for geolocation, our approach does not require *a priori* knowledge of distribution of baseline isotope values, and accommodates temporal variation in these baseline isotope values.

Critically, our approach can be applied retrospectively, and the influence of long-term climate variation on the spatial distribution of populations can be studied. Stable isotope-based techniques can be applied to any marine pelagic species (e.g. tuna, herring, turtles, seabirds etc.) for which long-term tissue archives are available or could be initiated, and would be particularly valuable in identifying regions suitable for marine no-take zones or protected areas.

Methods

Our samples come from archived collections of scales taken from wild Atlantic salmon returning to two distinct regions of the UK: the North East Coast drift net fishery, which samples a mixed stock originating in rivers from the North East coast of the UK³⁵, around 55°N and 1°W, and the Dorset River Frome stock from the south coast of England, around 50.5°N and 2°W. Both sampled stocks belong to the proposed southern European population. For both archives, we determined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of scales from approximately 10 1SW and 10 MSW fish for each available year between 1985 and 2002 (see supplementary information for a statistical justification of the sample numbers).

Scales are composite bioapatite-collagen structures. The mineralised component contains a minor inorganic carbonate component, but acid pre-treatment of scales results in biologically insignificant changes in the bulk isotopic composition³⁶. $\delta^{13}\text{C}$ values in the collagen component of fish scales are consistently enriched in $\delta^{13}\text{C}$ relative to muscle values reflecting the high proportion of glycine in collagen³⁷. Scale $\delta^{13}\text{C}$ values are, however, linearly related to the isotopic composition of other body

tissues across multiple genera, under differing diet conditions and growth rates^{56,58,59}, indicating a consistent relationship between scale collagen and diet $\delta^{13}\text{C}$ values.

Scales are incremental tissues growing allometrically with body size increase. Scale collagen is deposited only during growth, and is not turned over metabolically. Occasionally, scales are resorbed, but this is easily identified, and any scales showing resorption are not used for analyses. We therefore target collagen formed during spring–summer growth. Scales were briefly (c. 2–5 minutes) soaked in de-ionised water, manually cleaned using forceps and a scalpel to remove adherents such as lipids and guanine, and dissected under a transmitted light microscope. The last summer of growth at sea (indicated by widely spaced circuli) was excised to obtain a temporally distinct sample⁶⁰. In ISW fish, the summer section from the edge of the scale was sampled, while in MSW fish the summer immediately before the final winter at sea was sampled. Because of the three dimensional nature of growth of collagen in scales⁶⁰ both ISW and, to a lesser extent, 2SW samples will include a minor contribution of collagen laid down during the return migration. This additional collagen may contribute to the relatively high within year variance in seen in $\delta^{13}\text{C}$ values in ISW fish. The measured values represent the isotopic composition of fish tissues averaged over the last full season of marine growth (approximately 8 months, March – October). Samples were weighed to ~0.60mg, and the isotope ratios determined by elemental analysis isotope ratio mass spectrometry (EA-IRMS), using L-glutamic acid as an in-house calibration standard. Measurement precision assessed as 2 \times standard deviation of 16 replicate analyses of USGS40 glutamic acid for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ is, respectively, 0.7‰ and 0.1‰. Comparisons of carbon isotope values between populations were performed using ANOVA with geographic origin, year and sea age as factors. All statistical analyses were performed using the R statistical language⁶¹.

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Acknowledgements

This research was funded by Defra projects SF0250 and SF0246 to CNT. Cefas provided help, advice and samples from the North East Coast Driftnet Archive, with particular thanks to Barry Bendall and William Riley, and to CEH for help and samples from the River Frome Archive. Thanks also to Catherine Cole for help with sample preparation, to Mike Bolshaw for mass-spectrometry assistance and to Mark Moore and Elizabeth Kent for advice, all of the University of Southampton.

Author contributions

KMM prepared and analysed samples. Data were interpreted by KMM, CNT and PMRP with contribution from all authors, AM, ATI and WRCB provided access to samples and expertise on salmon ecology, DJSP provided SST temperature data and aided data processing. The project was designed by CNT, PMRP and AM. The manuscript was written by KMM, CNT and PMRP with contributions from all authors.

Additional information

Supplementary Information accompanies this paper at <http://www.nature.com/scientificreports>

Competing financial interests: Authors have no Competing Financial Interests

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How to cite this article: MacKenzie, K.M. *et al.* Locations of marine animals revealed by carbon isotopes. *Sci. Rep.* **1**, 21; DOI:10.1038/srep00021 (2011).