Global patterns and inferences of tuna movements and trophodynamics

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Abstract :

A global dataset of carbon stable isotope ($\delta^{13}\text{C}$) values from yellowfin, bigeye, and albacore tuna muscle tissue ($n = 4275$) was used to develop a novel tool to infer broad-scale movement and residency patterns of these highly mobile marine predators. This tool was coupled with environmental models and lipid content (C:N ratio) of tuna muscle tissues to examine ocean warming impacts on tuna ecology and bioenergetic condition across Longhurst provinces. Over a 16-year study period (2000–2015), latitudinal gradients in tuna $\delta^{13}\text{C}$ values were consistent, with values decreasing with increasing latitude. Tuna $\delta^{13}\text{C}$ values, reflecting modelled global phytoplankton $\delta^{13}\text{C}$ landscapes (“isoscapes”), were largely related to spatial changes in oxygen concentrations at depth and temporal changes in sea surface temperature. Observed tuna isoscapes ($\delta^{13}\text{C}_{\text{LScorr}}$), corrected for lipid content and the Suess effect (oceanic changes in CO_2 over time), were subtracted from model-predicted baseline isoscapes ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$) to infer spatial movement and residency patterns of the different tuna species. Stable isotope niche width was calculated for each Longhurst province using $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ and baseline-corrected nitrogen isotope ($\delta^{15}\text{N}_{\text{tuna-phyto}}$) values to further quantify isotopic variability as evidence of movements across isoscapes. A high degree of movement—defined as the deviation from expected range of $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values—was evident in four Longhurst provinces: Guinea current coast, North Atlantic drift, Pacific equatorial divergence, and the North Pacific equatorial counter current. The highest level of population dispersal (variability in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values) was observed in Longhurst provinces within the western and central Pacific Oceans and in the Guinea current coast. While lipid content was low in yellowfin and bigeye, high and variable lipid stores in albacore muscle were consistent with seasonal movements between productive foraging and oligotrophic spawning habitats. Our ability to characterize tuna movement patterns without ambiguity remains challenged by uncertainty in trophic discrimination

factors and ecological (e.g. diet variability) processes. However, this study illustrates that model-corrected $\delta^{13}\text{C}$ values are a valuable, relatively cost-effective tool for identifying potential areas of mixing across management zones, particularly when electronic tagging studies are limited or absent. Stable isotope analyses of tuna tissues can therefore be an additional tool for guiding spatial stock assessments on top predator movement, dispersal patterns, and how they may be altered under a changing climate.

Keywords : Albacore tuna, Bigeye tuna, Yellowfin tuna, Carbon isotope analysis, Movement indicators, Global ocean, Fisheries management

1. Introduction

Understanding how and why highly mobile species utilise and move between available habitats in time and space is vital to determining how successful stocks are managed (Evans et al., 2015). In recent years there has been considerable effort to empirically measure and forecast where and when highly mobile species are likely to occur. To date, this has largely been achieved through expensive tagging or bio-logging programs (Block et al., 2011) and habitat preference models that use environmental proxies (Eveson et al., 2015; Hobday et al., 2011; Lehodey et al., 2018; Sibert et al., 1999). Another important aspect in fisheries management and conservation biology is assessing population connectivity, including how much dispersal and mixing occurs among populations. Such information is currently acquired through extensive demographic datasets or using genetics, with the recent development of close-kin mark-recapture methods (Bravington et al., 2016). Many of these tools however still have foundational and logistical constraints (e.g. high cost, require large sample sizes, and limited number of experts and/or users). In contrast, a long-standing and widely utilized tool—analysis of spatial patterns of carbon stable isotope ($\delta^{13}\text{C}$) values in top predator tissues—is a potential complementary approach to assist in understanding both movement patterns and habitat use in marine predators (Bird et al., 2018a; Graham et al., 2010; Trueman et al., 2012; Trueman and St. John Glew, 2019).

Carbon stable isotope analysis has been used for over forty years to trace movements in estuarine and marine environments of a variety of consumers including crustaceans (Fry, 1981; Fry et al., 2003), cephalopods (Takai et al., 2000), seabirds (Jaeger et al., 2010), pinnipeds (Newsome et al., 2007), whales (Best and Schell, 1996; Schell et al., 1989), teleosts (Ménard et al., 2007), and elasmobranchs (Bird et al., 2018a). Early studies examined shrimp and whale movements based on tissue $\delta^{13}\text{C}$ values (Best and Schell, 1996; Fry, 1981; Schell et al., 1989). Shrimp movement detection was facilitated by the presence of primary producers with distinct $\delta^{13}\text{C}$ values at each foraging habitat while whale movements were inferred by spatial variability

in phytoplankton $\delta^{13}\text{C}$ values. At broad oceanic scales, $\delta^{13}\text{C}$ values of dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$) are influenced by temperature (Laws et al., 1995), oceanic partial pressure of CO_2 ($p\text{CO}_2$), phytoplankton growth, and phytoplankton community structure (Fry and Wainright, 1991; Hinga et al., 1994; Popp et al., 1998). These variations in baseline $\delta^{13}\text{C}$ values are driven by spatial differences in primary producers or abiotic conditions, which propagate up to top predators and provide a chemical tracer of movements across foraging grounds with different baseline values (isoscapes sensu West et al., 2010). Further studies have demonstrated success in linking isotopic variation to individual-level dietary differences and movement patterns (Araújo et al., 2007; Grecian et al., 2015; Shipley et al., 2019). Individual isotopic variability, quantifiable as isotopic niches based on scatter in bivariate isotope space (Jackson et al., 2011), can provide a relative measure of trophic and/or movement diversity within a group.

Before carbon isotope techniques can be applied to examine the feeding and behavioural ecology of consumers, spatiotemporal and biochemical factors need to be considered. Direct comparison of isotope values of consumers occupying different isoscapes requires some form of prior adjustment for spatial and temporal baseline variability. Over long time periods, plankton $\delta^{13}\text{C}$ values are known to decline (typically by 0 – 0.08‰ per year) due to the Suess effect (ocean absorption of fossil fuel-derived CO_2) (Quay et al., 2017), which needs to be accounted for in temporal studies. Spatial baseline adjustments can be applied using site-specific modelled phytoplankton isotope values (e.g. Navarro et al., 2013; Pethybridge et al., 2018), normalization using a secondary consumer of a known trophic position (e.g. Olson et al., 2010; Post, 2002), and compound specific stable isotope analyses (e.g. Popp et al., 2007). Within fish muscle tissue, bulk $\delta^{13}\text{C}$ values can also be influenced by lipid content, as lipids have a lower $\delta^{13}\text{C}$ value than proteins (Abelson and Hoering, 1961; Park and Epstein, 1961). Lipid effects can be accounted for with chemical extractions (e.g. Pinnegar and Polunin, 1999) or a posteriori mathematical correction using carbon to nitrogen (C:N) ratios as lipid-content proxies (e.g. Logan et al., 2008).

Trophic influences on $\delta^{13}\text{C}$ values also need to be accounted for in carbon isotope analyses. Biochemical processes alter $\delta^{13}\text{C}$ values between a consumer and its prey (trophic discrimination factor; TDF), and this results in an increase by approximately 0.5–2.0‰ (Caut et al., 2009; DeNiro and Epstein, 1978; McCutchan et al., 2003; Post, 2002; Sweeting et al., 2007). Controlled feeding studies show that carbon TDFs for fish muscle are generally at the higher end of this range with estimates of 1.5‰ found across a variety of species (Sweeting et al., 2007) and 1.8‰ for *Thunnus* muscle specifically (Madigan et al., 2012). Cephalopods, an important prey group of tunas (Olson et al., 2016), are less studied but existing controlled studies showed limited (<0.5‰) increases in mantle $\delta^{13}\text{C}$ values relative to diet (Hobson and Cherel, 2006). Estimates for coastal and open ocean zooplankton fall closer to 1‰ (France and Peters, 1997). Therefore, if the trophic position of yellowfin tuna (*Thunnus albacares*) in the equatorial Pacific Ocean is observed to be approximately 4.5‰ (Houssard et al., 2017; Lorrain et al., 2015; Popp et al., 2007), then the difference between the base of the food web and tuna $\delta^{13}\text{C}$ values ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$) should be approximately 2 to 8‰ given documented variability in TDFs (0.5-2.0‰ across taxa linking phytoplankton to tunas) and food chain length from tunas down through to lower trophic level species (Fig. 1). Variations from these values and/or a high degree of individual variability could be indicators of highly dynamic migration areas.

Most previous studies that have used stable isotopes to examine the movements of highly mobile marine animals have focused on regional scales and higher latitudes where regional gradients in $\delta^{13}\text{C}$ values are more apparent (Cherel and Hobson, 2007; Cunjak et al., 2005; Hobson, 1999; Rubenstein and Hobson, 2004; Witteveen et al., 2009). A recent analysis of shark

muscle $\delta^{13}\text{C}$ values examined latitudinal trends in relation to modelled phytoplankton $\delta^{13}\text{C}$ values to establish global trends in shelf, oceanic, and deep sea trophic geography of sharks (Bird et al., 2018a). Our study applied a similar approach to tunas and focused primarily on the tropics and subtropics to examine animal movements, potential environmental drivers, and global-scale trends. Using a compiled dataset of $\delta^{13}\text{C}$ values and C:N (a proxy for bioenergetic condition) values of yellowfin (*Thunnus albacares*), bigeye (*T. obesus*), and albacore (*T. alalunga*) tunas sampled over a 16-year period from the major ocean bodies, our study aims were to: (i) map spatial patterns at a global scale (i.e. develop carbon isoscapes), (ii) test the influence of biological and environmental factors on the temporal and spatial patterns, (iii) relate environmental, temporal, and spatial variables to tuna bioenergetic condition, and (iv) use modelled baseline and observed tuna $\delta^{13}\text{C}$ values to identify likely transitional zones of tuna movements. Movement was further inferred using calculated isotopic niches (Jackson et al., 2011) based on baseline-corrected $\delta^{13}\text{C}$ values (this study) and nitrogen stable isotope ($\delta^{15}\text{N}$) values (Pethybridge et al., 2018). Based on previous tagging and stable isotope studies that demonstrate limited movements of tunas (Evans et al., 2011; Graham et al., 2010; Houssard et al., 2017; Schaefer et al., 2007; Schaefer and Fuller, 2002), we hypothesized that the $\delta^{13}\text{C}$ values of tropical tunas (i.e. yellowfin and bigeye) would track latitudinal baseline gradients. Given documented north-south migrations of the temperate albacore tuna (Nikolic et al., 2017; Williams et al., 2015), we hypothesized that $\delta^{13}\text{C}$ values for this species would not track baseline values as extensive movements across isoscapes should create a disconnect between tuna $\delta^{13}\text{C}$ values and the baseline values at the site of capture (Graham et al., 2010). Ultimately, identifying the biological and environmental mechanisms responsible for the large-scale patterns or isoscapes will improve our understanding of regional movements of tunas. Such data can inform stock assessment models and better assist fisheries managers and policy makers in managing ecologically dynamic and commercially valuable open-ocean predators.

2. Methods

2.1. Isotope data compilation

Overall, 4275 $\delta^{13}\text{C}$ values were compiled from the muscle tissue of yellowfin (*Thunnus albacares*), bigeye (*T. obesus*), and albacore (*T. alalunga*) tunas from published and unpublished regional studies and assembled in a global database (Fig. 2; Table 1). Samples spanned a 16-year period from 2000 to 2015. Measurements of tuna size (fork length, cm) were taken, and dates, positions, and fishing gear type were provided for each sampling event. Data were classified by ocean basin (Pacific, Atlantic including Mediterranean Sea, Indian, and Antarctic Oceans) and Longhurst Biogeographical Province (Longhurst, 1998). Longhurst provinces are shown in Figure 2 and defined in Table S1.

2.2. $\delta^{13}\text{C}$ lipid correction

Our dataset consists of both bulk and lipid-extracted samples. Generally, for aquatic samples, C:N ratios < 3.5 correspond to low lipid content and by association minor lipid bias (Hoffman and Sutton, 2010; Logan et al., 2008; Post et al., 2007). Given unlikely lipid bias and potential error created by variable C:N_{lipid-free} among tuna species, no corrections were applied to samples with C:N values ≤ 3.5. For δ¹³C values with C:N values > 3.5, mathematical corrections were applied (Logan et al., 2008) to produce lipid corrected tuna δ¹³C values (δ¹³C_{Lcorr_tuna}; Table 2). The correction equation was based on a dataset of bluefin tuna (*T. thynnus*) muscle with a maximum C:N of 6.5 so samples with C:N > 6.5 (n=47) were excluded from δ¹³C analyses. The equation used was derived from Fry (2002):

$$\delta^{13}\text{C}_{\text{Lcorr_tuna}} = P - \frac{P * F}{C:N} + \delta^{13}\text{C}_{\text{Bulk}}$$

where δ¹³C_{Lcorr_tuna} is the lipid corrected δ¹³C value, C:N is %C/%N, P is an estimate of the isotopic difference between protein and lipid (7.489), and F is an estimate of the C:N value of lipid-free tissue (3.097). Mathematical corrections were applied to 39.5% (yellowfin), 40.5% (bigeye), and 51.7% (albacore) of all samples used in δ¹³C analyses (n=4228). To assess the effect of lipid correction on δ¹³C values and determine if any potential lipid bias remained in the mathematically corrected values, bulk and lipid corrected δ¹³C values were plotted against C:N for the subset of samples that underwent mathematical lipid correction (3.5 < C:N ≤ 6.5) (Fig. S1). Equivalent comparisons were made for baseline corrected δ¹³C values (δ¹³C_{tuna-phyto}) (Fig. S1).

2.3. Baseline δ¹³C values

Baseline δ¹³C predictions from a global model of ocean biogeochemistry and isotopes, including both δ¹³C and δ¹⁵N values (Schmittner and Somes, 2016), were used to assess and correct for spatial and temporal variability in isotopic baselines (Fig. S2). The model included a three-dimensional (1.8° x 3.6°, 19 vertical levels) ocean circulation model forced with prescribed (fixed) monthly climatological winds (Weaver et al., 2001). The two stable carbon isotopes, ¹²C and ¹³C, were included for dissolved inorganic carbon and organic carbon including phytoplankton, zooplankton, sinking detritus, and dissolved organic carbon. The main relevant processes incorporated in the model included air-sea gas exchange, physical transport, biological uptake, and remineralization of organic carbon. Model results were provided for each respective year of a hindcast from year 2000 of a pre-industrial simulation including increasing atmospheric CO₂ and decreasing δ¹³C-atmospheric CO₂ following Schmittner et al. (2013). All model results were averaged annually over 130 meters of surface ocean. To account for the Suess effect, model predicted phytoplankton δ¹³C values given for year 2000 were subtracted from the phytoplankton δ¹³C values that corresponded to the year of tuna sampling (δ¹³C_{phyto}), that is 2000-2015. The difference was used to correct for the Suess effect in tunas (δ¹³C_{LScorr}; Table 2) with an average decline of 0.05‰ per year over the 16-year period. Note that the model hindcast simulation also accounted for CO₂-driven warming over this period, which affects δ¹³C_{phyto} values through changes in circulation, air-sea gas exchange, and uptake fractionation that is CO₂ and temperature-dependent. These processes contribute to a larger decrease in δ¹³C_{phyto} than would be expected from the Suess effect alone. As additional biogeochemical and hydrological

processes are also affected by changes in atmospheric CO₂ and temperature in the model, annual differences represent more than just the Suess effect.

2.4. Variability in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ and isotopic niche areas to infer movement

To infer regional differences in the degrees of tuna movement and population residency, the $\delta^{13}\text{C}_{\text{Lcorr_tuna}}$ values were subtracted from the model-predicted and Suess-corrected $\delta^{13}\text{C}$ values at the base of the food web ($\delta^{13}\text{C}_{\text{Scorr_phyto}}$) as:

$$\Delta^{13}\text{C}_{\text{tuna-phyto}} = \delta^{13}\text{C}_{\text{Scorr_phyto}} - \delta^{13}\text{C}_{\text{Lcorr_tuna}} \text{ (Table 2)}$$

The expected range of tuna $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values (X) if tunas were feeding in the same isoscape is represented as:

$$X(\Delta^{13}\text{C}_{\text{tuna-phyto}}) = \text{TP}_{\text{Tuna}} * \text{TDF} - 1$$

where TP_{Tuna} is a trophic position estimate (~4.5-5.0) based on regional datasets of compound-specific nitrogen isotopes of amino acids determined in tuna from the equatorial Pacific Ocean (Choy et al., 2015; Houssard et al., 2017; Lorrain et al., 2015; Olson et al., 2010; Popp et al., 2007), and the TDF values per trophic position range from ~0.5 (typically for lower trophic orders; DeNiro and Epstein, 1978; Post, 2002) to ~2‰ (1.8‰ in tuna; Madigan et al., 2012). Given this knowledge, over the timescale of muscle isotopic turnover—likely on the order of months rather than weeks (Madigan et al., 2012)—the expected range of tuna $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values if tunas were feeding in the same isoscape (thus not moving between contrasting isoscapes) was between -2 and -8‰ (Fig. 1). As diet and trophic position were assumed to be relatively constrained for a given species and region, higher intra-species variability was interpreted as an indication of population dispersal and inclusion of more recent arrivals as well as individuals at or near steady state with local isotope baselines.

Based on trends in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values, we developed a classification table to infer both the degrees of tuna movement (or occupancy) and population dispersal in yellowfin, bigeye, and albacore tunas sampled in the different Longhurst provinces (Table 3). The inferred degree of spatial movement was assigned to a score from 0 to 4, with higher values implying higher inferred degrees of movement. The following scores and movement categories were assigned for each species-Longhurst province dataset based on the median and range (i.e. 1.5 times the interquartile range (IQR)): 0 and “*limited movement*” = $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ with a median and range within -4 to -6‰, because values were constrained within a range consistent with local baselines given TP and TDF assumptions; 1 and “*moderate movements by some individuals*” = $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ with a median the same as in 1 but an extended range of -2 to -4‰ or -6 to -8‰ and therefore increased variability; 2 and “*moderate movement*” = $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ with an increased median within either -2 to -4‰ or -6 to -8‰ and a range between -6 to -8‰; 3 and “*high degree of movement by some individuals*” = $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ with the same median defined in 2 but with a wider range of <-2 or >-8‰; and 4 and “*high degree of movement*” = $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ with a median outside of <-2 or >-8‰. Population dispersal was also categorized on a scale of 0 to 4 based on inter-site variability in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values that fell within 1.5 of the IQR for a given species and Longhurst province: 0 = “*no dispersal*” due to minimal variability ($1.5 * \text{IQR} < 1\%$); 1 = “*low dispersal*” (range: 1–2‰); 2 = “*moderate dispersal*” (range: 2–3‰); 3 = “*high dispersal*” (range: 3–4‰); and 4 = “*very high dispersal*” (range >4‰). Given a presumed TDF of 1.8‰ for tunas, scores 3 and 4 and corresponding high dispersal classifications would correspond to $\sim \geq 2$ TPs of variability across individuals if caused purely by trophic differences. Given

corresponding diet data for tuna in the regions sampled in the present study (Duffy et al., 2017), this level of individual trophic variability is not expected and therefore, mixing across isoscapes was considered the most likely source. For these analyses, we assumed that model predictions are equally accurate in terms of both regional median and inter-quartile ranges and that any residual effect of C:N on $\delta^{13}\text{C}$ values not accounted for with mathematical corrections can be ignored.

Movement was further inferred for each species and Longhurst region based on isotopic niches calculated using the Stable Isotope Bayesian Ellipse in R (SIBER; Jackson et al., 2011) and Stable Isotope Analysis in R (SIAR; Parnell et al., 2010) packages in R (R Core Team, 2019). Similar to our calculation table based on $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values, we assumed that increased intra-specific and intra-region isotopic variability and associated increased isotopic niche values were driven by movement across isoscapes. Niche calculations were made using $\delta^{13}\text{C}_{\text{Lcorr_tuna}} - \delta^{13}\text{C}_{\text{Scorr_phyto}}$ ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$) and $\delta^{15}\text{N}_{\text{tuna}} - \delta^{15}\text{N}_{\text{phyto}}$ (See Pethybridge et al., 2018 for nitrogen isotope baseline correction methods). Bayesian standard ellipse areas (SEA_B), reported as ‰^2 values, were calculated alongside Bayesian credible intervals to provide a measure of isotopic variability of baseline-corrected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of tuna muscle. The SEA contains approximately 40% of the data and provides a measure of the core niche area as it is effectively the equivalent to standard deviation for bivariate data (Batschelet, 1981; Jackson et al., 2011). In addition to SEA_B , total area (TA) and SEA corrected for small sample sizes (SEA_c) were also calculated as measures of isotopic niche width. SEA_c , reported as ‰^2 , provides a measure of the representative isotopic niche breadth of fish sampled from each region. TA (‰^2) is the convex hull area contained within the smallest polygon containing all carbon and nitrogen Δ values and as such reflects total isotopic diversity (Layman et al., 2007). More detailed information for SEA_c values was derived from calculations of eccentricity (E) and theta (θ°) (based on methods described by Reid et al., 2016; Shipley et al., 2019; Turner et al., 2010). Briefly, eccentricity is a measure of the relative contributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to observed variance within the standard ellipse area. Values closer to 0 indicate contributions of both delta values and values approaching 1 reflect variability driven by a single isotope tracer. Theta, reported in degrees, provides a measure of the relative angle of isotopic dispersion relative to $\delta^{13}\text{C}$ with values closer to 0° corresponding to $\delta^{13}\text{C}$ as the primary driver and values closer to 90° instead suggesting $\delta^{15}\text{N}$ as the primary influence. Negative theta values reflect opposing trends where $\delta^{13}\text{C}$ values increase with decreasing $\delta^{15}\text{N}$ values, which can provide evidence of baseline vs. trophic influences on intra-group isotopic variability as increases in trophic position would be expected to produce a positive relationship.

2.5. Tuna bioenergetic condition estimates

Tuna bioenergetic condition was compared across regions and in relation to environmental variables using muscle C:N as a proxy for lipid content and thus bioenergetic condition. Fish muscle C:N values increase linearly with lipid content due to the high percentage of carbon and the absence or minimal nitrogen content in lipids (Logan et al., 2015, 2008). A regression equation developed from Atlantic bluefin tuna muscle samples was used to convert C:N values to percent lipid content, $\% \text{ lipid} = 3.9972 * \text{C:N} - 11.4663$ (Logan et al., 2015). The C:N dataset used for the percent lipid estimates had a maximum C:N value of 7.3, which results in a percent lipid content estimate of 17.7%. Any samples in our C:N dataset with values > 7.3

are reported as >17.7%. Samples with C:N > 7.3 were converted to percent lipids only for mean estimates (Table 1). Chemical lipid extractions were applied to some of our samples (yellowfin: 36.9%, bigeye: 34.4%, albacore: 15.3%) prior to elemental composition analysis and therefore were not included in this condition analysis. Some muscle samples obtained from regions of the tuna other than caudal dorsal muscle (e.g. head, ventral) were also excluded from condition analyses since lipid content can vary across these different body regions in tunas (Balshaw et al., 2008). Following exclusion of lipid extracted and non-dorsal muscle samples, the remaining dataset available for C:N analyses contained 2205 samples.

2.6. Environmental data

A suite of available environmental variables was selected to explore physical forcing on tuna $\delta^{13}\text{C}$ values at the surface and at depth since these tunas are vertical foragers across epipelagic and mesopelagic zones (Olson et al., 2016). Surface variables included sea surface temperature (SST, °C) and chlorophyll-*a* (Chl-*a*, mg m⁻³). Monthly averaged NOAA Optimum Interpolation SST data were acquired from the NOAA National Centre for Environmental Information (<http://www.esrl.noaa.gov/psd/>) using AVHRR version 2 (Reynolds et al., 2007), available at <https://ncics.org/data/obs4mips/>. The spatial resolution of the SST data was a 0.25° grid, and this product was available for the years 2001–2014. For tuna sampling years outside this range, climatologies for the next closest year were used.

Monthly Chl-*a* concentrations were acquired from GlobColour data (<http://globcolour.info>) which has been developed, validated, and distributed by ACRI-ST, France and provides a continuous dataset of merged L3 Ocean Colour product from 1997 to 2016. Monthly means of net primary production (NPP, mg C m⁻²d⁻¹) were derived from a vertically generalized production model (VGPM, <http://www.science.oregonstate.edu/ocean.productivity>; Behrenfeld and Falkowski, 1997) available at a 9 km resolution which we interpolated onto a 1°x1° grid.

Variables at depth included the mixed layer depth (MLD, m), depth of the 12°C isotherms ($D_{\text{iso}12}$, m), and oxygen concentrations (mL L⁻¹) at three depths (375 m $\text{O}_{2\text{-}375\text{m}}$, 100 m below the MLD $\text{O}_{2\text{-}100\text{m}}$, and 50 m below the MLD $\text{O}_{2\text{-}50\text{m}}$), which were taken from daily CARS climatology (Dunn and Ridgway, 2002; Ridgway et al., 2002) updated using the 2006-2015 Argo-only dataset. The MLD climatology defined the depth of the mixed layer based on an absolute temperature difference of 0.2°C from the surface (de Boyer Montégut et al., 2004). The variables at depth do not vary annually as they are based on a climatology.

For all environmental variables, spatial linear interpolation was used to collocate data to the tuna sample location. For each tuna location, environmental variables were also obtained at the matching tuna sampling date minus 3 and 6 months to account for time delays for prey tissues to be incorporated in tuna muscle (months; Madigan et al., 2012). If environmental data were not available for a particular year, data for the next closest year were used.

2.7. Data analyses

Boxplots were used to compare $\delta^{13}\text{C}_{\text{corr}}$ values, $\Delta^{13}\text{C}_{\text{tuna-phyto}}$, C:N ratios and isotopic niche areas between regions and tuna species. These exploratory analyses were performed only for Longhurst province-species datasets with $n \geq 5$.

General trends in $\delta^{13}\text{C}_{\text{corr}}$ and $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values in relation to latitude expressed as distance from the equator and C:N were assessed using linear and non-linear regression, respectively. Normality was assessed visually using QQ plots.

2.8. Generalized additive mixed models and isoscapes

Generalized additive mixed models (GAMMs) were used to test potential predictors of $\Delta^{13}\text{C}_{\text{tuna-phyto}}$, $\delta^{13}\text{C}_{\text{LScorr}}$ values, and lipid content. The predictors included spatial (latitude and longitude), morphometric (tuna fork length), and environmental (SST, Chl-*a*, NPP, MLD, D_{iso} , and O_2) variables. Longhurst province was incorporated as a random effect to account for intra group correlations and overdispersal that frequently arises in spatial analyses (Wood, 2006). Before constructing GAMMs, matrix scatterplots and variance inflation factors (VIF) from the usdm package (Naimi, 2015) in R (R Core Team, 2019) were used to confirm that collinearity was not apparent among the explanatory variables. Individual GAMMs were fitted for each set of environmental variables at the matching sample date (D) and D minus 3, 6, and 9 months prior to tuna capture. For each tuna species, the best time-related environmental variable, determined by the percent deviance explained (DE%, or pseudo R-squared), was retained and used in subsequent models (Tables S3 and S4).

GAMMs were constructed in R using the gamm4 package (Wood, 2006) and the Gaussian family with an identity link function. Smoothing splines were used to examine non-linear fits for all marginal terms considered in the model while a scale-invariant tensor product was used to model the covariates for geographical location. Model selection was performed manually using a backward elimination approach, and the best model fit was selected using the Akaike information criterion for small sample sizes (AIC_c) and DE%. To determine the amount of variation explained by each predictor variable, we fitted a separate model for individual predictor variables. Subsequent models were then fitted, including each of the remaining smooth terms, one at a time, to assess additional variation explained. To test the performance of each model, standard diagnostic checks were performed on the residuals from the model, and constant variance was observed.

A GAMM based on two-dimensional thin plate regression splines fitted to the geographical location and interpolated at a $\sim 2^\circ$ resolution was used to visually explore broad-scale patterns in predicted $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ and lipid content. Due to the potential effect of year, isoscapes were produced for both the earlier (2000–2007) and later (2008–2015) periods of our analysis.

3. Results

3.1. Lipid corrections and tuna $\delta^{13}\text{C}$

Both bulk and $\delta^{13}\text{C}_{\text{Lcorr_tuna}}$ datasets had negative correlations with C:N while $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values only declined for the bulk $\delta^{13}\text{C}$ dataset (Fig. S1). Bulk $\delta^{13}\text{C}$ values were lower ($-17.9 \pm 2.1\text{‰}$) than lipid corrected ($-16.3 \pm 1.6\text{‰}$) values with a modelled maximum offset of 4.3‰ for high lipid samples (Fig. S1). Within the C:N range for which lipid corrections were applied

($3.5 < C:N \leq 6.5$), the modelled decrease in $\delta^{13}C$ values with increasing C:N was 3.3 and 6.2‰ for $\delta^{13}C_{Lcorr_tuna}$ and bulk $\delta^{13}C$ values, respectively. For baseline-corrected $\delta^{13}C$ values ($\Delta^{13}C_{tuna-phyto}$), the offset between tuna and baseline values decreased by 2.1‰ for bulk $\delta^{13}C$ values while modelled isotope spacing increased slightly ($< 1\%$) for $\delta^{13}C_{Lcorr_tuna}$ values (Fig. S1).

3.2. Global and ocean region observations

Global mean $\delta^{13}C_{LScorr}$ values were lowest in albacore ($-17.2 \pm 1.0\%$) and similar in bigeye ($-15.9 \pm 1.0\%$) and yellowfin ($-15.7 \pm 0.9\%$) tunas (Table 1). The range of observed $\delta^{13}C_{LScorr}$ values was greatest in albacore (7.0‰) and smallest in bigeye (5.2‰). Across ocean regions, highest mean $\delta^{13}C_{LScorr}$ values were observed in Longhurst provinces within the eastern Pacific Ocean and central tropical Pacific Ocean for yellowfin and bigeye and the western Pacific Ocean for albacore (Figs 3-5; S3). The lowest mean $\delta^{13}C_{LScorr}$ values were observed in the AUSE Longhurst province of the western Pacific and NASW and GFST provinces in the western North Atlantic Ocean for yellowfin and bigeye (Figs 3-4; S3). For albacore, the lowest $\delta^{13}C_{LScorr}$ values were in the eastern Atlantic in the NADR and CNRY provinces (Fig 5; S3).

Differences between $\delta^{13}C$ values of tuna and phytoplankton ($\Delta^{13}C_{tuna-phyto}$; Table 2), used to report degrees of spatial movement and population dispersal, were globally similar among species with means varying between -5.0 to -5.3‰ (Table 1). Median $\Delta^{13}C_{tuna-phyto}$ across Longhurst provinces ranged from -4.6 to -8.3‰, -3.9 to -7.9‰, and -4.0 to -7.0‰ for yellowfin, bigeye, and albacore, respectively (Figs. 3-5). Minimum differences between $\Delta^{13}C_{tuna-phyto}$ values were within the anticipated -2 to -8‰ range, but maximum differences exceeded this range for yellowfin and bigeye in several regions (Figs. 3,4). Elevated values ($> -8\%$) were observed in the GUIN (Atlantic) and PEQD (Pacific) Longhurst provinces for both yellowfin and bigeye translating to a “*high degree of movement by some individuals*” classification (Table 3). Similar maximum values were observed for yellowfin in the PNEC province (Fig. 3) which were also classified as “*high degree of movement*” (Table 3). For bigeye, the GFST (Atlantic) province included high $\Delta^{13}C_{tuna-phyto}$ differences (maximum of -7.6‰) (Fig. 4). While none of the maximum albacore values exceeded -8‰, values for bordering provinces in the Northeast Atlantic (NADR and NECS) were -7.9 and -7.7‰, respectively, and therefore were classified as “*high degree of movement by some individuals*” and “*moderate movement*”, respectively (Table 3). ARCH, TASM, and SANT, provinces in the western Pacific and Antarctic, had similarly high (-7.4 to -7.7‰) maximum values (Fig. 5) and “*moderate movement*” classifications for albacore.

Regional variability in $\Delta^{13}C_{tuna-phyto}$ values, used to report levels of population dispersal, differed between and within the Longhurst provinces with ranges among individual tuna of 0.0 to -4.9‰ (yellowfin), 0.0 to -5.2 (bigeye), and -0.5 to -5.2‰ (albacore) (Figs. 3-5). The largest ranges ($> -3.6\%$) among non-outlier values were found in the bordering WARM and PEQD regions of the equatorial Pacific for both yellowfin and bigeye (Figs. 3,4), which were assigned a classification of “*very high dispersal*” (Table 3). Yellowfin in the GUIN region also had “*very high dispersal*” with a range of 4.7‰. AUSE (yellowfin), SPSG (both yellowfin and bigeye), and ARCH (both yellowfin and bigeye) regions in the Pacific had similarly high ranges (Fig. 3) and were assigned the “*high dispersal*” classification (Table 3). For albacore, the greatest ranges ($> -3.6\%$) occurred in the bordering ARCH and SPSG Longhurst provinces (Fig. 4) and had a dispersal classification of “*very high*” (Table 3). Relatively low regional variability was observed in the Indian Ocean for all species (Figs. 3-5), and in albacore from the MEDI province (the

tropical yellowfin and bigeye tunas were not sampled from this region) (Fig. 5). These regions all had population dispersal scores of “no”, “low”, or “moderate dispersal” (Table 3).

SEA_B, SEA_C, and TA values were highest for Longhurst provinces in the Pacific Ocean for all three tuna species (Table S2). For albacore, SEA_B, SEA_C, and TA values from the SPSG were elevated (e.g. SEA_C>10) relative to all other sampled Longhurst regions (Fig. 5; Table S2). For bigeye and yellowfin, highest SEA_B, SEA_C, and TA values were observed in the SPSG, WARM, and PEQD regions (Table S2).

Eccentricity values fell close to 1 for most provinces (mean across Longhurst provinces $\geq$ 0.8 for all three tuna species) while theta was closer to 90° (absolute mean across Longhurst provinces $> 70^\circ$ for all three tuna species) indicating that most of the intra-specific variability was driven by variation in $\delta^{15}\text{N}$ values (Table S2). Theta values were negative for many provinces (37.5%, 31.3%, and 44.4% of provinces for yellowfin, bigeye, and albacore, respectively), which reflects increasing $\delta^{13}\text{C}$ values with decreasing $\delta^{15}\text{N}$ values in these regions (Table S2).

C:N values were generally low for yellowfin and bigeye tunas but higher and more variable for albacore tuna (Figs. 3-5). For yellowfin and bigeye, median values for all provinces were < 4 (4.5% lipid content), but several outliers (with median C:N values ~ 5 , 8.5% lipid content) were observed in the western and central Pacific Ocean (WCPO) in the WARM province (Figs. 3,4). In the WCPO, similar outliers with elevated C:N values were present in the WARM (yellowfin) and NPTG (bigeye) provinces. For the Indian Ocean, yellowfin with elevated C:N values (C:N ~ 4 -5) were present in the MONS province (Fig. 3). Based on regressions of muscle C:N and lipid content, median values for yellowfin and bigeye correspond to $< 3\%$ lipid content. For albacore, the north Atlantic Ocean had the highest C:N values with a median value > 4.5 (6.5% lipid content) in the NADR and NECS and individual values as high as 8 ($> 17.7\%$ lipid content). While the regional median C:N was < 3.9 (4.1% lipid content) for albacore in the ARCH and AUSE provinces of the Southwest Pacific Ocean, many outliers had elevated C:N between 4 and 6 (4.5% to 12.5% lipid content) (Fig. 5).

3.3. Model results

The best model (i.e. lowest AIC_c value) for $\delta^{13}\text{C}_{\text{LScorr}}$ values of all species combined spatial, environmental, and year variables (DE% = 65.3% in yellowfin, 70.0% in bigeye, and 80.7% in albacore) (Table S3). According to AIC_c, year was one of the best standalone predictive variables in all tuna species, with more negative $\delta^{13}\text{C}_{\text{LScorr}}$ values predicted in later sampling years with intercepts reached at 2006 or 2007 (Fig. 6). Spatial variables were also ranked highly for all species with an inverse relationship occurring between latitude and $\delta^{13}\text{C}_{\text{LScorr}}$ values with higher values around the equator and lower values of $\delta^{13}\text{C}_{\text{LScorr}}$ at high latitudes (Fig. 6; Fig. S3). There were no clear relationships with longitude.

Similarly, linear regressions of $\delta^{13}\text{C}_{\text{LScorr}}$ values with latitude expressed as distance from the equator all had significant negative correlations (Fig. S4; All tuna: $R^2=0.43$; $F_{1,4226}=3152$; $p<0.001$, yellowfin: $R^2=0.06$; $F_{1,1617}=106.4$; $p<0.001$, bigeye: $R^2=0.04$; $F_{1,932}=36.5$; $p<0.001$, albacore: $R^2=0.52$; $F_{1,1781}=1781$; $p<0.001$). The intercept of the best fit lines for all tuna combined was 5‰ above the intercept of modelled phytoplankton $\delta^{13}\text{C}$ values while separation for individual tuna species were 5.5‰ (yellowfin), 5.2‰ (bigeye), and 3.8‰ (albacore) (Fig. S4). The slope of the best fit line for all tuna combined was -0.05 (‰ change in $\delta^{13}\text{C}$ per degree

of latitude) relative to -0.08 for associated modelled phytoplankton. Yellowfin and bigeye best fit line slopes (-0.02) were similar to associated phytoplankton (-0.03 for both datasets) while the slope for the albacore best fit line (-0.05) was less steep than the associated phytoplankton baseline (-0.11). While all regressions showed a significant negative correlation between modelled phytoplankton $\delta^{13}\text{C}$ values and latitude ($P < 0.001$ for all comparisons), R^2 values varied across datasets. Lower values were observed associated with the sampling locations for yellowfin ($R^2 = 0.10$) and bigeye ($R^2 = 0.13$) while modelled phytoplankton $\delta^{13}\text{C}$ values associated with the albacore dataset had an R^2 of 0.82.

For $\Delta^{13}\text{C}_{\text{tuna-phyto}}$, the full tuna dataset had a significant negative relationship with latitude ($R^2 = 0.09$; $F_{1,4232} = 443.5$; $p < 0.001$), but this relationship was mainly driven by albacore ($R^2 = 0.51$; $F_{1,1674} = 1778$; $p < 0.001$) (Fig. S4). For the tropical tunas, bigeye had a weak negative relationship ($R^2 = 0.01$; $F_{1,934} = 9.5$; $p < 0.01$) while yellowfin $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ was not correlated with latitude ($R^2 = 0.00$; $F_{1,1620} < 0.01$; $p = 0.98$) (Fig. S4).

Smooth terms for most environmental variables were significant in all tuna species (Table S3). Oxygen concentration at depth was consistently the best ranked environmental model (according to AIC_c). For all species, predicted $\delta^{13}\text{C}_{\text{LScorr}}$ values declined after oxygen concentrations reached 4 mL L^{-1} (Fig. 6). The next best ranked environmental variable was SST with $\delta^{13}\text{C}_{\text{corr}}$ values predicted to increase at higher temperatures with the predicted intercepts reached at 25.8°C, 25.9°C, and 25.0°C for yellowfin, bigeye, and albacore, respectively (Fig. 6). D_{Iso12} consistently showed a parabolic curve in which $\delta^{13}\text{C}_{\text{LScorr}}$ values were highest at about 250, 300, and 550 m depth for yellowfin, bigeye, and albacore, respectively. As Chl-*a* and NPP increased, $\delta^{13}\text{C}_{\text{LScorr}}$ values were predicted to increase in yellowfin and decrease in bigeye and albacore. Trends with MLD were less clear.

Length was a less efficient predictor of $\delta^{13}\text{C}_{\text{LScorr}}$ values in all tuna species, globally. Global patterns varied among species; decreasing in bigeye, increasing in albacore, and the trend unclear in yellowfin (data not shown).

Model results of $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ were largely similar to those for $\delta^{13}\text{C}_{\text{LScorr}}$ values with the best models (i.e. those with the lowest AIC_c values) including oxygen at depth and the spatial and temporal variables (Fig. 7; Table S4). Predictive ability was slightly higher ($\text{DE}\% = 71.0\%$ in yellowfin, 71.5% in bigeye, and 84.0% in albacore). For all tuna species, the most significant standalone variable was year followed by oxygen at depth. Annual changes in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ closely matched corresponding $\delta^{13}\text{C}_{\text{LScorr}}$ patterns. Similar to $\delta^{13}\text{C}_{\text{LScorr}}$, oxygen at depth was the best environmental variable; values of $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ declined with increasing oxygen at depth for all three species with the caveat that values then increased at highest oxygen concentrations ($> 4 \text{ mL L}^{-1}$) for albacore. Relationships between $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ and SST were the inverse of corresponding $\delta^{13}\text{C}_{\text{LScorr}}$; $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ instead declined as SST increased. For latitude, $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ increased in northern latitudes relative to the equator for all three tuna species. In southern latitudes, albacore $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ showed a similar pattern while yellowfin and bigeye instead showed slight declining trends with distance from the equator (Fig. 7).

The model predictive ability of C:N ratios was reasonably good for all tuna species (59.0 to 65.0 $\text{DE}\%$) (Table S5). The best model (i.e. lowest AIC_c value) for yellowfin and bigeye was a variable model that included year and the spatial variables while oxygen at depth was most influential for albacore (Table S5).

3.4. Spatio-temporal patterns

All tuna species showed strong spatio-temporal patterns of $\delta^{13}\text{C}_{\text{LScorr}}$ values with distinct geographical regions identified in the GAMM predicted and interpolated isoscapes (Fig. S3). Clear differences between the two selected time periods were observed with higher values predicted in the earlier (2000-2007) sampling years for each of the ocean basins. Largest temporal differences were observed in the Pacific Ocean and in the southwestern Indian Ocean. In both sampling periods, predicted $\delta^{13}\text{C}_{\text{LScorr}}$ values were highest in the western central Pacific Ocean and lowest in the North Atlantic Ocean and southwestern Pacific and Indian Oceans for all tuna species.

Predicted $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ varied spatially during both periods for the three tuna species (Fig. 8). During 2000-2007, the most negative $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values, suggesting higher degrees of spatial movement, for bigeye and yellowfin were in the eastern tropical Pacific while albacore values were most negative in the southern sampling extent of our western and central Pacific dataset. During 2008-2015, bigeye and yellowfin data were only available for the Pacific and Indian Oceans, where most negative values occurred in the central Pacific. For albacore, most negative values were in the Northeast Atlantic region (Fig. 8).

Maps of model predicted C:N values for each tuna species sampled over the study period showed few spatial gradients (Fig. 9). Yellowfin values were consistently low across ocean regions and sampling periods. Bigeye C:N values were low and uniform throughout much of the sampled area except for some elevated values in the central Pacific Ocean. For albacore, C:N values were highest in the Atlantic Ocean (Fig. 9).

4. Discussion

An understanding of top predator movements and trophodynamics in the open ocean is crucial to informing stock assessments of commercially important species, and in predicting and determining shifts in a changing climate. Here we provide evidence of potential tuna movement and residency patterns, illustrating how spatial isotope analyses can provide insight into the habitat use of large migratory predators to directly inform conservation and management efforts. Given stable isotope theory, we assumed greater regional residency where the difference between corrected-tuna and model-derived phytoplankton $\delta^{13}\text{C}$ values ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$, ‰) was between -2 and -8‰. By correcting for known lipid and Suess effects and adjusting for baseline variability our study demonstrates a novel and rigorous approach employing tuna $\delta^{13}\text{C}$ values to reflect spatiotemporal changes in movement patterns at a global scale. Predictive models of $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values allowed us to determine which environmental variables were explaining observed temporal, spatial, and ontogenetic patterns in tuna foraging habitats. Combining baseline-corrected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data to calculate isotopic niche width allowed for further assessment of individual isotopic variability as an indicator of population dispersal across regional isoscapes. Assessing additional variability in percent lipid as derived from C:N values further assisted in understanding tuna movements and trophodynamics.

4.1. Temporal, spatial, and environmental gradients

Tuna $\delta^{13}\text{C}_{\text{LScorr}}$ values declined across sampling years for all three tuna species, despite correcting for Suess and additional climate effects on phytoplankton. The decline was continuous across sampling years for albacore while yellowfin and bigeye declines were slightly delayed until 2003 (Fig. 6). This observed decline was thoroughly explored using time-series analysis and theoretical modelling (Lorrain et al., 2020). Analyses by Lorrain et al., (2020) showed that our observed temporal declines are most likely due to temporal shifts in phytoplankton community structure and/or physiology that differ across ocean basins (greater temporal decline in tuna muscle $\delta^{13}\text{C}$ in the Pacific than Atlantic and Indian Oceans).

In general, phytoplankton and zooplankton baseline $\delta^{13}\text{C}$ values increase with increasing SST toward the equator (Magozzi et al., 2017; McMahon et al., 2013). Here we demonstrate similar patterns for three tuna species indicating, in agreement with previous literature (e.g. Bird et al., 2018a), that marine carbon isoscapes can be directly linked with top predators. Overall adherence to these latitudinal trends also suggests relatively constrained movements within the timescale of muscle isotopic turnover (months; Madigan et al., 2012) as foraging across a broad latitudinal gradient was expected to blur baseline differences in phytoplankton and zooplankton $\delta^{13}\text{C}$ values (exceptions discussed below). These baseline gradients would not be apparent in higher trophic level predators if e.g. the tuna sampled in the present study frequently traversed these latitudinal isoscapes within months prior to capture. A global analysis of shark muscle $\delta^{13}\text{C}$ values found a similar trend for sharks foraging in continental shelf, but not pelagic, waters (Bird et al., 2018a). Similar patterns have been documented for yellowfin and bigeye in the Pacific based on latitudinal gradients in bulk $\delta^{15}\text{N}$ values (Graham et al., 2010; Houssard et al., 2017; Olson et al., 2010). Popp et al. (2007) demonstrated that latitudinal patterns in yellowfin muscle bulk $\delta^{15}\text{N}$ values were indicative of baseline effects based on amino acid stable isotope analysis (AA-SIA). Sharks inhabiting the continental shelf and the three tuna species included in our analysis—based solely on similarity in latitudinal trends in muscle $\delta^{13}\text{C}$ and underlying baseline $\delta^{13}\text{C}$ values—appeared to have constrained movements. Mean $\delta^{13}\text{C}$ differences between phytoplankton and all three tuna species ($\sim 5\text{‰}$) were similar to the 4.6‰ global average difference reported for sharks (Bird et al., 2018a) and consistent with a presumed average tuna TP of 4.5 to 5.0 based on collective expected TDFs in the trophic pathway to tunas (Caut et al., 2009; France and Peters, 1997; Hobson and Cherel, 2006; Madigan et al., 2012; Sweeting et al., 2007) (Fig. 1). Preservation of latitudinal baseline $\delta^{13}\text{C}$ gradients at the global scale is not surprising for yellowfin or bigeye as these tropical tunas tend to have mainly east-west movements and more constrained north-south movements in most of their global distribution (Evans et al., 2011; Fonteneau and Hallier, 2015; Schaefer et al., 2007; Schaefer and Fuller, 2002, 2009).

Species undertaking extensive north-south migrations would be expected to have only a weak or no correlation with latitudinal baseline values as foraging across different isoscapes should cause tissue $\delta^{13}\text{C}$ values to reflect a mix of baseline values rather than solely the baseline of their sampling location. Open ocean shark $\delta^{13}\text{C}$ values, for example, did not closely match baseline latitudinal trends, which could be due to large scale movements and foraging across isoscapes and a consequent homogenization of latitudinal baseline values (Bird et al., 2018a). Albacore tuna are known or presumed to undertake long distance north-south migrations between foraging and spawning grounds (Nikolic et al., 2017; Williams et al., 2015) and therefore a similar homogenization and disassociation from baseline gradients was expected for

this species. While muscle tissue may not reach isotopic steady state at any given foraging ground for highly migratory species, some degree of resident feeding will reflect at least a fraction of the local $\delta^{13}\text{C}$ baseline. Our assumption that muscle $\delta^{13}\text{C}$ values of highly migratory species would blur isotopic baselines due to feeding and movement across isoscapes may have been overly simplistic with regards to species with directed movements between spawning and foraging habitats. Tunas have been described as “energy speculators” that undertake long migrations in search of productive foraging grounds (Brill, 1996). Upon reaching a productive foraging ground, tunas would begin to incorporate local $\delta^{13}\text{C}$ baseline values in their tissues. For example, Atlantic bluefin tuna are known to undergo extensive north-south migrations throughout the North Atlantic (Mather et al., 1995), but their mean muscle stable isotope values still reflect local isoscapes (Logan, 2009; Logan et al., 2015). However, individual isotopic variability is high, likely due to past migrations from different isoscapes and different arrival times to the areas of capture (Estrada et al., 2005; Logan et al., 2015). While albacore $\delta^{13}\text{C}$ values tracked baseline values across latitudes, further exploration of this relationship revealed that the rate of change for tuna $\delta^{13}\text{C}$ values was far less than that observed across the same locations for modelled phytoplankton and so the isotopic spacing between tuna and local baselines varied negatively with latitude (Fig. S4). This latter pattern is consistent with albacore retaining some baseline isotope values from prior north-south migrations; fish foraging in higher latitudes with lower baseline $\delta^{13}\text{C}$ values would have positively biased separation from local baselines while fish foraging near the equator with elevated phytoplankton baseline values would be negatively biased from previous foraging in high latitudes. Yellowfin and bigeye muscle $\delta^{13}\text{C}$ relationships with phytoplankton were instead closely linked, which is consistent with spatially constrained movements.

The extent to which highly migratory predator muscle $\delta^{13}\text{C}$ values will reflect isotope gradients is related to the duration of residency and feeding intensity within a given isoscape as well as tissue turnover rates. A fish would be expected to reflect local baselines if it remains resident in that region for a time sufficient for the sampled tissue to reach isotopic steady state. While migratory tunas may not reside and feed in any given area for a sufficient duration to reach isotopic steady state, muscle tissue from the relatively small (fork length ~ 80-90 cm) tunas sampled in our study should at least partly reflect local baselines given the elevated metabolic rates and regional endothermy attributes of these species (Dickson and Graham, 2004; Olson et al., 2016) and relationships between size, metabolic rate, and isotopic turnover rates (Thomas and Crowther, 2015; Vander Zanden et al., 2015). By contrast, pelagic sharks from the Bird et al. (2018a) analysis would presumably have slower isotopic turnover rates based on estimates from a representative shark species that exhibits ram ventilation (Logan and Lutcavage, 2010) and larger average size (178 ± 61.0 cm TL) (Bird et al., 2018a, 2018b). These larger pelagic sharks with slower isotopic turnover rates would likely not reflect local baselines due to the mismatch between regional residency and isotopic turnover. For example, muscle $\delta^{15}\text{N}$ values of shortfin mako sharks (*Isurus oxyrinchus*) of a similar size (178-232 cm FL) sampled in southern New England waters did not reflect known seasonal diet shifts and associated migrations between offshore and shelf waters (MacNeil et al., 2005). Shortfin makos are regional endotherms (Carey and Teal, 1969) with among the highest measured routine metabolic rates of any shark species (Sepulveda et al., 2007), so muscle tissue of other large pelagic sharks would also be unlikely to reflect local isoscapes from seasonal foraging grounds. These differences in size, metabolic rate, and associated isotopic incorporation rates may explain the disconnect from baseline trends for

pelagic shark $\delta^{13}\text{C}$ values (Bird et al., 2018a) as opposed to the significant correlations observed in our tuna dataset.

Our models showed that spatiotemporal patterns in tuna $\delta^{13}\text{C}_{\text{LScorr}}$ and $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values were largely related to changes in oxygen concentrations at depth. The oxygen minimum layer was the most powerful environmental predictor of baseline-corrected tuna $\delta^{15}\text{N}$ values for the same tuna sampled in this study (Pethybridge et al., 2018) of which tuna trophic position was shown to decline under reduced oxygen concentrations. Tuna $\delta^{13}\text{C}_{\text{LScorr}}$ and $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ instead generally increased under reduced oxygen conditions (Figs. 6 and 8). Therefore, relationships between tuna isotope values and oxygen at depth could be influenced by vertical $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes since baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values tend to decrease and increase with depth, respectively (Altabet et al., 1991; Miller et al., 2008; Richards et al., 2019). As the model-derived phytoplankton $\delta^{13}\text{C}$ values were based on surface waters, model corrections would not account for vertical baseline shifts. If declining trends in tuna $\delta^{13}\text{C}_{\text{LScorr}}$ and $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values with increasing oxygen at depth are a result of vertical baseline differences, this relationship would suggest that tuna vertical feeding is influenced by oxygen concentration, which in turn would provide support for foraging habitat alteration with ocean warming. These relationships would be expected for yellowfin as this species is more vertically constrained and limited by oxygen concentrations ($>3.5 \text{ ml O}_2 \text{ l}^{-1}$ required; Brill et al., 2005). Bigeye instead routinely feed in the mesopelagic zone (Lam et al., 2014; Schaefer and Fuller, 2002), can tolerate low oxygen concentrations ($<1.5 \text{ ml O}_2 \text{ l}^{-1}$; Brill et al., 2005), and thus would not be expected to vary foraging habitat across a higher oxygen concentration gradient. The decline in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ with increasing dissolved oxygen concentrations at depth follows a steeper gradient for bigeye than yellowfin, which is consistent with bigeye only being impacted by the lowest oxygen concentrations (i.e. $<1.5 \text{ ml O}_2 \text{ l}^{-1}$) and yellowfin vertical distribution and foraging being influenced across a broader range of low dissolved oxygen values (i.e. $<3.5 \text{ ml O}_2 \text{ l}^{-1}$). Albacore tolerance of low dissolved oxygen is less than bigeye and similar to yellowfin (Arrizabalaga et al., 2015; Sund et al., 1981). While albacore $\delta^{13}\text{C}_{\text{LScorr}}$ values decline with increasing oxygen at depth, the more parabolic $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ relationship with oxygen concentration may reflect combined influences of vertical $\delta^{13}\text{C}$ baselines, trophic position, and body condition across different vertical foraging habitats (Table S5; Pethybridge et al., 2018). The apparent tracking of vertical $\delta^{13}\text{C}$ baseline gradients in tuna muscle with oxygen concentration at depth suggests feeding at depth follows the relative physiological tolerances of these tuna species. Consequently, foraging habitat could be impacted by habitat compression resulting from the predicted expansion of the oxygen minimum layer with ocean warming (Oschlies et al., 2008; Stramma et al., 2012).

4.2. Spatial movement and population dispersal patterns

While variability and uncertainty in trophic discrimination factors (TDFs) for tunas and underlying lower trophic level taxa limit our ability to interpret modelled differences between tuna and phytoplankton $\delta^{13}\text{C}$ values, some general patterns emerged. High $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values near or beyond the extremes of the range presumed based on trophic enrichment (-2 to -8‰) and high individual variability ($\geq 3\text{‰}$) provided evidence of potential movements and dispersal across isoscapes (Table 3). While trophic diversity cannot be completely ruled out as an alternative explanation for these patterns, $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values near or outside of our assumed -2 to -8‰ would require TDFs across trophic levels to be consistently at the higher or lower range of TDFs

expected for these species. The higher tuna-phytoplankton $\delta^{13}\text{C}$ offsets observed in several regions could be the result of higher TDFs across trophic linkages in these food webs, but presuming tuna TPs of ~ 4.5 , these greater offsets would require all trophic linkages to be enriched in ^{13}C relative to diet by almost 2‰. Several controlled feeding studies have shown a positive relationship between fish muscle TDFs and temperature (Bloomfield et al., 2011; Martino et al., 2019), which could bias spatial trends in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values. However, $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values in our dataset were lower in the warmer SST regions near the equator relative to higher latitudes, suggesting factors other than TDF variability are driving these patterns. Similarly, variability in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values consistent with our “*high dispersal*” and “*very high dispersal*” classifications (Table 3) would require $\geq$ two trophic levels of dietary segregation among individuals in a given foraging location over the timescale of muscle isotopic turnover (months), a degree of individual variability not consistent with past diet studies (Duffy et al., 2017). Tuna size was not included in our best GAMMs (i.e. those with lowest AIC_c values), which, given that tuna diet and TP often vary ontogenetically (Olson et al., 2016), suggests observed $\delta^{13}\text{C}$ variability was explained more by spatial baseline than trophic differences.

Moderate to high degrees of movement were observed for all three tuna species in several regions of the Atlantic and Pacific oceans (Table 3). The elevated values relative to planktonic baselines are not all due simply to higher tuna TP in these regions, as corresponding TP estimates based on model-corrected $\delta^{15}\text{N}$ were actually below global mean estimates for most of the oceanic regions containing these Longhurst provinces (Pethybridge et al., 2018). Even with some degree of individual variability in TP and inherent variability in TDFs, the wide ranges of $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values observed in our dataset for certain regions exceeded expected ranges (3–4‰) and likely relate to movements across carbon isoscapes. Large isotopic ellipse areas and variability in baseline-corrected $\delta^{13}\text{C}$ values further reflect movements across isoscapes as observed ranges would require trophic separation of greater than two trophic levels across individuals based on a presumed tuna $\delta^{13}\text{C}$ TDF of 1.8‰ (Madigan et al., 2012). This shows that our classification of both movement and dispersal based on baseline-corrected $\delta^{13}\text{C}_{\text{LScorr}}$ values is a useful tool, particularly when combined with results from complementary global analyses of tuna stomach contents and trophic position and verified with existing tagging data.

Moderate to high movement and dispersal were consistently reported among the tuna species within the WCPO. The WCPO is a large and dynamic area that includes both oligotrophic and nutrient-rich waters (Brown et al., 2014; Le Borgne et al., 2011) therefore both variable baseline-corrected $\delta^{13}\text{C}$ and bioenergetic condition are consistent with movements and feeding across these differing water masses. High variability in the diet diversity and TP of these tuna species has been reported in this area (Duffy et al., 2017; Pethybridge et al., 2018), consistent with mixing across isoscapes. In addition, bigeye in the WCPO also showed high individual C:N variability (Fig. 4). Based on previous tagging studies within this region, bigeye undertake long distance movements (Fonteneau and Hallier, 2015; Schaefer et al., 2015), while yellowfin display higher residency, particularly in the WARM province (Rooker et al., 2016), a result similar to our study where yellowfin were assigned a classification of “*low movement*” in the same area (Table 3). Following model baseline corrections, $\delta^{13}\text{C}$ values remained most variable for tunas in the WCPO, particularly the SPSG province for which albacore were classified as having “*very high dispersal*.” Phytoplankton carbon isoscapes are highly variable across this region of the Pacific (Magozzi et al., 2017) while particulate organic matter (POM) $\delta^{15}\text{N}$ isoscapes vary by as much as 10‰ (Houssard et al., 2017). Based on similarities in baseline POM and tuna $\delta^{15}\text{N}$ isoscapes from the WCPO, Houssard et al. (2017) concluded that yellowfin

and bigeye had constrained movements within this ocean region. While latitudinal baseline isoscapes generally matched tuna $\delta^{15}\text{N}$ in Houssard et al. (2017) and $\delta^{13}\text{C}$ values in our study, individual variability within Longhurst provinces is sufficiently high for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to suggest a degree of mixing and foraging within the WCPO.

Another pattern consistent among tuna species was moderate degrees of movement reported in the GFST province in the Northwest Atlantic Ocean based on tuna $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ median values of -4 to -6‰. The GFST province borders southerly waters with zooplankton-based isoscapes with higher $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ values (McMahon et al., 2013). Electronically tagged bigeye have been shown to travel between the northern waters represented by our isotope dataset and more southerly waters extending as far south as the Brazilian shelf (Lam et al., 2014). Recent movements from these southerly isoscapes would produce the elevated $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ and negative theta values observed in our dataset as well as lower TP estimates reported in Pethybridge et al. (2018).

Only albacore were sampled from the NADR province in the Northeast Atlantic Ocean, of which the reported “*high degrees of movement*” agree with existing tagging data showing that albacore travelled to southerly and offshore waters mainly southwest off the Iberian Peninsula (Cosgrove et al., 2014). Zooplankton carbon isoscapes for this region are elevated relative to NECS and NADR waters while corresponding $\delta^{15}\text{N}$ isoscapes are fairly homogenous (McMahon et al., 2013). Similar to the elevated $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ observed in GFST tunas, the elevated median $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ observed for NADR albacore could be due to movements from these offshore waters with higher baseline $\delta^{13}\text{C}$ values. Despite the elevated $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values, ranges of these values in addition to SEA values were more constrained suggesting fairly homogenous movements for these NADR albacore. Albacore diet diversity generally decreases with increasing latitude and so more constrained isotopic niches for this species in the Northeast Atlantic could be partly due to a corresponding lack of individual variability in diet in this region (Duffy et al., 2017).

Yellowfin and bigeye sampled from the GUIN province in the eastern Atlantic had the highest estimated degrees of movement observed in this study, based on $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values. The global model used for $\delta^{13}\text{C}$ baseline corrections could potentially underestimate phytoplankton $\delta^{13}\text{C}$ near this coastal upwelling zone, which would result in artificially high estimates of $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values. Bigeye in the GUIN showed little $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ variability and tagging data have shown fairly constrained movements for this region (Carruthers et al., 2010), which further suggests the observed difference may not be indicative of movements across isoscapes. In contrast, yellowfin in the GUIN province had the greatest variability in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values (4.7‰) which corresponds to “*very high dispersal*” and high SEA_c . While absolute baseline-corrected $\delta^{13}\text{C}$ values may be inaccurate due to modelling deficiencies, the high variability in estimates across individuals does suggest some influence of movement across isoscapes for yellowfin. Diet diversity is low for yellowfin in this and other coastal upwelling regions (Duffy et al., 2017), therefore wide isotopic niche space is not likely due to trophic diversity. Many conventionally-tagged yellowfin in the Atlantic travelled to the eastern central Atlantic Ocean (ECAO) region from distant waters in the western Atlantic and Gulf of Mexico while others displayed more localized movements within the ECAO (Carruthers et al., 2010). Yellowfin from the ECAO also showed a high degree of variability in estimated TP using baseline-corrected $\delta^{15}\text{N}$ (Pethybridge et al., 2018), which is consistent with influences of movements from different isoscapes combined with more constrained movements for other individuals within this region.

Another consistent pattern among species was the classification of “*limited movement*” in the EAFR province in the coastal waters in the southwestern Indian Ocean. In fact, limited to low

degrees of movement were found for all tunas sampled in southwestern Indian Ocean provinces (ARAB, MONS, EAFR, ISSG). Limited tagging data exist for these provinces, but diet diversity and TP have been shown to be low for the same tuna species sampled in the present study (Duffy et al., 2017; Pethybridge et al., 2018). Levels of population dispersal and SEA values were also relatively low within the southwestern Indian Ocean, suggesting residency.

4.3. Condition

Total lipid content is used as a proxy for bioenergetic condition and can reflect a requirement of energy for life history events such as reproduction or migration (Marshall et al., 1999). For albacore, the higher and more variable lipid content likely reflects its migration range over a larger spread of latitudes than yellowfin and bigeye (Childers et al., 2011; Williams et al., 2015). Albacore encounter a more diverse mix of both productive temperate waters with abundant, energy-rich prey as well as more oligotrophic waters in the tropics where prey is less abundant and lower energetic value (Duffy et al., 2017). As yellowfin and bigeye movements are more constrained latitudinally, they also forage in less productive waters. Albacore in the eastern North Atlantic undertake seasonal migrations to foraging grounds in the Bay of Biscay with muscle lipid stores increasing across the summer to fall foraging period (Goñi and Arrizabalaga, 2010). Muscle lipid stores also increase with albacore size in the Bay of Biscay (Goñi et al., 2011), with a peak at 80 cm FL followed by a declining trend (Goñi and Arrizabalaga, 2010). High but variable lipid stores in albacore sampled from the eastern North Atlantic Ocean (NAO) likely reflect this documented gradient as individuals were sampled across different sizes, months, and locations. Previous analyses of muscle lipid content in Pacific albacore found elevated values (13–19%) in fish sampled in higher latitudes ($>40^{\circ}\text{N}$), a region not included in our analysis but consistent with the greater lipid stores observed for our most northerly samples in the Atlantic Ocean (Rasmussen et al., 2006). While the median value was low, many albacore sampled from the Southwest Pacific Ocean (SWPO) had elevated C:N values. Muscle lipid stores for albacore in this region vary with SST and like eastern Atlantic albacore (Goñi et al., 2011) with length (Pethybridge et al., 2015a, 2015b). Lower lipid values in many SWPO individuals could relate to recent energy expenditures associated with long distance movements for reproduction. More detailed analyses of this broader SWPO region revealed spatial C:N gradients with highest values in the Tasman Sea and Central offshore bioregions as well as in inshore waters off the south-central coast of Australia, an area of higher productivity (Pethybridge et al., 2015b). Albacore in lower latitudes off New Zealand feed on energy-rich prey like krill and have elevated muscle lipid stores while albacore feeding in more tropical waters have a more diverse but less energy-rich diet (Williams et al., 2015) and correspondingly low muscle lipid stores (Fig. 9). As documented by Dhurmeea et al. (2018), albacore in the central and southwestern Indian Ocean had low muscle lipid content, which could relate to a capital-income breeder strategy in this region in which fish rely more on local foraging than stored energy from previous feeding migrations.

Yellowfin and bigeye tunas in the Atlantic, Indian, and Pacific Oceans all have been reported to have low lipid content in white muscle tissue ($<5\%$) (Aubourg et al., 1996; Medina et al., 1995; Peng et al., 2013; Sardenne et al., 2018, 2016; Zudaire et al., 2014). Elevated lipid stores were instead concentrated mainly in liver tissue in these species (Sardenne et al., 2018, 2016; Zudaire et al., 2014). Some outliers with elevated C:N values may have been biased by sampling location. While some samples were identified as being taken from non-dorsal muscle

locations and consequently excluded from C:N analyses, sample location was not verified for all remaining samples. Some of the higher lipid content samples may have been derived from regions with higher lipid content than dorsal muscle in tuna (Balshaw et al., 2008). For albacore, the best model (i.e. lowest AIC_c value) included only dissolved oxygen (D.O.) at 375 m depth, and the deviance explained was high (65%), which could relate to differences in vertical distribution and associated dietary differences. Goñi and Arrizabalaga (2010) noted ontogenetic increases in vertical range in the water column and associated dietary differences as a possible explanation for observed pronounced seasonal changes in older (age 3 and 4 years) relative to younger albacore. Pethybridge et al. (2018) observed an increase in albacore TP in relation to D.O. at 375 m while C:N instead followed a declining trend, suggesting a possible reduction in foraging efficiency or prey quality for albacore feeding at higher TPs and/or at greater depths.

4.4. Caveats and Next Steps

Regional estimates of tuna residency based on differences between tuna muscle and phytoplankton $\delta^{13}\text{C}$ are limited by several sources of uncertainty and variability related to trophic and physiological processes. As $\delta^{13}\text{C}$ TDFs vary across taxa and environmental conditions (McCutchan et al., 2003), potential variability in tuna-phytoplankton $\Delta^{13}\text{C}$ values is relatively high. Even fish held under controlled environmental conditions and fed a common diet have some degree of inherent variability in tissue $\delta^{13}\text{C}$ values (Barnes et al., 2008) that will contribute to uncertainty in relating individual isotopic variability to movement or other ecological processes. Thus, our resolution of residency evaluation is fairly coarse. The uncertainty considered in our analysis for $\delta^{13}\text{C}$ spacing between local phytoplankton and tuna (~2-8‰) exceeds spatial isoscapes across our sampling regions. In addition to variability associated with TDFs for tunas and underlying food web components, TP of tunas, as generalist predators, will also vary across regions and size classes (Houssard et al., 2017; Olson et al., 2016), further contributing to variability in tuna-phytoplankton $\delta^{13}\text{C}$ spacing unrelated to movement.

Lipid biases on $\delta^{13}\text{C}$ values were largely addressed using mathematical corrections rather than chemical extractions for our dataset, which can result in error (Abrantes et al., 2012; Sardenne et al., 2015). While our lipid-corrected $\delta^{13}\text{C}$ values were negatively related to C:N, this relationship did not persist for values that were both lipid and baseline corrected (Fig. S1) suggesting the former relationship was due to underlying negative relationships between tuna condition and baseline $\delta^{13}\text{C}$ gradients rather than lipid bias. Indeed, albacore, the species with the highest muscle lipid content in our dataset (Table 1), had highest C:N values in regions with low baseline $\delta^{13}\text{C}$ values (e.g. Northeast Atlantic) (Magozzi et al., 2017) and low C:N values in regions with elevated baseline $\delta^{13}\text{C}$ values (e.g. equatorial Pacific, Magozzi et al., 2017). The accuracy of lipid correction models largely relates to the similarity between the type of samples used to generate equation parameters and the dataset to which the equation is applied (Logan et al., 2008). Our samples were corrected using parameters that were tissue and genus specific, which were shown to give reliable predictions for yellowfin and bigeye tuna white muscle (Sardenne et al., 2015) and thus likely did not bias our $\delta^{13}\text{C}$ analyses.

Residency based on isoscapes is also relative to the proximity and magnitude of bordering isoscape gradients. Evidence of movement for all three tuna species in the WCPO

based on high $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ variability and wide isotopic niches is enhanced by the more distinct isoscapes in this region. Foraging and movements across isoscapes in this region are more easily detected and distinguished from more constrained variability potentially resulting from trophic differences, relative to other ocean regions with less pronounced isoscape gradients. Consequently, a carbon isoscape approach to estimating residency and movements of tunas and other highly migratory species may only be suitable for assessing movements across broader isoscapes much as isotope-based food web analyses are best applied in distinguishing among isotopically distinct prey (Fry, 2006). Potential applicability of isotope-based evaluations of movement would also be limited to cases where management zones occupy multiple isoscapes. Relatedly, the resolution of movement distance estimates will be limited to the spatial scale of bordering isoscapes. Relatively constrained movements could still impart high intraspecific isotopic variability if fish are foraging across the boundaries of bordering isoscapes.

Additionally, temporal variability in baseline, lower trophic level, and tuna $\delta^{13}\text{C}$ values relative to the timing of sampling can also influence residency estimates. Timing of sampling will influence the ability to detect any movements across isoscapes with declining detections for samples collected following greater durations of residency in a given region. Movements of prey species across isoscapes rather than movements of the tunas themselves could further impart observed individual variability in tuna $\delta^{13}\text{C}$ values. Seasonal variability in baseline $\delta^{13}\text{C}$ values driven by changes in primary producer populations, blooms, or abiotic conditions (Goering et al., 1990; Ostrom et al., 1997) could also impart variability in tuna $\delta^{13}\text{C}$ values in the absence of movements across isoscapes.

Finally, various model assumptions and an unbalanced sampling design also may have influenced our regional movement assessments. Our assessment of movement and dispersion assumed that the model is equally accurate across all Longhurst provinces, which is likely not the case. While a modelled carbon isotope baseline correction approach allows for evaluations of isotope patterns across isoscapes, modelled estimates are prone to biases, which potentially created unique values for our datasets in the GUIN province. Sample sizes also varied by species and Longhurst province, which would affect our dispersal classifications as range would be expected to increase with sample size. Dispersal estimates would be negatively biased for regions with more limited sample sizes. The model derived correction for the Suess effect also represents higher values than those reported in the literature, as it incorporates other climate effects on carbon isotope fractionation in the water column. More observations are needed to better validate the spatial and temporal changes of $\delta^{13}\text{C}_{\text{DIC}}$ and $\delta^{13}\text{C}_{\text{POC}}$ over the global ocean to have better confidence in baseline variation corrections on tuna $\delta^{13}\text{C}$ values.

A variety of additional data as well as a more hypothesis-driven sample collection approach would further refine the general observations derived from the current study which took a meta-data analysis approach. A balanced sampling design across Longhurst provinces would aid in direct comparisons of movement and dispersal classifications across regions. Compound-specific stable isotope analysis (CSIA) is an emerging tool for distinguishing trophic and movement-based influences on bulk stable isotope values (McMahon and McCarthy, 2016; McMahon and Newsome, 2019) and smaller samples of AA- $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data could be paired with larger bulk datasets like our tuna muscle dataset to further resolve trophic vs. movement influences on bulk patterns (e.g. Houssard et al., 2017; Popp et al., 2007). Inclusion of data from more rapid turnover tissues (e.g. liver) would also help define duration of residency through

comparisons with the slower turnover white muscle tissue used in our study and local baseline values (MacNeil et al., 2005; Sardenne et al., 2018). Comparing isotopic offsets between tissue types among individuals in a given region would provide another means of assessing homogeneity of movements and trophic status (Bean and Logan, 2019; Fry et al., 2003). Rapid turnover tissues would also more likely reflect local baselines and trophic information, consequently reducing potential biases of local baseline corrections for fish that recently migrated prior to sampling. Combining isotope data with other techniques (e.g. electronic tagging) or tracers (e.g. organochlorines, Dickhut et al., 2009; or mercury, Houssard et al., 2019) would also strengthen results. The current dataset could be better refined in future work using existing isotope or tagging data to develop a sampling plan more directly designed to quantify dynamics of residency, movements, and bioenergetic condition.

5. Conclusions

Despite limitations associated with our dataset, our analysis was able to document several important spatial-temporal and environmental relationships. Our GAMM analyses showed large-scale latitudinal gradients in tuna muscle $\delta^{13}\text{C}$ consistent with previously documented spatial variability at the base of these food webs. Preservation of these gradients at higher trophic levels is consistent with a general degree of residency within the carbon isoscape regions occupied by the tuna species in the present study, but a more detailed analysis is required to fully assess residency and movement across isoscapes. For example, while albacore muscle $\delta^{13}\text{C}$ values preserved underlying latitudinal baseline patterns, the slope of $\delta^{13}\text{C}$ change with distance from the equator differed from the underlying baseline suggesting some degree of mixing across isoscapes. High individual variability in $\delta^{13}\text{C}$ spacing between phytoplankton and tuna muscle in several regions also suggested exceptions to the general residency pattern as observed variability (e.g. 5‰ for YFT in the WARM province) was likely due to mixing across isoscapes rather than any purely trophic differences. The WCPO showed particularly high variability in baseline-corrected $\delta^{13}\text{C}$ and wide isotopic niche space beyond what would be expected from trophic and inherent variability, reflective of movements across isoscapes in this region. Carbon, and through inclusion in isotopic ellipses, nitrogen stable isotopes of tropical and temperate tunas provided insight into both global and regional patterns of movements as well as biological, temporal, and environmental associations. Continued application of these approaches will contribute to our understanding of tuna movement and ecology as climate change continues to modify habitats (Erauskin-Extramiana et al., 2019) and underlying food webs (Le Borgne et al., 2011) for these mobile top predators.

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Figure 1. Diagram of representative food chain with tuna occupying a trophic position of 5, showing upper and lower bounds of estimated $\Delta^{13}\text{C}$ between tuna and phytoplankton. The upper estimate (blue) assumes all trophic transfers impart a 2‰ increase in $\delta^{13}\text{C}$ to the consumer, which translates to a $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ value of -8‰. The lower estimate (red) assumes all trophic transfers impart a 0.5‰ increase in $\delta^{13}\text{C}$ to the consumer, which translates to a $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ value of -2‰. The 0.5‰ and 2‰ trophic discrimination factor (TDF) estimates are based on the lower and upper ends, respectively, of reported TDFs for representative taxa in pelagic food webs that include tuna. Values in black are best estimates based on controlled feeding experiments on taxa representative of each trophic step: ^aFrance and Peters 1997; ^bSweeting et al. 2007; ^cCaut et al. 2009; ^dHobson and Cherel 2006; ^eMadigan et al. 2012). Phytoplankton and tuna images: Tracey Saxby, IAN Image Library (<http://ian.umecs.edu/imagelibrary/>). Zooplankton image: Jane Hawkey, IAN Image Library. Anchovy image: Dieter Tracey, IAN Image Library. Squid image: Jane Thomas, IAN Image Library.

Figure 2. Map of Longhurst provinces and overlapping sampling locations for yellowfin, bigeye, and albacore tuna. See Supplementary Table S1 for code names and related sampling details.

Figure 3. Boxplots of yellowfin tuna (A) lipid and Suess corrected carbon isotopes values of tuna ($\delta^{13}\text{C}_{\text{LScorr}}$); (B) difference between lipid corrected carbon isotope values of tuna and model-derived Suess corrected phytoplankton carbon isotope values ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$); (C) C:N ratios; and (D) standard ellipse area (SEA) as an indicator of isotopic niche area, for each Longhurst province (Table S1) in this study. Biome: C – Coastal, T – Trade wind; W – Westerly. For boxplots (A-C), the dotted line corresponds to the global median value, the black line is the region median, the shaded box includes the interquartile range (IQR), whiskers represent 1.5 IQR, and individual points are outliers outside of the IQR. For (B) the dark and light grey band highlight $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values that fall between -4 to -6‰ and -2 to -8‰, respectively (that define limited and moderate degrees of tuna movement; see Table 2). SEA density plots (D) represent the credibility intervals of the Bayesian SEA with shaded boxes encompassing the 50th, 75th, and 95th credibility intervals for each Longhurst province. Black circles and red x-marks represent the mode SEA and SEA corrected for small sample sizes (SEA_c).

Figure 4. Boxplots of bigeye tuna (A) lipid and Suess corrected carbon isotopes values of tuna ($\delta^{13}\text{C}_{\text{LScorr}}$); (B) difference between lipid corrected carbon isotope values of tuna and model-derived Suess corrected phytoplankton carbon isotope values ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$); (C) C:N ratios; and (D) standard ellipse area (SEA) as an indicator of isotopic niche area, for each Longhurst province (Table S1) in this study. Biome: C – Coastal, T – Trade wind; W – Westerly. For boxplots (A-C), the dotted line corresponds to the global median value, the black line is the region median, the shaded box includes the interquartile range (IQR), whiskers represent 1.5 IQR, and individual points are outliers outside of the IQR. For (B) the dark and light grey band highlight $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values that fall between -4 to -6‰ and -2 to -8‰, respectively (that define limited and moderate degrees of tuna movement; see Table 2). SEA density plots (D) represent the credibility intervals of the Bayesian SEA with shaded boxes encompassing the 50th, 75th, and 95th credibility intervals for each Longhurst province. Black circles and red x-marks represent the mode SEA and SEA corrected for small sample sizes (SEA_c).

Figure 5. Boxplots of albacore tuna (A) lipid and Suess corrected carbon isotopes values of tuna ($\delta^{13}\text{C}_{\text{LScorr}}$); (B) difference between lipid corrected carbon isotope values of tuna and model-derived Suess corrected phytoplankton carbon isotope values ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$); (C) C:N ratios; and (D) standard ellipse area (SEA) as an indicator of isotopic niche area, for each Longhurst province (Table S1) in this study. Biome: C – Coastal, T – Trade wind; W – Westerly. For boxplots (A-C), the dotted line corresponds to the global median value, the black line is the region median, the shaded box includes the interquartile range (IQR), whiskers represent 1.5 IQR, and individual points are outliers outside of the IQR. For (B) the dark and light grey band highlight $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values that fall between -4 to -

6‰ and -2 to -8‰, respectively (that define limited and moderate degrees of tuna movement; see Table 2). SEA density plots (D) represent the credibility intervals of the Bayesian SEA with shaded boxes encompassing the 50th, 75th, and 95th credibility intervals for each Longhurst province. Black circles and red x-marks represent the mode SEA and SEA corrected for small sample sizes (SEA_c).

Figure 6. Relationships between predicted lipid- and Suess-corrected ($\delta^{13}\text{C}_{\text{LScorr}}$) values of tunas and observations of standalone variables: year, latitude, oxygen at depth, and SST for (A) yellowfin, (B) bigeye, and (C) albacore tunas. The dashed horizontal red lines represent the intercept (or zero line) in each plot. The solid blue areas bracketing the response curves show the confidence limits of the model and are twice the standard error.

Figure 7. Relationships between difference between lipid corrected carbon isotope values of tuna and model-derived Suess corrected phytoplankton carbon isotope values ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$) and observations of standalone variables: year, latitude, oxygen at depth, and SST for (A) yellowfin, (B) bigeye and (C) albacore tunas. The dashed horizontal red lines represent the intercept (or zero line) in each plot. The solid blue areas bracketing the response curves show the confidence limits of the model and are twice the standard error.

Figure 8. GAMM produced isoscapes of the difference between lipid corrected carbon isotope values of tuna and model-derived Suess corrected phytoplankton carbon isotope values ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$) in (A) yellowfin, (B) bigeye, and (C) albacore tunas sampled between 2000 – 2007 and 2008 – 2015.

Figure 9. GAMM produced isoscapes of C:N ratios representing condition of (A) bigeye, (B) yellowfin, and (C) albacore tunas sampled between 2000 – 2015.

Figure S1. (A) Tuna muscle $\delta^{13}\text{C}$ and (B) baseline-corrected $\delta^{13}\text{C}$ ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$) values (‰) in relation to bulk C:N values pre (green squares) and post (blue circles) mathematical correction for lipid content.

Figure S2. Model-data comparison of $\delta^{13}\text{C}$ of particulate organic carbon (POC) in the surface layer (0-50 meters) of the ocean: (A) Observations of $\delta^{13}\text{C}$ -POC in the data compilation from (Goericke and Fry, 1994), which were collected during 1970-1990; (B) Model $\delta^{13}\text{C}$ -POC (Schmittner and Somes, 2016) averaged over the same time period (1970-1990) in a hindcast simulation forced by observed increasing atmospheric CO_2 and decreasing $\delta^{13}\text{CO}_2$ (i.e. Suess effect) as described in Schmittner et al. (2013); and (C) $\delta^{13}\text{C}$ -POC versus latitude of observations in the Atlantic (red squares), Pacific (green circles), and Indian (blue diamonds), along with zonally-averaged model simulations from 1970-1990 when the observations were sampled (solid line) as well as from 2000-2009 (dotted line), which shows lower values due to the Suess effect.

Figure S3. GAMM produced isoscapes of lipid and Suess corrected $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_{\text{LScorr}}$) in (A) yellowfin, (B) bigeye, and (C) albacore tunas sampled between 2000–2007 and 2008–2015.

Figure S4. Tuna muscle (lipid and Suess-corrected) and modelled phytoplankton (Suess corrected) (A) $\delta^{13}\text{C}$ values and (B) $\delta^{13}\text{C}$ separation ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$) in relation to distance from the equator.

Table 1. Global observations of tuna number (n) per time period, length, $\delta^{13}\text{C}$ values of tuna corrected for lipid content and the Suess effect ($\delta^{13}\text{C}_{\text{corr_tuna}}$), and differences between $\delta^{13}\text{C}_{\text{Lcorr_tuna}}$ and $\delta^{13}\text{C}_{\text{Scorr_phyto}}$ values ($\Delta^{13}\text{C}_{\text{tuna-phyto}}$), C:N ratio and lipid content. Mean $\pm$ standard deviations are indicated. Sample sizes in parentheses refer to C:N ratio and lipid content data. A breakdown of sample sizes by species and region, and associated references can be found in Table S1.

	Unit	Yellowfin	Bigeye	Albacore
2000-2007, n	-	1118 (790)	561 (455)	343 (247)
2008-2015, n	-	503 (32)	378 (30)	1372 (651)
Length	cm	94.3 $\pm$ 37.9	84.8 $\pm$ 34.2	82.4 $\pm$ 16.8
$\delta^{13}\text{C}_{\text{LScorr_tuna}}$	‰	-15.7 $\pm$ 0.9	-15.9 $\pm$ 1.0	-17.2 $\pm$ 1.0
$\delta^{13}\text{C}_{\text{LScorr_tuna}}$ min/max	‰	-19.3/-12.9	-18.4/-13.2	-20.0/-13.2
$\Delta^{13}\text{C}_{\text{tuna-phyto}}$	‰	-5.3 $\pm$ 1.1	-5.0 $\pm$ 1.1	-5.2 $\pm$ 1.2
C:N ratio	-	3.6 $\pm$ 0.3	3.5 $\pm$ 0.3	4.1 $\pm$ 1.1
Lipid content	%	2.8 $\pm$ 1.0	2.6 $\pm$ 1.2	4.8 $\pm$ 4.3

Table 2. Summary of variables used in the global tuna analysis, based on $\delta^{13}\text{C}$ values.

Variable	Definition	Application
$\delta^{13}\text{C}_{\text{Lcorr_tuna}}$	Tuna muscle $\delta^{13}\text{C}$ values corrected for lipids by chemical extraction and/or mathematical correction or deemed to not require correction (i.e., C:N<3.5)	Lipid corrected values to be normalized with baseline phytoplankton $\delta^{13}\text{C}$ values for global tuna comparisons
$\delta^{13}\text{C}_{\text{Scorr_phyto}}$	Model-derived baseline phytoplankton $\delta^{13}\text{C}$ values corrected for the Suess effect	Baseline correction for global tuna comparisons
$\Delta^{13}\text{C}_{\text{tuna-phyto}}$	$\delta^{13}\text{C}_{\text{Scorr_phyto}} - \delta^{13}\text{C}_{\text{Lcorr_tuna}}$	Movement and residency classifications and isotopic niche calculations
$\delta^{13}\text{C}_{\text{LScorr}}$	Tuna muscle $\delta^{13}\text{C}$ values corrected for lipids and the Suess effect	Global tuna isoscapes

Table 3. Classification of spatial movement (or occupancy) and population dispersal in yellowfin, bigeye, and albacore tuna sampled in the different Longhurst provinces (Table S1) based on trends in $\Delta^{13}\text{C}_{\text{tuna-phyto}}$ values presented in this study (Figures 2-3 B). Spatial movement is scaled from 0 to 4 with 0: limited movement (median and range falls within -4 to -6‰); 1: moderate movements by some individuals (median within -4 to -6‰, with range within -2 to -4 or -6 to -8‰); 2: moderate movement (median within either -2 to -4 or -6 to -8‰ with range between -2 and -8‰); 3: high degree of movement by some individuals (median within either -2 to -4 or -6 to -8‰, but range <-2 or >-8‰); and 4: high degree of movement (median is outside <-2 or >-8‰). Population dispersal was scaled from 0-4 with 0: no dispersal (range < 1‰); 1: low dispersal (range 1-2‰); 2: moderate dispersal (range 2-3‰); 3: high dispersal (range 3-4‰); and 4 very high dispersal (range >4‰). Blank spaces indicate areas where sample size was ≤ 5 . Most limited (0) and highest (4) movement scores are highlighted in red and bold, respectively. Range corresponds to 1.5 of the interquartile range represented by the boxplot whiskers.

Ocean	Biome	Longhurst Province	Spatial movement			Population dispersal		
			Yellowfin	Bigeye	Albacore	Yellowfin	Bigeye	Albacore
Atlantic	W	MEDI			1			1
Atlantic	C	NECS			2			1
Atlantic	C	CNRY			1			1
Atlantic	C	GUIN	4	3		4	1	
Atlantic	TW	ETRA	1	1		2	2	
Atlantic	TW	WTRA		0			1	
Atlantic	TW	NATR		0			1	
Atlantic	W	NADR			2			
Atlantic	W	GFST	2	2	1	1	2	0
Atlantic	W	NASW	0	1	1	1	1	1
Pacific	TW	SPSG	1	1	1	3	3	4
Pacific	TW	PEQD	3	3		4	4	
Pacific	TW	PNEC	3	2		2	1	
Pacific	C	CCAL	2			0		
Pacific	TW	NPTG	2	1		2	3	
Pacific	TW	WARM	1	1	1	4	4	1
Pacific	TW	ARCH	1	1	1	3	3	4
Pacific	C	SUND	1			1		
Pacific	W	TASM			2			1
Pacific	C	AUSE	1	1	0	3	2	2
Indian	TW	MONS	1	1	1	2	1	0
Indian	W	ARAB	1	0		2	0	
Indian	TW	ISSG			1			1
Indian	C	EAFR	0	0	0	1	1	0
Antarctic	W	SSTC			2			1
Antarctic	W	SANT			2			2

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.