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Identifying migrations in marine fishes through stable-isotope analysis

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The isotopic composition of many elements varies across both land and ocean surfaces in a predictable fashion. These stable-isotope ratios are transferred into animal tissues, potentially providing a powerful natural geospatial tag. To date, most studies using stable isotopes as geolocators in marine settings have focussed on mammals and seabirds conducting large ocean-basin scale migrations. An increasing understanding of isotopic variation in the marine environment, and improved sampling and analytical techniques, however, means that stable isotopes now hold genuine promise as a natural geolocation tag in marine fishes. Here, the theoretical background underpinning the use of stable isotopes of C, N and O in otolith, scale and muscle tissues as geolocation tools in the marine environment is reviewed, and examples of their applications are provided.

Key words: chemical proxy; fishes; movement; oceanic; tracking.

INTRODUCTION

Significant global declines in most commercially exploited pelagic marine fish populations over recent decades (Hutchings & Reynolds, 2004) have cast an unfavourable light over the current state of knowledge on open-ocean ecology. Direct information on the behaviour and movement of fishes, and the conditions they experience in the marine environment has, to date, largely stemmed from fishing effort and tagging studies (Jennings *et al.*, 2001). In the case of fishery data (Bolle *et al.*, 2005), however, such studies are complicated by biased spatio-temporal sampling, and tagging studies are reliant on either a significant chance of recapture of the tagged animals, or the transmission of recorded information back to the researchers (Block *et al.*, 2011). Tagged fishes in many marine populations have a very low chance of recapture (ICES, 2009); thus, passive tagging operations must be extensive in order to provide meaningful data. While the cost and size of active tags is becoming cheaper, they are relatively expensive, and even the flagship international project, the TOPP strand of the Census of Marine life (Block *et al.*, 2011), was restricted to <5000 tags. Effective tagging of any type is usually extremely expensive, as it relies on sufficient fishes tagged to make recapture likely, or to

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provide a margin of error for failures in tags that transmit data. At present, satellite tagging technologies are not practical for monitoring on a temporal and spatial scale relevant for routine stock management, particularly for widely dispersed mixed stock fisheries. The unprecedented picture of migration revealed by the relatively small number of satellite tags deployed so far demonstrates the relative paucity of understanding of spatial behaviour of pelagic fishes. Fishes that are present in the lowest abundances at sea are likely to be higher priorities for conservation, yet often present poorer candidates for tagging studies, as the likelihood of recapture is low. These types of fishes are also the most difficult to track within mixed stocks.

Natural chemical tags, where the compositions of fish tissues reflect that of the ambient body of water or local food web, provide a potential solution, as every captured (or commercially landed) fish contains some chemical information that could potentially be used to gain information on location and movement. Where incrementally grown tissues, or a range of tissues with known and different growth rates are available, patterns of movement throughout time may be recovered retrospectively from a single individual. Natural chemical tags are clearly an attractive complement to genetic and tagging studies of stock structure, but are relatively under used for tracking migration in fully marine fishes largely because of uncertainties underpinning the spatial distribution of stable-isotope values across ocean basins, the mechanism and biochemistry of isotope fractionation in biological systems, and the time represented by different biological tissues.

Chemical tags are used to study movements in fishes with three main conceptual approaches. (1) linking the composition measured in fish tissues to the composition measured in a finite number of potential sites of origin identified *a priori*. This is the approach used in most otolith trace-element studies. This method requires no theory or prediction of the distribution of elements of isotopes, and is best suited to trace-element based testing of explicit hypotheses of individual or stock movements. This approach, however, requires *a priori* identification of potential sites (observer bias) and demands contemporaneous sampling of biologically and isotopically comparable specimens at each site. This approach is therefore best suited to relatively small-scale, targeted studies in well-characterised accessible localities. (2) Determining movements of fish across known geochemical gradients, for example from fresh to salt water, from inshore to offshore habitats, or across temperature gradients. This method requires some prior understanding of the chemistry underpinning spatial variation in the geochemical tracer, and has more predictive power. The efficacy of this approach is clearly linked to the stability, predictability and understanding of the chemical gradient in question. (3) True geolocation where the chemical composition of fish tissues is matched to a spatially explicit prediction or measurement of the distribution of the chemical signal. This is the most powerful, but most challenging application, requiring accurate theories and measurements of spatial variation in chemical abundances across ocean basins, and a thorough understanding of the biochemistry of tracer uptake into the tissue of interest. At present, this is a goal rather than a reality.

The use of trace element composition to track location and stock structure in marine fishes is reviewed in a companion paper in this volume (Sturrock *et al*., 2012). In this paper the use of stable isotopes in tracking fishes is reviewed, particularly focussing on approaches (2) and (3) above.

STABLE-ISOTOPE THEORY

The ratio of stable isotopes of elements such as H, O, C, N and S varies throughout ecosystems due to differences in reaction kinetics between the light and heavy isotopes. The fractionation of stable isotopes during biochemical reactions provides a chemical link between prey and consumer tissues, and consequently stable isotopes have long been used to study diet segregation and trophic ecology (DeNiro & Epstein, 1978; 1981; Wada *et al*., 1991, 1993). The isotopic composition of either ambient water and the base of the food chain, however, vary in time and space (often referred to as baseline effect, Hobson, 1999; Newsome *et al*., 2010), complicating interpretation of diet. Increasingly, researchers are recognizing that this baseline effect contains spatial information that can be used to interpret movements and migrations in fully marine species (Barnes *et al*., 2009; Graham *et al*., 2010). To date, most applications using stable isotopes to infer spatial information in marine species have involved marine mammals and seabirds (Cherel *et al*., 2009; Newsome *et al*., 2010), with surprisingly few extensions to fishes. In terrestrial environments, stable isotopes of Sr are also useful in tracking animal movements (Barnet-Johnson *et al.,* 2008; Bendry *et al*., 2009), but the isotopic composition of Sr is effectively uniform in the open ocean, and Sr will not be considered further in this review. Similarly, the isotopic behaviour of S is relatively poorly known in open-ocean pelagic systems. Here the principles responsible for spatial patterns in baseline C, N and O stable-isotope ratios are outlined, the pros and cons behind the various tissues available for sampling discussed, and some case study examples presented where stable isotopes have been used to track migrations in marine animals (fishes where possible). A brief summary of studies using a stable-isotope approach to track migration in marine fishes is presented in Table I.

Throughout this review, all stable-isotope data are discussed in delta (δ) notation, describing the difference in the ratio of the heavy and light isotopes in the sample compared to a standard: *e.g.* $\delta^a X‰ = [R_{\text{sample}}(R_{\text{standard}} - 1)^{-1}]$, where a is the atomic mass of the heavy isotope in question (*e.g.* 13 for C), and R is the ratio of the heavy v. the light isotope. The standard typically used for carbon isotopes is Vienna PeeDee Belemnite (VPDB), for oxygen isotopes VPDB or Vienna standard mean ocean water (VSMOW) and air for nitrogen.

Before discussing the mechanisms underpinning spatial variation in stable isotopes, it is important to consider the fish tissues that will host stable-isotope information.

TISSUES

Any tissue containing the isotope in question may potentially be sampled. As O, C and N are structural elements, almost any tissue is suitable for stable-isotope analysis. In practice, however, most stable-isotope studies sample muscle, blood, liver, scale or otolith tissues, and otolith aragonite is the only biomineral discussed here. Biomineralized tissues represent a special case, as structural elements such as O, H and C are derived largely from ambient water (rather than from diet), and stable isotopes of oxygen, in particular, are precipitated at or close to equilibrium with ambient waters. Organic tissues are synthesized from metabolised products and their isotopic composition is referenced to local food chains rather than dissolved water isotopes.

TABLE I. Summary of research to date on the use of stable isotopes in tracking marine migrations in fishes

Stable isotopes	Reference	Species	Tissue	Locations
$\delta^{13}C$, $\delta^{15}N$	Abrantes *et al.* (2011)	*Notorynchus cepedianus*	White muscle	South-east Tasmania
$\delta^{13}C$, $\delta^{15}N$	Borrell *et al.* (2011)	*Rhincodon typus*	White muscle	Arabian Sea
$\delta^{13}C$, $\delta^{15}N$	Hussey *et al.* (2011)	*Sphyrna lewini;* (*Carcharhinus obscurus*)	White muscle	South-western Indian Ocean
$\delta^{13}C$, $\delta^{18}O$	Longmore *et al.* (2011)	*Coryphaenoides rupestris*	Otolith	North-east Atlantic Ocean
$\delta^{13}C$	MacKenzie *et al.* (2011)	*Salmo salar*	Scales	North Atlantic Ocean
Amino acid $\delta^{13}C$	McMahon *et al.* (2011)	*Lutjanus ehrenbergii*	Otolith, white muscle	Red Sea
$\delta^{13}C$, $\delta^{18}O$	Clarke *et al.* (2010)	*Menidia menidia*	Otolith	North-east Atlantic Ocean
$\delta^{15}N$	Graham *et al.* (2010)	*Thunnus albacores*; *Thunnus obesus*	White muscle	Equatorial Pacific Ocean
$\delta^{15}N$	Olson *et al.* (2010)	*Thunnus albacores*	White muscle	Eastern Pacific Ocean
$\delta^{13}C$, $\delta^{15}N$	Papastamatiou *et al.* (2010)	*Carcharhinus melanopterus*	White muscle	Palmyra atoll, central Pacific Ocean
$\delta^{13}C$, $\delta^{18}O$	Wells *et al.* (2010)	*Makaira nigricans; Tetraptus albidus*	Otolith	Western North Atlantic Ocean
$\delta^{13}C$, $\delta^{18}O$	Shiao *et al.* (2009)	*Thunnus maccoyii*	Otolith	Central Indian Ocean
$\delta^{13}C$, $\delta^{15}N$	Nagelkerken *et al.* (2008)	*Haemulon flavolineatum*	White muscle	Caribbean Sea, Western Atlantic Ocean
$\delta^{13}C$, $\delta^{18}O$	Rooker *et al.* (2008)	*Thunnus thynnus*	Otolith	North Atlantic Ocean, Mediterranean Sea
$\delta^{13}C$, $\delta^{15}N$	Verweij *et al.* (2008)	*Ocyurus chrysurus*	Otolith, white muscle	Curaçao, Caribbean Sea
$\delta^{13}C$, $\delta^{15}N$	Menard *et al.* (2007)	*Thunnus albacores*; *Xiphias gladius*	White muscle	Western Indian Ocean
$\delta^{13}C$, $\delta^{15}N$	Kerr *et al.* (2006)	*Carcharodon carcharias*	Vertebrae	Eastern North Pacific Ocean
$\delta^{13}C$, $\delta^{18}O$	Ayvazian *et al.* (2004)	*Arripis georgianus*	Otolith	South-western Australia
$\delta^{13}C$, $\delta^{18}O$	Gao & Beamish (2003)	*Hippoglossus stenolepis*	Otolith	Bering Sea, North-east Pacific Ocean
$\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$	MacAvoy *et al.* (2002)	*Nezumia* sp.; *Synaphobranchus* sp.; *Ophichthus cruentifer; Dysommina rugosa; Eptatretus* sp.	White muscle	Gulf of Mexico
$\delta^{13}C$, $\delta^{18}O$	Begg & Weidman (2001)	*Melanogrammus aeglefinus*	Otolith	North-west Atlantic
$\delta^{13}C$	Schwarcz *et al.* (1998)	*Gadus morhua*	Otolith	Scotian Shelf, North-west Atlantic

For all tissues, some estimate of the length of time represented by the tissue is needed. Many tissues sample multiple body pools of C, N and O, and these body pools may be composed of elements derived directly from diet, or from the replacement (turnover) of biosynthesized tissues (Carleton & Martinez del Rio, 2010). The relative proportion of elements derived from a body turnover pool will influence the time period represented by any tissue sample, and estimating the time represented by the sampled tissue is a critical aspect of stable-isotope analyses. Models describing tissue turnover rates are derived from diet-switching experiments using exponential (Hesslein *et al*., 1993) or reaction progress variable (Cerling *et al*., 2007) approaches to provide estimates of the number of isotopic turnover pools, the rates of exchange in each pool and the proportional contribution of different turnover pools to whole body isotope kinetics. Several such experiments have been performed on fishes (Hesslein *et al*., 1993; Jardine *et al*., 2004; Trueman *et al*., 2005; Miller, 2006). Hobson *et al*. (2010) provide a recent review of the concept of tissue isotope turnover in the context of animal migrations.

MUSCLE, LIVER AND BLOOD

White muscle is the tissue of choice for many stable-isotope studies of fishes, largely due to its ease of sampling and sample handling. Muscle tissue is metabolically active, however, and the time represented by any muscle sample can be difficult to constrain. In rapidly growing juvenile fishes, relatively little turnover of synthesized tissues occurs and the body pool of the atoms used to synthesize muscle tissue is relatively tightly coupled to diet. Muscle tissue may then reflect weeks to months of life. In slow growing adult fishes, turnover may provide a high proportion of atoms to the total body pool available for biosynthesis, and a single muscle sample will represent months (or years in sharks and deep water fishes with very slow metabolic rates). Clearly muscle may be an inappropriate tissue to reconstruct short-term movements. Liver and blood (whole blood, red blood cells or plasma) are more metabolically active than muscle, and thus may integrate isotopes over a shorter duration than muscle, but the precise timescale represented is poorly understood. Blood plasma appears to contain carbon and nitrogen derived from both tissue recycling and diet whereas carbon in red blood cells appears more directly related to dietary inputs (Carleton & Martinez del Rio, 2010). Again, more experimental work is needed to constrain these relationships, particularly in slow growing adult fishes.

OTOLITHS AND SCALES

Incrementally grown tissues such as otoliths and scales provide an attractive solution to the problem of sample duration described above. Otoliths are metabolically inactive, providing a complete life history record of the isotopic composition of the fish. Otoliths are largely composed of the calcium carbonate polymorph aragonite, and this mineral component reflects the oxygen and (in a more complex fashion) the carbon isotope composition of dissolved carbonate in seawater. Otolith aragonite forms at (or close to) isotopic equilibrium with oxygen in ambient seawater. The relationship between the isotopic composition of the otolith aragonite and that of ambient seawater is also dependent on temperature. This means that the otolith preserves a record of the isotopic composition and temperature of seawater inhabited by the fish throughout its lifetime. The isotopic composition of seawater is itself largely

controlled by salinity. Otolith oxygen isotopes thus provide an extremely powerful tool to explore migration and movement in fishes, particularly across temperature and salinity gradients. The superb sclerochronological properties of otoliths also mean that ontogenetic migrations can be recovered retrospectively, and otolith isotopes are very well suited to studying migrations in larval and juvenile fishes that are too small for direct tagging.

The carbon in otolith aragonite is delivered to the otolith *via* the blood and is ultimately derived from both dissolved inorganic carbonate (DIC) in the ambient sea-water, and from metabolic carbon in blood (Kalish, 1991; Solomon *et al*., 2005). Because of the strong fractionation of carbon isotopes during photosynthesis, dietary carbon is isotopically depleted compared to ambient DIC, typically by >15‰, and the isotopic composition of carbon in otolith aragonite is a weighted average of these two components. The proportion of metabolically derived carbon in blood varies with metabolic rate, so that the isotopic composition of carbon in otolith aragonite varies with the isotopic composition of the two sources (DIC and diet), and with the metabolic rate of the fish at the time of otolith deposition (Weidman & Milner, 2000; Wurster *et al*., 2005; Høie *et al*., 2004*a*, *b*). Disentangling these sources of variation is complex, and consequently few studies use the isotopic composition of carbon in otolith aragonite to reconstruct movements. Ashford & Jones (2007), however, used a strong gradient in DIC $\delta^{13}C$ values to discriminate between stocks of Patagonian toothfish *Dissostichus eleginoides* Smitt 1898.

Otoliths also contain a minor (typically <10%) protein-rich organic component, which can be used as a substrate for C and N analyses (Elsdon *et al*., 2010). Unfortunately, the low sample mass of the organic matrix restricts the potential for sequential isotopic analyses, and, in slow growing fishes, the temporal resolution available using otolith matrix proteins may be lower than in muscle or blood. The ability to sample retrospectively, either within a single fish or using historical archives of otoliths, is a powerful incentive to utilize otolith proteins as a target for stable-isotope analyses. Recent advances in compound specific stable-isotope analyses aid the interpretation of the carbon isotope composition of the otolith matrix (McMahon *et al*., 2011), and are likely to be useful tracers of fish movements in the near future. Otoliths provide the best tissue substrate for oxygen isotope-based studies of migration.

Scales are also incrementally grown tissues, composed of the mineral apatite on a collagenous base plate. The apatite layer is usually very thin (<50 μm) and is not suitable for high-resolution oxygen isotope analyses. The collagen base layer can be used for carbon and nitrogen analysis and the temporal span of the sample can be guided by the apatite increments, however, the collagen grows by a process of underplating, so that all but the final apatite growth increments are underlain by collagen that is younger than the apatite. Consequently, sampling should be either limited to the last season of growth, or some assessment should be made of the relative proportion of collagen laid down contemporaneously with the apatite and later collagen (Hutchinson & Trueman, 2006).

GEOGRAPHIC HETEROGENEITY IN BASELINE ISOTOPES

In terrestrial systems, predictable gradients in the stable-isotope ratios of hydrogen, oxygen and strontium have been used to create static isotope maps, commonly termed

isoscapes (Bowen & Wilkinson, 2002; Bowen *et al*., 2005; West *et al*., 2010). The inherent predictability stems from inorganic features such as local geology and the hydrological cycle (Bowen & Wilkinson, 2002; Bowen *et al*., 2005). The derived isoscapes can then be used to determine the geographic location of an animal by matching the isotopic composition of its tissues (with appropriate models of isotopic fractionation between tissue and diet and tissue integration time) to an area of the isoscape with similar isotope values. Crucially, such assignments should be statistically derived and based on likelihood envelopes that consider uncertainties associated with individual variation and generation of the isoscape model (Wunder, 2010). This approach is rather more complicated in marine environments, as while large spatial variations in stable-isotope compositions exist, the underlying isotopic variation is not static but varies dynamically with changes in climate, ocean circulation and plankton community composition.

OXYGEN ISOTOPE VARIABILITY IN THE GLOBAL OCEAN AND IN OTOLITHS

The oxygen isotope composition of seawater ($\delta^{18}O_w$) is largely controlled by mixing between seawater and fresh water (*i.e.* salinity). As the isotopic composition of rain water varies with latitude and altitude, the linear relationship between salinity and $\delta^{18}O_w$ also varies between and within ocean basins. The oxygen isotope composition of seawater is relatively well constrained, at least in surface waters, and a global compilation of $\delta^{18}O_w$ values is described by Bigg & Rohling (2000), and available from Schmidt *et al*. (1999). Most isotopic variation occurs in high latitudes, influenced by the negative values of precipitation at high latitudes, and input of glacial melt water. Additionally, surface $\delta^{18}O_w$ values may be particularly high in restricted basins where evaporation is intense such as the Red Sea. The isotopic composition of oxygen in deeper waters is less well constrained, but may vary considerably over relatively short vertical scales due to highly differentiated sources of water masses. For example, Mediterranean outflow water (MOW), which spills over the Craminal Sill in the Strait of Gibraltar into the North Atlantic Ocean, has a relatively positive $\delta^{18}O_w$ value due to the high rates of evaporation in the Mediterranean Basin. MOW flows west and northwards forming a discrete layer *c*. 500–1000 m depth until at least the Porcupine Seabight (50° 30′ N; 12° 30′ W). Vertical profiles through the water column show distinct isotopic excursions when MOW is encountered. It is therefore dangerous to use either surface water values or surface-derived relationships between salinity and $\delta^{18}O_w$ values to infer likely $\delta^{18}O_w$ values at depth.

The isotopic composition of oxygen in otoliths ($\delta^{18}O_{oto}$) is related by a simple linear equation to the isotopic composition ($\delta^{18}O_w$) and temperature (T) of ambient seawater:

$$T = \gamma(\delta^{18}O_{oto} - \delta^{18}O_w) + \beta \quad (1)$$

In order to use otolith oxygen isotope ratios as geolocators, therefore, an accurate (empirical) assessment of parameters γ and β must be made, and the isotopic composition of seawater in the area of interest must be known or estimated. Several experimental studies or compilations of field-derived measurements have been made

to evaluate γ and β using a range of freshwater, anadromous and marine species from temperate and tropical waters (Kalish, 1991; Patterson *et al*., 1993; Thorrold *et al*., 1997; Stephenson *et al*., 2001; Høie *et al*., 2004*a*; Storm-Suke *et al*., 2007).

If parameters γ and β are assumed to be constant (*i.e.* if the discrepancies between the measured estimates are assumed to be an artefact of errors estimating ambient $\delta^{18}O_w$ values and measurement uncertainties), then a broad prediction of the geographic variation expected in otolith oxygen isotopes in surface dwelling fishes can be produced by coupling global compilations of ocean $\delta^{18}O_w$ values (Schmidt *et al*., 1999) with measurements of mean annual sea surface temperature (SST) (*e.g.* Fig. 1).

Considering that analytical resolution in otoliths is on the order of 0·1‰ it can be seen that on broad ocean-basin scales, oxygen isotope $\delta^{18}O$ analyses can provide useful migration information. Specific research questions may be particularly well-suited; identifying for instance latitudinal migrations between tropical spawning and temperate feeding as seen in many tuna species, migrations from the high arctic to boreal seas and east–west migrations within the North Atlantic and North Pacific Oceans. On a more local scale, certain seas are identified as isotopically distinct largely due to increased evaporation (Red Sea), or high freshwater input (North Sea), and oxygen isotope analyses may be particularly well suited to studying movements between these restricted water bodies and the open ocean. Note that Fig. 1 is based on a small dataset of <4000 individual measurements, unevenly distributed throughout seasons and across ocean basins, and recorded over >30 years. Controlling for these variables would probably result in more tightly defined predicted otolith isoscapes. To date, there are relatively few direct measurements of the isotopic composition of ocean water, but this may improve rapidly with the development of relatively low-cost, high-throughput techniques for isotope analyses using optical spectrometers. On a more local scale, seasonal fluctuations in temperature and salinity may result in more variable spatial patterns than shown in Fig. 1. In this case otolith oxygen isotopes may hold more promise for geolocation, but it must be stressed that accurate estimates of temperature, salinity and salinity to $\delta^{18}O_w$ relationships are required.

Experimental and field-based determinations of the parameters γ and β vary between species (Kalish, 1991; Høie *et al*., 2004*a*; Longmore *et al*., 2011) but debate continues as to whether the inconsistencies represent true physiological differences in fractionation of oxygen between species, or are artefacts of incompletely constrained experiments. The uncertainty currently associated with these parameters is significant and limits the precision available for otolith oxygen isotopes as a direct geolocation tool (Høie *et al*., 2004*b*; Hanson *et al*., 2010).

EXAMPLES OF USE

The isotopic distinction in $\delta^{18}O_w$ values between restricted water masses and the open ocean was exploited by Schloesser *et al*. (2010) to identify natal origin in Atlantic bluefin tuna *Thunnus thynnus* (L. 1758) from Canadian waters. *Thunnus thynnus* are managed as two separate stocks, divided at 45° W longitude. The western stock spawns in the Gulf of Mexico and the eastern stock spawns in the Mediterranean Sea. The current management strategy assumes no mixing between eastern and western stocks, but continued declines of the stocks have (in part) called this assumption into question. As described above, Mediterranean Sea waters are

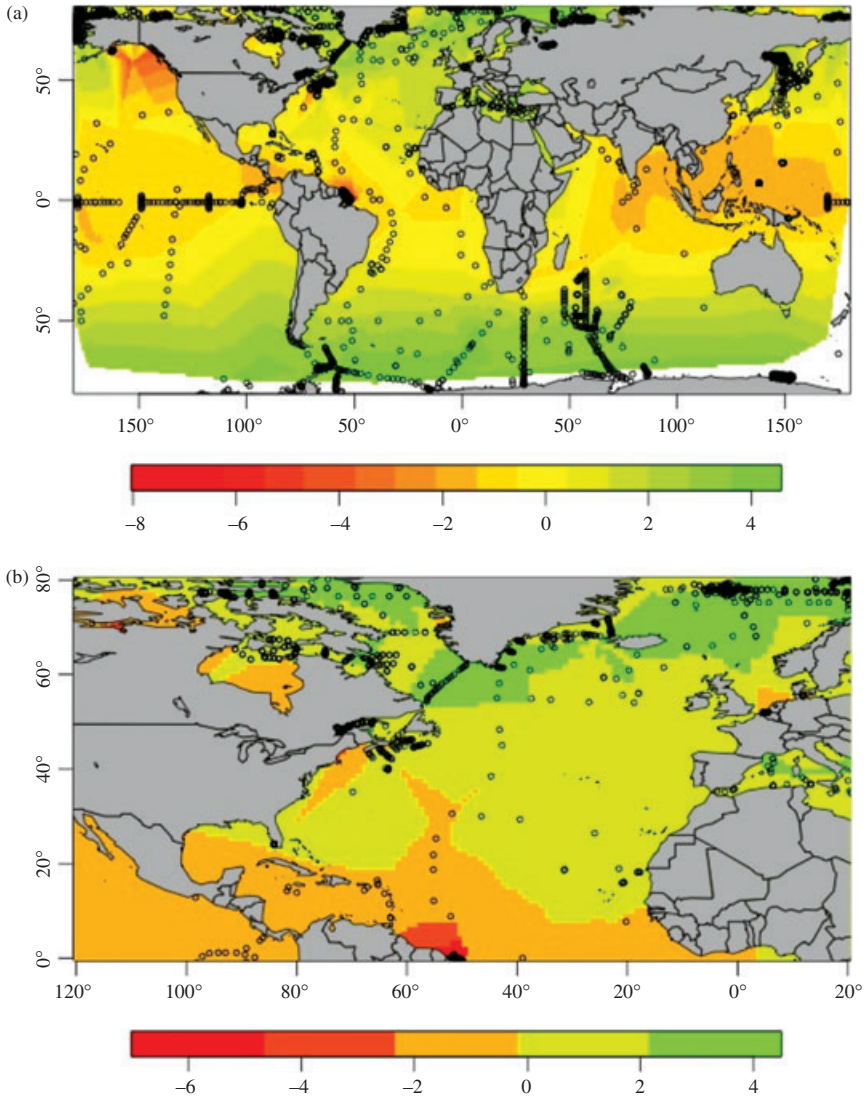

FIG. 1. Modelled spatial variations in isotopic composition of oxygen in otoliths ($\delta^{18}O_{oto}$) based on global surface water (0–20 m) measured $\delta^{18}O_w$ values (Schmidt *et al*., 1999), using equation (1) and parameters γ and β from Høie *et al.* (2004*a*): (a) global variations and (b) variations predicted for the North Atlantic Ocean. ○, locations of samples used to generate the interpolated model predictions. Note that this simplistic model assumes constant parameters for the otolith fractionation equation, and is based on a small number of direct coupled measurements of $\delta^{18}O_w$ values and sea surface temperature. These data are unevenly spaced spatially and temporally, and the resulting model is presented only for illustrative purposes.

isotopically enriched in ^{18}O due to the high evaporation rates, low riverine input and restricted circulation. By contrast, waters of the Mid-Atlantic Ocean Bight have relatively negative $\delta^{18}O_w$ values. To test whether *T. thynnus* caught in the Gulf of St Lawrence (GSL) originated in Mediterranean spawning grounds, Schloesser

et al. (2010) initially confirmed the isotopic separation in otoliths of juveniles recovered from the two spawning grounds, and then compared these values with cores of otoliths recovered from large adult fish caught in the GSL between the 1970s and 2000s. Almost all otolith cores from adults fell into the range described by juveniles from the mid Atlantic Bight region, suggesting very limited mixing between eastern and western stocks in the GSL *T. thynnus* fishery. A particularly significant aspect of this study is the ability to test patterns of stock mixing retrospectively. In the Schloesser *et al*. (2010) study, no change in stock origin or mixing was detected in the three decades sampled.

A clear example of the use of $\delta^{18}O_{oto}$ values to constrain migrations across an environmental gradient is the reconstruction of ontogenetic depth migrations in fishes from the continental slope. Many slope-dwelling fishes are thought to have pelagic or meso-pelagic larval phases, but larval and juvenile forms are rarely found or identified in trawl surveys. In benthic trawl surveys, deep water fishes often show a pattern of increasing size with depth, but it is not clear if this represents ontogenetic migration or increased longevity at depth. The existence and duration of a larval phase has clear implications for potential stock structure and genetic isolation, but the location of juvenile and larval deep-water fishes is very uncertain, even in commercially important species such as orange roughy *Hoplostethus atlanticus* Collett 1889 and roundnose grenadier *Coryphaenoides rupestris* Gunnerus 1765. Ontogenetic profiles of $\delta^{18}O_{oto}$ values across otoliths from adult fishes caught in trawl samples between 500 and 1500 m depth on the Irish continental slope have been measured in *H. atlanticus* (Shephard *et al*., 2009; C. N. Trueman, unpubli. data) and in *C. rupestris* (Longmore *et al*., 2011). Representative profiles of *H. atlanticus* are shown in Fig. 2. All three species show evidence of a relatively warm and shallow larval and early juvenile phase. Consistent ontogenetic migrations towards deeper waters are seen in *C. rupestris*, whereas *H. atlanticus* shows a more complex migration history with a deep late juvenile period followed by rise to intermediate depths at first maturity and subsequent ontogenetic migration to deeper waters. The more pelagic blue whiting *Micromesistius poutassou* (Risso 1827) shows no evidence of migration to deeper waters. Using equation (1) and making estimates of parameters γ and β from literature values, and $\delta^{18}O_w$ values from CTD profiles, an estimate of depth at age can be made, but these estimates contain combined uncertainties associated with estimating parameters in the temperature fractionation equation (Longmore *et al*., 2011).

A similar study assessing variation in $\delta^{18}O_{oto}$ values across a salinity gradient was given by Hanson *et al*. (2010), showing the outward migration of Atlantic salmon *Salmo salar* L. 1758 from fresh to seawater. In this study, $\delta^{18}O_{oto}$ values were determined by ion probe, giving spatial resolution across the otolith of <30 μm, which equates to *c*. 2 weeks of life. The timing of the smolt migration is very clearly expressed in otolith isotopes. Hanson *et al*. (2010) attempted to use the subsequent $\delta^{18}O_{oto}$ values together with a fractionation equation derived for the related Arctic charr *Salvelinus alpinus* (L. 1758) (Storm-Suke *et al*., 2007), and estimates of SST and salinity in the North Atlantic Ocean to identify areas of marine feeding. This was not particularly successful, suggesting marine feeding areas that are consistently warmer than expected from tagging and fisheries information. The lack of success probably reflects inaccuracies in either estimates of $\delta^{18}O_w$ and equation parameters γ and β.

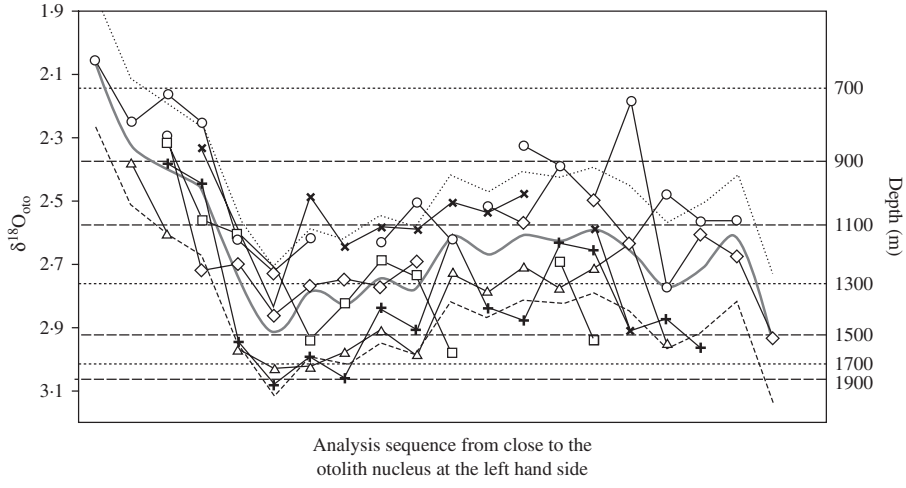

FIG. 2. Ontogenetic trends in isotopic composition of oxygen in otoliths ($\delta^{18}O_{oto}$) values in the otoliths of *Hoplostethus atlanticus* from the Irish continental slope. Isotope tracks are displayed with the focus (juvenile portion) to the left hand side and aligned based on the clear isotopic maximum found in the juvenile portion of life. ——, a moving average of the six fish measured (-□-, 1 right otolith; -△-, 8 left otolith; -◇-, 13 left otolith; -✕-, 3 right otolith; -○-, 15 left otolith; -+-, 9 left otolith); - - -, ±2 S.D. Numbers on the right hand side show the depth (m) equivalent to each $\delta^{18}O_{oto}$ measurement following methods outlined by Shephard *et al.* (2009) and Longmore *et al.* (2011).

In summary, while direct geolocation (comparison of measured values to the position on a map) may stretch current analytical capabilities and theoretical understanding, otolith oxygen isotopes are particularly well-suited to studying migrations across temperature and salinity gradients. As ion probe and other spatial sampling techniques improve, otolith isotope geolocation may become a viable option for tracking movements of fully marine fishes, particularly when fish move through salinity gradients.

HYDROGEN ISOTOPES

Hydrogen isotopes vary widely in continental precipitation as the relatively large difference in mass between ^{1}H and ^{2}H results in large isotopic fractionation during evaporation and precipitation of water. The resulting hydrogen isotope maps (isoscapes) provide the basis for studies of location in terrestrial mammals (Cormie *et al.*, 1994), birds (Hobson & Wassenaar, 1997) and insects (Hobson *et al.*, 1999). While precipitation-based hydrogen isoscapes are relatively well understood, however, the use of hydrogen isotopes to track movement in aquatic, and particularly marine, ecosystems is rather more problematic. In high latitude environments, strong isotopic gradients in both oxygen and hydrogen in water may provide sufficient separation to track seasonal migration (Hobson *et al.*, 2010). Hydrogen isotope biochemistry, however, is complicated by the relative ease of exchange of hydrogen with body waters and environmental waters after tissue formation. In an isotopically homogenous, relatively controlled freshwater system, the hydrogen isotope composition of four fish species varied considerably, potentially reflecting dietary

and metabolic influences related to tissue turnover, protein age and location (DeSoto *et al*., 2011). While hydrogen isotope analyses may hold some promise for tracking migrations in marine fishes, particularly in high latitude regions, more controlled studies are needed to understand competing influences on tissue hydrogen isotope composition.

CARBON AND NITROGEN BASELINES

Most marine food chains are ultimately supported by phytoplankton production, and the isotopic composition of C and N in phytoplankton is transferred through the food chain. The isotopic composition of carbon and nitrogen in particulate organic matter (POM) varies significantly at the point of assimilation, leading to basin-scale gradients in carbon and nitrogen isotope composition that have been used to track the migrations of fishes and marine mammals (Hobson & Schell, 1998; Graham *et al*., 2010). At smaller spatial scales, carbon and nitrogen isotopic compositions are highly variable both spatially and temporally, complicating the use of static isoscape maps.

The nitrogen isotope composition of POM is controlled by the isotopic composition of the nutrient source, the mechanism of fixation of N into organic tissues, and the effective size of the available nutrient pool. Recent reviews of nitrogen isotope variation in marine systems are given by Montoya (2007) and Graham *et al*. (2010). In most ocean systems, primary production is fuelled by nitrate (NO_3^-), and the isotopic composition of phytoplankton is controlled by the isotopic composition of nitrate and the amount of nitrate utilization. In most regions all nitrate is used by phytoplankton, so the averaged composition of phytoplankton integrated over a season will be the same as the initial isotopic composition of nitrate. In highly productive regions with sub-oxic deep water, bacterial denitrification can drive sub-surface dissolved NO_3^- to much more positive values. Upwelling of this positive nitrate leads to strong spatial gradients in surface water $\delta^{15}N$ (NO_3^-). In nutrient-limited zones such as the Southern Ocean, incomplete assimilation of dissolved NO_3^- leads to relatively negative $\delta^{15}N$ values in POM. Finally, in nutrient-rich low-chlorophyll regions, bacterial N_2 fixation occurs resulting in relatively negative $\delta^{15}N$ values. As POM $\delta^{15}N$ values are dependent on dynamic processes such as nutrient depletion and upwelling, both absolute POM $\delta^{15}N$ values and the spatial distribution of $\delta^{15}N$ POM values are subject to temporal variation on seasonal, annual and decadal scales.

CARBON BASELINES

$\delta^{13}C$ values in components of a marine ecosystem also reflect the isotopic signature of primary productivity at the base of the food chain (Wada *et al*., 1991). Carbon isotope variation in POM is controlled by the concentration and isotopic composition of dissolved CO_2, phytoplankton growth rates, cell geometry and taxonomy. SST acts as a master control, as cooler waters contain more dissolved nutrients, including CO_2, leading to greater preferential uptake of the lighter isotope, *e.g.* ^{12}C. In warmer waters, however, there is less available CO_2 resulting in relatively positive $\delta^{13}C$ POM values. Temperature also controls phytoplankton growth rate: where nutrients are not limiting, plankton cells grow faster under warmer conditions and exhibit less preferential uptake of the lighter isotope, incorporating all available nutrient sources

in order to maintain their growth at high rates (Popp *et al.*, 1998; Hofmann *et al.*, 2000; Ngochera & Bootsma, 2011). As SSTs increase, stratification limits nutrient availability, which suppresses diatom growth in favour of smaller-celled nanoplankton. Diatoms produce POM with relatively elevated $\delta^{13}C$ values. The combination of lower CO_2 availability, higher growth rate and nutrient limitation under warmer temperatures generally leads, therefore, to enrichment of ^{13}C and thus elevated $\delta^{13}C$ values. This is often reported as a latitudinal gradient in $\delta^{13}C$ values, with lower, warmer latitudes having more positive phytoplankton $\delta^{13}C$ values (Lorrain *et al.*, 2009). In warmer waters with a well-developed thermocline, plankton growth is nutrient-limited, resulting in relatively negative plankton $\delta^{13}C$ values in the subtropical gyres. In stratified waters, or under intense bloom conditions, preferential removal of ^{12}C into POM results in a progressive elevation in POM $\delta^{13}C$ values as the phytoplankton bloom progresses, thus a strong bloom that has been productive for a long time in warm conditions would be expected to contain organic carbon that is considerably enriched in ^{13}C compared to a smaller, shorter bloom in cooler, less stratified conditions (Hofmann *et al.*, 2000; Fry, 2006; Trueman & Moore, 2007).

The species composition of primary producers is also important in determining isotopic values. As a bloom advances and phytoplankton cells decay, ammonium becomes a major source of nitrogen. Certain enzymes important in ammonium uptake, *e.g.* phosphoenol carboxykinase (PEPCK) and phosphoenolpyruvate carboxylase (PEPC), are associated with decreased isotopic discrimination and therefore cause relatively positive $\delta^{13}C$ values in diatoms (PEPCK only) and dinoflagellates (PEPC and PEPCK) (Lara *et al.*, 2010). This probably inundates the cells with undiscriminated carbon ions, as opposed to ribulose-1,5-biophosphate carboxylase oxygenase (RuBisCo), which they also contain but which is more discriminatory in its isotopic uptake. Diatoms are also fast-growing compared with many other types of phytoplankton, which may lead to increased isotopic enrichment through greater efficiency in the use of source nutrients. Hence, locally elevated values of $\delta^{13}C$ within the trophic web may indicate either prevalence of diatoms in the phytoplankton, or rapid primary production incorporating all available isotopes of carbon, rather than preferentially incorporating ^{12}C in a manner common to slower rates of production (Wainright *et al.*, 1993).

As in N, plankton $\delta^{13}C$ values broadly vary with large-scale features such as SST, resulting in predictable ocean-basin scale isotopic gradients (Hofmann *et al.*, 2000; Tagliabue & Bopp, 2008; Graham *et al.*, 2010). Small-scale variation in SST on seasonal, annual and decadal scales, however, will again alter the absolute $\delta^{13}C$ values in POM in any area and the spatial distribution of $\delta^{13}C$ values over wider regional scales (Rolff, 2000). The result of these spatial variations in C and N isotopes is a relatively high degree of climate-linked regional temporal and spatial variation super-imposed on broad ocean-basin scale isoscapes (Hofmann *et al.*, 2000; Tagliabue & Bopp, 2008; Graham *et al.*, 2010; Newsome *et al.*, 2010).

KEY EXAMPLES OF USE OF C AND N TO TRACK MIGRATIONS

$\delta^{13}C$ values in marine megafaunal tissues have been found to relate strongly to foraging habitat baseline $\delta^{13}C$ values, often with isotopic separation seen between migration start and end points, allowing discrimination between separate feeding

populations (Hobson & Schell, 1998; Lee *et al*., 2005; Cherel *et al*., 2009). Stable carbon isotopes have been used to track seasonal and ontogenetic migrations of cetaceans and pinnipeds (Best & Schell, 1996; Lee *et al*., 2005; Mendes *et al*., 2007; Cherel *et al*., 2009) by relating tissue δ^{13}C values to the δ^{13}C values of bulk primary production in different water bodies and latitudes.

The pioneering work of Best & Schell (1996), Hobson & Schell (1998), Lee *et al*. (2005) and Cherel *et al*. (2009). took advantage of the strong isotopic gradient in δ^{13}C values between the Bering and Chukchi Seas, and repeated sampling of sequentially growing tissues such as baleen to track regular, repeated seasonal migrations between breeding and feeding grounds. Similarly, several workers have used the strong and predictable isotopic gradient in the Southern Ocean to track foraging ecology in seabirds (Cherel & Hobson, 2007) and pinnipeds (Cherel *et al*., 2009). Jaeger *et al*. (2010) validated the use of isotopic gradients in tracking foraging ecology in wandering albatrosses *Diomedea exulans* by using satellite tags. Mendes *et al*.'s (2007) work focussed on ontogenetic series of carbon isotopes in sperm whale *Physeter macrocephalus* teeth, supporting a gradual poleward migration post-puberty with an age-related decline in δ^{13}C values.

Fishes, however, are often more difficult to study than mammals and birds due to their cryptic nature and the difficulties involved in capture and sampling; they are not terrestrially accessible on breeding colonies or through stranding events, thus samples must be taken from fisheries or from research surveys. On local scales, isotopic gradients associated with changes in production sources have been used to track habitat use and movements between discrete regions. Fuji *et al*. (2011) recorded an isotopic gradient in prey mysid species along an estuary, and used this to demonstrate ontogenetic migrations in the temperate seabass *Lateolabrax japonicus* (Cuvier 1828) between freshwater and estuarine zones of the estuary, and demonstrate the nutritional benefit of migration into freshwater zones. Rodgers *et al*., (2008) explored isotopic gradients between coasts and fjords in southern New Zealand to investigate recruitment patterns and juvenile migrations in blue cod *Parapercis colias* (Forster 1801).

In coastal marine habitats, Papastamatiou *et al*. (2010) integrated telemetry and isotopic work to identify movement patterns and nutrient use in sharks between lagoons within the Palmyra Atoll National Wildlife Refuge. Onshore–offshore gradients in both δ^{13}C and δ^{15}N values were used by Tanaka *et al*. (2010) to demonstrate seasonal migrations and stock origin in commercially exploited populations of anchovy *Engraulis japonicus* Temminck & Schlegal 1846. This study confirmed anecdotal fishery knowledge, showing that spring-caught juvenile fish were spawned and foraged in offshore habitats prior to fishery interception, whereas autumn-caught fish had recently migrated to the offshore fishing ground after foraging in inshore waters. Finally, Dempson *et al*. (2010) used carbon isotopes in *S. salar* to show that fish originating in either North America or Ireland must feed in different regions due to differences in scale and muscle isotope values.

COMPOUND SPECIFIC STABLE-ISOTOPE ANALYSES IN MARINE MIGRATION RESEARCH

All of the studies above are based on either prior knowledge of an existing isotopic gradient or coupled measurements of spatially separated prey items and

fishes. Relatively few studies have attempted to geolocate fishes directly from stable-isotope values. Recently, stable-isotope analyses have been performed on individual compounds such as amino acids. Amino acids in a consumer's protein may be either synthesized *de novo* in the body, derived purely from diet, or a mixture of both. Amino acids that are not synthesised *de novo*, but obtained directly from diet are termed source amino acids in terms of nitrogen and essential amino acids in terms of carbon. The degree of *de novo* synthesis varies between organisms, but amino acids such as glycine, histidine and phenylalanine are commonly reported as source amino acids and glutamic acid, aspartic acid, leucine and proline typically show stronger trophic fractionation effects (Boecklen *et al*., 2011). Source or essential amino acids provide a direct measure of the isotopic composition of the consumer's diet. If a lack of *de novo* synthesis is conserved in the food chain, source amino acids may provide a relatively direct measure of the isotopic composition of primary production that avoids some of the complication associated with mixed baseline and trophic isotope effects (McClelland & Montoya, 2002; Popp *et al*., 2007; McMahon *et al*., 2010). To date, few studies have examined migration in marine fishes using a compound-specific amino acid approach (Popp *et al*., 2007; Lorrain *et al*., 2009; McMahon *et al*., 2011), and compound-specific isotope techniques are relatively time consuming and expensive, limiting their use in statistically meaningful studies. In the future, compound specific stable-isotope analyses are likely to become increasingly important both for direct studies of migration, and as a means to better understand the biochemistry underpinning stable-isotope fractionation.

Graham *et al*. (2010) provide one of the most extensive studies of stable isotopes in pelagic fishes, investigating foraging behaviours in Pacific yellowfin *Thunnus albacares* (Bonnaterre 1788) and bigeye tuna *Thunnus obesus* Lowe 1839. Analysing a large dataset of muscle samples from across the tropical Pacific Ocean, Graham *et al*. (2010) demonstrated high variance in nitrogen isotope composition. Compound-specific isotope analyses prove that the variation cannot be explained by changes in trophic level, and must therefore reflect differences in the isotopic composition at the base of the food chain (Popp *et al*., 2007). As tuna muscle integrates dietary isotope values over a period of at least 2–4 months (Graham *et al*., 2010), the high spatial variance preserved in the whole muscle samples implies a relatively low degree of movement and mixing in *T. albacares* and *T. obesus* within the equatorial Pacific Ocean. These conclusions are in agreement with passive and active tagging studies also suggesting relatively restricted spatial movements in *T. albacares* and *T. obesus* (Graham *et al*., 2010).

Studies such as those mentioned above are used to track marine animals across ocean-scale features, but are reliant on *a priori* knowledge of ocean conditions and likely migratory pathways. It is, however, possible to determine where fishes have been retrospectively. As discussed, the factors that control $\delta^{13}C$ values in open marine systems are directly and indirectly driven by the temperature of the surface waters. As $\delta^{13}C$ values are largely conserved during trophic transfer, temporal trends in SST in regions of feeding will covary with animal tissue $\delta^{13}C$ values. Using the covariation principle outlined above, MacKenzie *et al*. (2011) compared time series of carbon isotope compositions of scales from different populations of *S. salar* collected over a period of 18 years to contemporaneous records of SST to identify the most likely regions of marine feeding (Fig. 3). The matching of long-term records in the isotopic composition of fishes to remotely sensed data has the potential for application to

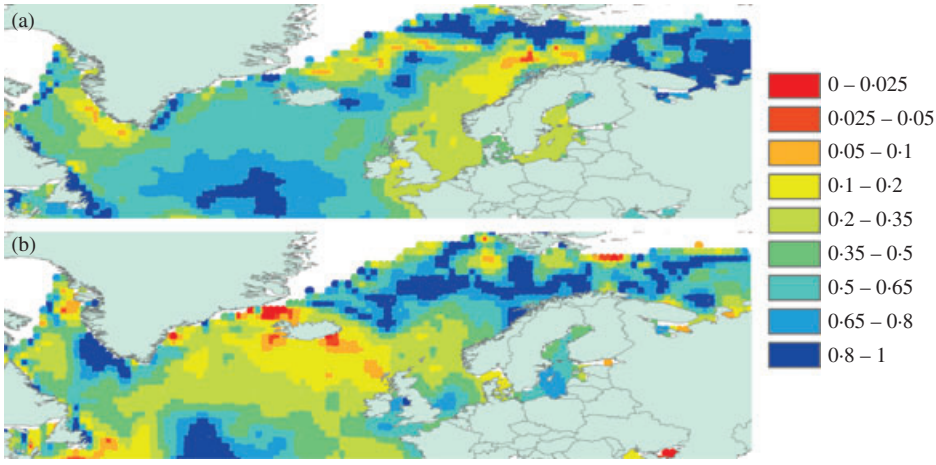

FIG. 3. Locations of marine feeding grounds of two sea-winter *Salmo salar* returning to (a) the north-east coast of the U.K. and (b) the U.K. River Frome (50° 41′ N; 02° 05′ W) predicted from the covariance of scale carbon isotope and sea surface temperature time series. Colours represent the significance (*p*-values) of (autocorrelation adjusted) correlations. After MacKenzie *et al.* (2011).

many different fish species. The advantage of this approach, other than avoiding the expense and pitfalls of tagging as mentioned above, is that, using fish tissues collected over a period of time, it allows for retrospective identification of feeding location. In the case of scale tissues, the sampling is also minimally invasive and non-destructive.

CONCLUSIONS

While the isotopic compositions of muscle, scale and otolith tissues have been extremely useful in tracking marine movements of a range of species, as discussed above, natural biological variability within and between species means that these tissues are grown and remodelled at differing rates. These rates are often an unknown factor in analyses, meaning that the timeframe for any locational information is usually based on informed guesswork. As such there is a great need for empirical studies of tissue growth and turnover rates in species of interest, such as those carried out by Trueman *et al.* (2005). Additionally, the power of tag-recapture or satellite telemetry tagging studies could be increased if they were carried out in concert with measurements of the isotopic compositions of tissues grown during such studies. Improvements to current measurements of baseline isotopic variation, allowing model validation, would also immeasurably improve the ability to track and locate fishes at sea.

Graham *et al.* (2010) suggested the coupling of tissue turnover times, isoscapes and multiple tissue measurements to provide directional migration models; this would be a very powerful approach under relatively static isotopic conditions. If this tracking method were combined with the use of diffusion-advection individual-based models (IBM) to generate possible tracks, and maximum likelihood, or Bayesian methods to

select the most likely migration routes, it would allow for the incorporation of more dynamic isotopic conditions at sea, such as those seen in C and N isotope ratios. In regions with isotopic gradients on similar spatial scales to migration patterns this approach could provide a viable natural geolocational tag.

It is important to keep in mind that chemical tracers should not be viewed as an alternative geolocation tool to be used in isolation. The power of chemical tags comes from their independence of most of the assumptions underpinning tagging or genetic methods. As with most branches of natural sciences, the clearest and most accurate picture will be built from a combination of complementary techniques.

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