

A review of ecogeochemistry approaches to estimating movements of marine animals

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Abstract

Ecogeochemistry—the application of geochemical techniques to fundamental questions in population and community ecology—has been used in animal migration studies in terrestrial environments for several decades; however, the approach has received far less attention in marine systems. This review includes comprehensive meta-analyses of organic zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at the base of the food web, dissolved inorganic carbon $\delta^{13}\text{C}$ values, and seawater $\delta^{18}\text{O}$ values to create, for the first time, robust isoscapes for the Atlantic Ocean. These isoscapes present far greater geographic variability in multiple geochemical tracers than was previously thought, thus forming the foundation for reconstructions of habitat use and migration patterns of marine organisms. We review several additional tracers, including trace-element-to-calcium ratios and heavy element stable isotopes, to examine anadromous migrations. We highlight the value of the ecogeochemistry approach by examining case studies on three components of connectivity: dispersal and natal homing, functional connectivity, and migratory connectivity. We also discuss recent advances in compound-specific stable carbon and nitrogen isotope analyses for tracking animal movement. A better understanding of isotopic routing and fractionation factors, particularly of individual compound classes, is necessary to realize the full potential of ecogeochemistry.

Animal migrations are among nature's most spectacular and biologically significant phenomena (Dingle 1996). In an evolutionary context, the ability to move determines the genetic structure of geographically separated populations. For instance, homing to natal populations may lead to genetic isolation and significant adaptation to local environments, but only if dispersal is sufficiently low to allow local genetic variation to occur. The demographic implications of migration and dispersal to populations are equally compelling. Movement rates will determine colonization patterns of new habitats, the resiliency of populations to harvest, and the effectiveness of spatial management options designed to reverse declines in ocean biodiversity and marine-capture fisheries. The importance of an understanding of migration and connectivity is particularly timely as organisms are faced with adapting to global climate change (Roessig et al. 2004; Munday et al. 2009).

Most classic examples of long-distance migration come from terrestrial environments. In contrast, marine ecologists have, at least until recently, known remarkably little about migration, dispersal, and migratory connectivity in marine organisms (Cowen et al. 2007). This ignorance stems from the inherent logistic challenges when working in a vast and largely opaque environment and with animals capable of traveling thousands of kilometers on seasonal time scales. New archival tag technology is shedding light on some remarkable long-distance migrations by large tunas (Block et al. 2005) and sharks (Skomal et al. 2009). Acoustic tags are similarly expanding our knowledge of fish movements over smaller spatial scales (Parsons et al. 2003; Luo et al. 2009). However, not all marine species, or life

stages, are amenable to archival or acoustic tags. Many marine fish and invertebrates begin life as microscopic larvae that are difficult, if not impossible, to tag using conventional artificial markers (Thorrold et al. 2002). Similarly, even the most basic aspects of the early life history of many elasmobranchs remain unknown, largely because neonates of many species are so rarely observed (Sims et al. 1997; Wilson and Martin 2004). Quantifying animal movement, therefore, remains a major challenge for researchers applying spatially explicit population models to conservation and management questions in marine environments (Botsford et al. 2009).

Recently, new approaches using isotopic and elemental tags as natural markers have been developed that may provide new insights on animal movements in ocean ecosystems (Graham et al. 2010; Hobson et al. 2010; Ramos and Gonzalez-Solis 2012). These techniques represent a new direction for the field of ecogeochemistry, a term first used to describe the application of stable carbon (C) and nitrogen (N) isotopes to infer diet and trophic structure in bats (Mizutani et al. 1991). The expansion of ecogeochemistry to include the use of geochemical markers in movement studies is logical as both types of studies use many of the same isotope systems and associated analytical techniques. The term “ecogeochemical markers,” therefore, refers to elemental and isotope ratios in biological tissues that are used to reconstruct movement or dietary histories of animals, and is similar to an earlier term “biogeochemical markers” reviewed by Schlesinger (1997) and discussed in the context of animal migration by Rubenstein and Hobson (2004). Our terminology is, however, less ambiguous as biogeochemistry more accurately refers to the study of biotic controls on chemical transformations in the environment (Elder 1988; Dittmar and Kattner 2003).

Ecogeochemistry is a potentially valuable approach to delineate metapopulation structure that is necessary for

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successful spatial management of many marine-capture fisheries (Crowder and Norse 2008). Natural tagging techniques rely upon geographic differences in isotope or trace element abundance that are recorded in the chemical composition of body tissues. The approach overcomes several significant difficulties with conventional techniques for studying movement (Thorrold et al. 2002). Ecogeochemical markers are induced by the environment, rather than administered by the researcher, and therefore all animals within a specified location are labeled without having to be captured and tagged. Similarly, because every individual is marked there is no need to recapture tagged animals. The approach is therefore well suited for rare species that may be unavailable to researchers for significant periods of their life history. Artificial tags also come with significant tagging and handling effects that limit their use to large-bodied animals. Natural ecogeochemical markers, on the other hand, do not affect behavior or mortality rates (Thorrold et al. 2002).

Whereas natural geochemical tags have been used to track movements of animals in terrestrial systems, there has been comparatively little use of the technique in ocean environments. One reason for this apparent oversight is that the degree of geographic variation in isotope and element abundances across marine environments may not be fully appreciated (Hobson 1999; Rubenstein and Hobson 2004). We present the results of a comprehensive meta-analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at the base of the food web and seawater $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values to create, for the first time, robust isoscapes for the Atlantic Ocean. We review several additional tracers, including trace-element-to-calcium ratios and trace element stable isotopes, to examine diadromous migrations. We also discuss recent advances in compound-specific stable carbon and nitrogen isotope analyses for tracking animal movement. We conclude by highlighting the value of an ecogeochemistry approach by examining case studies on population connectivity including dispersal and natal homing, functional connectivity, and migratory connectivity.

Geographic variation

To be successfully applied in the field, an ecogeochemistry approach must do each of the following (Hobson et al. 2010): (1) establish a geochemical map that characterizes distinct geochemical signatures in different habitats, (2) constrain tissue turnover rates that determine the period of spatial integration of geochemical signatures for a particular animal tissue, and (3) identify isotope or elemental fractionation factors between consumer and diet, or between animals and the ambient environment, that may offset geochemical signatures in animal tissues from baseline isoscape values. Whereas terrestrial isoscapes have been used to track long-distance migrations of birds and mammals for many years (Hobson 1999; Rubenstein and Hobson 2004), the degree of geographic variation in marine isotopes has only recently been recognized (West et al. 2010).

Here we synthesize geographic variability in inorganic (dissolved inorganic carbon [DIC] $\delta^{13}\text{C}_{\text{DIC}}$ and seawater

$\delta^{18}\text{O}_{\text{SW}}$) and organic (zooplankton $\delta^{13}\text{C}_{\text{PLK}}$ and $\delta^{15}\text{N}_{\text{PLK}}$) isoscapes of the Atlantic Ocean, and discuss the primary mechanisms generating this isoscape variability. These maps are necessarily constrained over space and time scales by the available data coverage. Caution should therefore be used when interpreting isoscape patterns in areas with low sample densities. All $\delta^{18}\text{O}_{\text{SW}}$ data are available on the Global Oxygen-18 Database (Schmidt et al. 1999). Similarly, seawater DIC $\delta^{13}\text{C}_{\text{DIC}}$ data were mined from the Global Data Analysis Project (Key et al. 2004). Data for both the $\delta^{18}\text{O}_{\text{SW}}$ and $\delta^{13}\text{C}_{\text{DIC}}$ isoscapes were limited to the top 100 m of the Atlantic Ocean. Zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were collated from extensive searches of Institute for Scientific Information Web of Science, Google Scholar, the Open Access library Pangaea (www.pangaea.de), and several other online data repositories. We limited the zooplankton isoscape search to samples described as net plankton (< 1 mm), collected in the euphotic (< 150 m depth) and not preserved in formalin. The zooplankton isoscapes comprise a range of species, but consisted predominantly of copepods and similar-sized zooplankton. In order to achieve the best spatial coverage, no attempts were made to sort data temporally, either by season or year. However, most samples were collected no earlier than 1990. References for the data presented in the isoscapes are organized by isotope in Tables 1 and 2.

Isoscapes were generated using Ocean Data View (ODV) version 4.5.0 (Brown 1998; Schlitzer 2002). Isotope data were displayed as color-shaded maps based on contouring of the original data using the Data Interpolating Variational Analysis (DIVA) gridding software (Barth et al. 2010). DIVA gridding takes into account coastlines, subbasins, and advection. Calculations rely on a finite-element resolution and take into account the distance between analysis and data (observation constraint), the regularity of the analysis (smoothness constraint), and physical laws (behavior constraint).

The gridding algorithms used in ODV provided estimations of isotope values at arbitrary (x, y) points based on observational data values at sampling locations (x_i, y_i) , $i = 1 \dots n$. We used misfit plots to assess the accuracy of the gridding algorithm. Misfits represent the difference between the observational data and the associated modeled value at the same location calculated by the gridding algorithm. In general, misfits should show no systematic spatial patterns, the mean of the misfits should be close to zero, and the standard deviation of the misfits close to the error in the data. We plotted gridding misfits onto the isoscape maps to visually assess the spatial distribution and magnitude of the misfits.

Inorganic $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isoscapes—The $\delta^{13}\text{C}$ values of DIC in surface ocean waters are influenced by physical and biological processes that create noticeable latitudinal gradients in the inorganic carbon isoscape (Figs. 1A, 2A). Air–sea gas exchange causes fractionation via two equilibration processes: the slow, ~ 10 yr process (Broecker and Peng 1974) of equilibration between atmospheric CO_2 and oceanic DIC that includes all the inorganic carbon species, and the relatively quick equilibration process of CO_2 alone.

Table 1. Regional breakdown of references and sample sizes for the dissolved inorganic carbon $\delta^{13}\text{C}_{\text{DIC}}$ (Figs. 1A, 2A) and seawater $\delta^{18}\text{O}_{\text{SW}}$ (Figs. 1B, 2B) inorganic isoscapes of the Atlantic Ocean. na = no data available.

Region	Latitude range	Longitude range	Sample size (<i>n</i>)		References	
			$\delta^{13}\text{C}_{\text{DIC}}$	$\delta^{18}\text{O}_{\text{SW}}$	$\delta^{13}\text{C}_{\text{DIC}}$	$\delta^{18}\text{O}_{\text{SW}}$
Northwest Atlantic	80°N to 35°N	80°W to 45°W	53	1998	Key et al. 2004	Schmidt et al. 1999
	35°N to 23°N	80°W to 70°W	30	61	Key et al. 2004	Schmidt et al. 1999
Northeast Atlantic	80°N to 35°N	45°W to 20°E	563	1694	Key et al. 2004	Schmidt et al. 1999
	35°N to 23°N	30°W to 5°W	131	7	Key et al. 2004	Schmidt et al. 1999
Mediterranean Sea	43°N to 30°N	5°W to 20°E	na	474	Key et al. 2004	Schmidt et al. 1999
Sargasso Sea	35°N to 23°N	70°W to 30°W	578	14	Key et al. 2004	Schmidt et al. 1999
Gulf of Mexico	30°N to 20°N	100°W to 80°W	na	75	Key et al. 2004	Schmidt et al. 1999
Tropical Atlantic	23°N to 23°S	90°W to 15°E	512	747	Key et al. 2004	Schmidt et al. 1999
Southern Atlantic	23°S to 55°S	70°W to 20°E	392	136	Key et al. 2004	Schmidt et al. 1999
Southern Ocean	55°S to 80°S	70°W to 20°E	248	798	Key et al. 2004	Schmidt et al. 1999
Total			2507	6004		

In areas of CO_2 invasion, such as the North Atlantic, surface waters have relatively low $\delta^{13}\text{C}$ due to the introduction of isotopically light atmospheric CO_2 . In areas of outgassing, like equatorial upwelling zones, surface waters become ^{13}C enriched (Lynch-Stieglitz et al. 1995).

Photosynthetic marine organisms preferentially take up the lighter carbon isotope (^{12}C) with a $\delta^{13}\text{C}$ fractionation value of approximately -19‰ between $\delta^{13}\text{C}_{\text{DIC}}$ and fixed organic carbon (Lynch-Stieglitz et al. 1995). Organic material is then remineralized as it sinks and water masses at depth are therefore low in $\delta^{13}\text{C}_{\text{DIC}}$ value relative to surface waters, typically approaching 0‰ . Upwelling events can result in significant, low surface $\delta^{13}\text{C}_{\text{DIC}}$ value anomalies (Kroopnick 1985).

The observed variation in $\delta^{13}\text{C}_{\text{DIC}}$ is much smaller than the potential range if the effects of the dominant regional processes acted in isolation. Photosynthetic organisms prefer to incorporate ^{12}C , leading to isotopically heavier DIC values in surface vs. deep waters, with variation in nutrient availability driving the amount of photosynthesis and therefore the amount of fractionation. However, this pattern is nearly offset due to temperature-driven air–sea gas exchange fractionation, leading to a relatively small range of geographic variation (Lynch-Stieglitz et al. 1995; Gruber et al. 1999). In terms of large-scale trends, there is a maximum in surface-water $\delta^{13}\text{C}_{\text{DIC}}$ values near the sub-Antarctic Front due to photosynthetic activity, and minimum surface-water $\delta^{13}\text{C}_{\text{DIC}}$ values in the Southern Ocean due to upwelling (Gruber et al. 1999). Worldwide, anthropogenic input of isotopically light CO_2 into the atmosphere has depleted surface ocean $\delta^{13}\text{C}_{\text{DIC}}$ values, with a decrease of about 0.2‰ per decade in the Atlantic Ocean (Quay et al. 2003). The largest changes in $\delta^{13}\text{C}_{\text{DIC}}$ can be seen in the equatorial and polar regions, with little or no change in the Southern Ocean. On seasonal time scales, sub-Arctic latitudes ($> 50^\circ\text{N}$) experience summertime $\delta^{13}\text{C}_{\text{DIC}}$ increases of up to 1‰ , and in the Sargasso Sea, near Bermuda, time-series data show annual oscillations in $\delta^{13}\text{C}$ values of 0.2‰ to 0.3‰ due to changes in net community production, air–sea exchange, and vertical transport (Gruber et al. 1999).

Oxygen isotope values of seawater ($\delta^{18}\text{O}_{\text{SW}}$) show substantial regional and ocean basin-scale variability that can

facilitate tracking habitat use and movement in the marine environment on a variety of scales (Figs. 1B, 2B). Seawater $\delta^{18}\text{O}$ values are generally linearly correlated with salinity due to the combined effects of evaporation and freshwater input (Epstein and Mayeda 1953). Evaporation acts to move water molecules with light oxygen isotopes into the vapor phase more quickly than the heavy isotopologues, and at the same time increases surface-water salinity. Meteoric water $\delta^{18}\text{O}$ values are also lower than $\delta^{18}\text{O}_{\text{SW}}$ values, with the magnitude of the effect dependent on the water source (Gat 1996). For instance, $\delta^{18}\text{O}$ values in river waters along the east coast of the U.S.A. vary from -2‰ (Vienna Standard Mean Ocean Water) in the St. Johns River, Florida, to -11‰ in the Connecticut River (Walther and Thorrold 2008). Freshwater discharge, in turn, lowers $\delta^{18}\text{O}_{\text{SW}}$ values of coastal ocean waters and, in the case of large rivers like the Amazon and the Orinoco in the tropics and the MacKenzie and Ob in the Arctic, can produce anomalously low $\delta^{18}\text{O}_{\text{SW}}$ values that penetrate hundreds of kilometers into the Atlantic Ocean (Cooper et al. 2005). However, some coastal regions, particularly shallow, enclosed or semi-enclosed bays with limited freshwater input, can become hypersaline and produce anomalously high $\delta^{18}\text{O}$ values (Lloyd 1966).

More positive $\delta^{18}\text{O}_{\text{SW}}$ values are typically observed in highly evaporative subtropical gyres and semi-enclosed marginal basins, including the Mediterranean Sea (maximum $\delta^{18}\text{O}_{\text{SW}} = 1.7\text{‰}$ [Rohling and Rijk 1999]) and the Red Sea (maximum $\delta^{18}\text{O}_{\text{SW}} = \sim 1.6\text{‰}$ [Ganssen and Kroon 1991]). The most negative $\delta^{18}\text{O}$ values are often found at high latitudes (nearly -20‰ in the Arctic Ocean) and regions of extensive freshwater input. There are, however, at least two exceptions to the general pattern of decreasing $\delta^{18}\text{O}_{\text{SW}}$ values with latitude. The California Current exhibits relatively low $\delta^{18}\text{O}_{\text{SW}}$ values for its latitude, due to advection of ^{18}O -depleted subpolar water toward the equator along the eastern boundary of the North Pacific Ocean. Conversely, the northeastern North Atlantic exhibits high $\delta^{18}\text{O}_{\text{SW}}$ values for its latitude due to poleward advection of ^{18}O -enriched low-latitude water via the Gulf Stream. Vertical profiles of $\delta^{18}\text{O}$ generally tend to show less variation than the horizontal surface variation, trending towards 0‰ with depth (Schmidt et

Table 2. Regional breakdown of references and sample sizes for the zooplankton $\delta^{13}\text{C}_{\text{PLK}}$ (Figs. 1C, 2C) and $\delta^{15}\text{N}_{\text{PLK}}$ (Figs. 1D, 2D) organic isoscapes of the Atlantic Ocean.

Region	Latitude range	Longitude range	Sample size (<i>n</i>)		References	
			$\delta^{13}\text{C}_{\text{PLK}}$	$\delta^{15}\text{N}_{\text{PLK}}$	$\delta^{13}\text{C}_{\text{PLK}}$	$\delta^{15}\text{N}_{\text{PLK}}$
Northwest Atlantic	80°N to 35°N	80°W to 45°W	203	69	Peterson and Howarth 1987; Fry 1988; Fry and Quinones 1994; France et al. 1995; Calvert 2000; Lesage et al. 2001; Hobson et al. 2002; Lamb and Swart 2008; Lysiak 2009; Pomerleau et al. 2011; K. McMahon unpubl. data	Peterson and Howarth 1987; Fry 1988; Hobson and Montevecchi 1991; Fry and Quinones 1994; Calvert 2000; Waser et al. 2000; Tittlemier et al. 2000; Lesage et al. 2001; Hobson et al. 2002; Montoya et al. 2002; Estrada et al. 2003; Lamb and Swart 2008; Lysiak 2009; Pomerleau et al. 2011; K. McMahon unpubl. data
Northeast Atlantic	35°N to 23°N	80°W to 70°W	12	2	Hobson et al. 1995; Calvert 2000; Hofmann et al. 2000; Polunin et al. 2001; Sato et al. 2002; Das et al. 2003; Le Loc'h and Hily 2005; Tamelander et al. 2006; Le Loc'h et al. 2008; Petursdottir et al. 2008, 2010; Hirsch 2009; Pajuelo et al. 2010; Kurten et al. 2012; K. McMahon unpubl. data	Hobson et al. 1995; Waser et al. 2000; Calvert 2000; Sato et al. 2002; Bode et al. 2003, 2007; Jennings and Warr 2003; Mahaffey et al. 2004; Kiriakoulakis et al. 2005; Sommer et al. 2005; Tamelander et al. 2006; Le Loc'h et al. 2008; Petursdottir et al. 2008, 2010; Hirsch 2009; Pajuelo et al. 2010; Kurten et al. 2012; K. McMahon unpubl. data
	80°N to 35°N	45°W to 20°E	72	68		
Mediterranean Sea	35°N to 23°N	30°W to 5°W	17	41	Pinnegar et al. 2000; Polunin et al. 2001; Stuck et al. 2001; Carlier et al. 2007; Harmelin-Vivien et al. 2008; Fanelli et al. 2009, 2011	Pinnegar et al. 2000; Stuck et al. 2001; Bode et al. 2007; Carlier et al. 2007; Harmelin-Vivien et al. 2008; Fanelli et al. 2009, 2011
	43°N to 30°N	5°W to 20°E	13	15		
Sargasso Sea	35°N to 23°N	70°W to 30°W	9	3	Sackett et al. 1965; Fry and Quinones 1994; Hofmann et al. 2000; K. McMahon unpubl. data	Altabet and Small 1990; Fry and Quinones 1994; Montoya et al. 2002; K. McMahon unpubl. data
Gulf of Mexico	30°N to 20°N	100°W to 80°W	29	12	Macko et al. 1984; Holl et al. 2007; Lamb and Swart 2008	Thayer et al. 1983; Macko et al. 1984; Holl et al. 2007; Lamb and Swart 2008
Tropical Atlantic	23°N to 23°S	90°W to 15°E	53	69	Sackett et al. 1965; Hofmann et al. 2000	Checkley and Entezroth 1985; Calvert 2000; Montoya et al. 2002; McClelland et al. 2003; Mahaffey et al. 2004; Abed-Navandi and Dworschak 2005; K. McMahon unpubl. data

Table 2. Continued.

Region	Latitude range	Longitude range	Sample size (<i>n</i>)		References	
			$\delta^{13}\text{C}_{\text{PLK}}$	$\delta^{15}\text{N}_{\text{PLK}}$	$\delta^{13}\text{C}_{\text{PLK}}$	$\delta^{15}\text{N}_{\text{PLK}}$
Southern Atlantic	23°S to 55°S	70°W to 20°E	68	35	Sackett et al. 1965; Matsuura and Wada 1994; Hofmann et al. 2000; Schmidt et al. 2003; Quillfeldt et al. 2005; Laakmann and Auel 2010; Kohler et al. 2011	Matsuura and Wada 1994; Sigman et al. 1999; Schmidt et al. 2003; Mahaffey et al. 2004; Quillfeldt et al. 2005; Laakmann and Auel 2010; Kohler et al. 2011; K. McMahon unpubl. data
Southern Ocean	55°S to 80°S	70°W to 20°E	70	51	Wada et al. 1987; Hofmann et al. 2000; Dunton 2001; Nyssen et al. 2002; Corbisier et al. 2004; Quillfeldt et al. 2005; Stowasser et al. 2012	Wada et al. 1987; Sigman et al. 1999; Dunton 2001; Nyssen et al. 2002; Schmidt et al. 2003; Quillfeldt et al. 2005; Stowasser et al. 2012
Total			546	365		

al. 1999). However, as with horizontal variation, vertical profiles of $\delta^{18}\text{O}$ generally follow the salinity profile patterns.

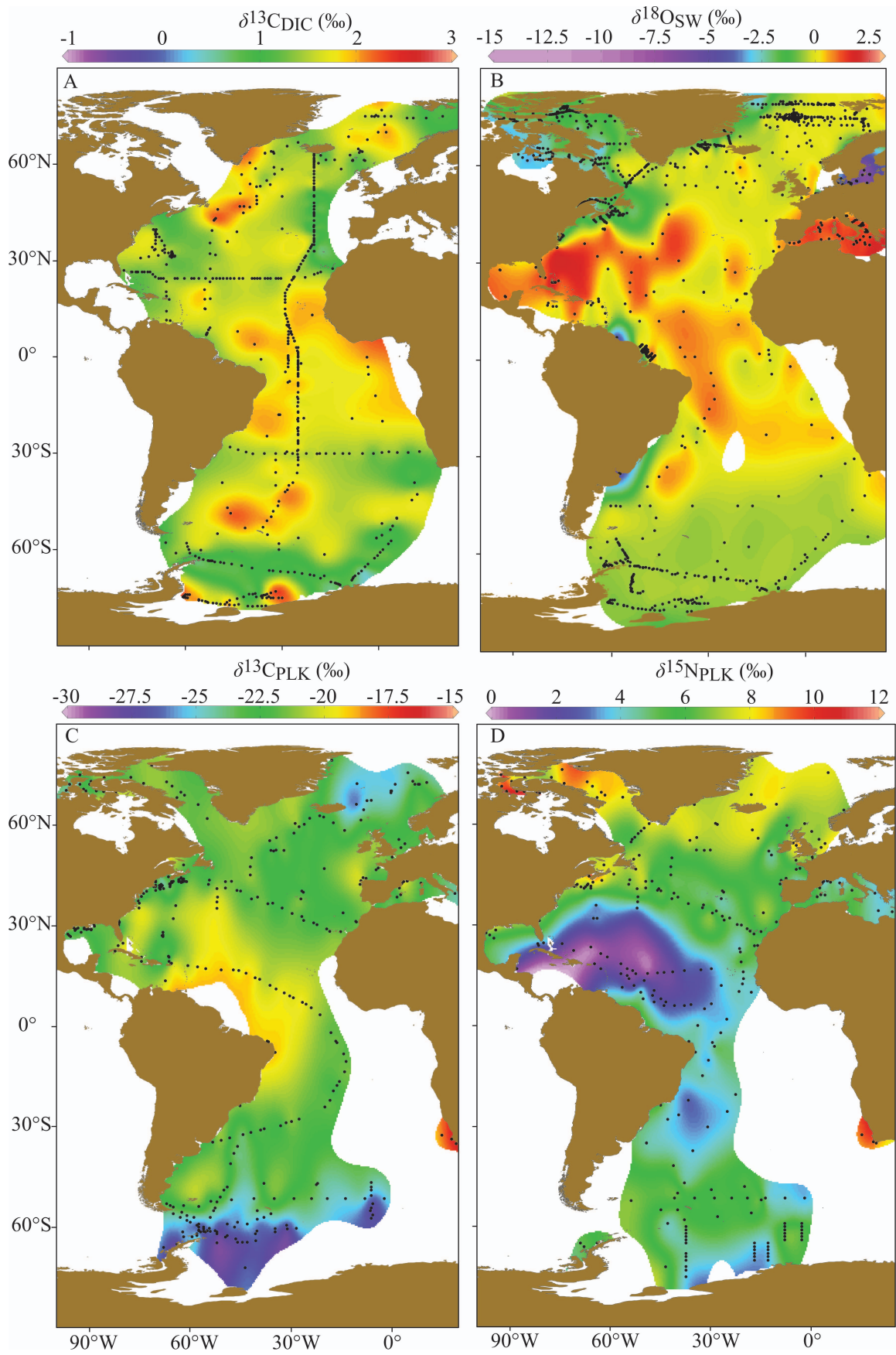
Organic isoscapes—We synthesized results from published organic stable carbon and nitrogen isotope data for zooplankton in the Atlantic Ocean (Table 2). Isoscapes of zooplankton carbon ($\delta^{13}\text{C}_{\text{PLK}}$ [Figs. 1C, 2C]) and nitrogen ($\delta^{15}\text{N}_{\text{PLK}}$ [Figs. 1D, 2D]) show substantial variation spatially, on regional and ocean basin scales. The $\delta^{13}\text{C}$ value of primary producers is strongly influenced by the $\delta^{13}\text{C}_{\text{DIC}}$ value of the local DIC pool (Fig. 1A), and thus spatial variability in $\delta^{13}\text{C}$ at the base of the food web ($\delta^{13}\text{C}_{\text{Base}}$) is primarily driven by the same physical parameters (temperature and $[\text{CO}_2]_{\text{aq}}$) that influence $\delta^{13}\text{C}_{\text{DIC}}$ values. However, internal biological parameters can also influence phytoplankton $\delta^{13}\text{C}$ values and thus obscure these patterns (Fry and Wainright 1991; Hinga et al. 1994; Kelly 2000). Nearshore and benthic systems with higher nutrient concentrations, and thus higher productivity, are typically more ^{13}C enriched than offshore, pelagic systems (France 1995). This gradient can be particularly pronounced in regions of strong upwelling or seasonal coastal phytoplankton blooms (Pancost et al. 1997). In addition, tighter terrestrial–littoral and benthic–pelagic coupling in nearshore systems can increase inputs from ^{13}C -heavy benthic algae and C_4 marsh plants (France 1995).

While nitrogen isotopes are commonly used to calculate trophic position of consumers in the marine environment, the microalgae that support marine food webs typically have $\delta^{15}\text{N}_{\text{Base}}$ values that change spatially and seasonally due to incomplete consumption of nitrogenous nutrients (Altabet and Francois 2001; Lourey et al. 2003), and differential utilization of nitrogen sources (nitrate, ammonium, N_2) in space and time (Dugdale and Goering 1967; Caraco et al. 1998; Dore et al. 2002). In the Atlantic Ocean, the lowest $\delta^{15}\text{N}_{\text{PLK}}$ values are found in the oligotrophic

Sargasso Sea, where diazotrophic cyanobacteria fix N_2 (0‰) into organic nitrogen (Montoya et al. 2002). In the higher latitudes of the Atlantic, NO_3^- (~ 5‰) is the major source of nitrogen for marine phytoplankton. Decomposition of particulate organic matter (POM) results in preferential losses in ^{14}N and creates a gradient of increasing $\delta^{15}\text{N}_{\text{POM}}$ with depth in the ocean that is particularly evident in areas of high productivity (Saino and Hattori 1980).

There can be significant variability in $\delta^{15}\text{N}_{\text{POM}}$ and $\delta^{15}\text{N}_{\text{PLK}}$ values on smaller spatial scales as well. Anthropogenic sources of nitrogen, including fertilizers, sewage and agricultural animal waste, and atmospheric deposition via fossil fuel burning, can have significant effects on coastal $\delta^{15}\text{N}_{\text{POM}}$ (Heaton 1986; Hansson et al. 1997). Local eutrophication from fertilizers and increased urbanization can lead to increases in primary production and denitrification, both of which generate an enriched $\delta^{15}\text{N}_{\text{POM}}$ isotopic signal (McClelland et al. 1997) that can be reflected in the $\delta^{15}\text{N}$ values of tissues in resident fishes and invertebrates (Griffin and Valiela 2001).

Both $\delta^{13}\text{C}_{\text{PLK}}$ and $\delta^{15}\text{N}_{\text{PLK}}$ values at the base of coastal food webs can also show significant temporal variability (Fig. 3), owing to changes in primary productivity and nutrient sources, microbial nitrogen cycling, temperature, and phytoplankton species growth rates and composition (Cifuentes et al. 1988; Goering et al. 1990; Ostrom et al. 1997; Caraco et al. 1998). Temporal variability can be pronounced on small spatial scales, as shown in the seasonal patterns of $\delta^{13}\text{C}_{\text{POM}}$ and $\delta^{15}\text{N}_{\text{POM}}$ values in the Delaware Estuary (Cifuentes et al. 1988). In early spring, POM reached a maximum of -17% in $\delta^{13}\text{C}$ and a minimum of $+2.3\%$ in $\delta^{15}\text{N}$. By summer, after the spring bloom had passed, the $\delta^{13}\text{C}_{\text{POM}}$ maximum disappeared and more negative values, down to -26% , were recorded within the estuary, whereas a $\delta^{15}\text{N}_{\text{POM}}$ maximum of $+18.7\%$ was located in the central portion of the estuary. The large seasonal variability was associated with shifts in available N sources, as NH_4^+



utilization far exceeded NO_3^- in the winter, and increases in productivity and decreases in nutrient availability during the spring bloom. The transfer of temporal variability in isotope values at the base of food webs to upper trophic consumers tends to diminish with increasing trophic level. Relatively slow tissue turnover rates in higher-trophic-level consumers may effectively lead to temporal averaging of much of the observed seasonal variability baseline values (Goering et al. 1990; O'Reilly et al. 2002). However, there is evidence that seasonal differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ can be observed in upper-trophic-level consumers in at least some situations (Goering et al. 1990; Riera and Richard 1997; Vizzini and Mazzola 2003).

Seasonal variability in isoscape structure can even be seen at regional and ocean basin scales. In general, seasonal variability is higher at high latitudes, with larger variations in temperature and productivity compared to low-latitude, tropical systems. Seasonal deviations in copepod $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the highly productive late-winter and early-spring months compared to the summer and early-fall months were similar on the western and eastern sides of the North Atlantic (Fig. 3). $\delta^{13}\text{C}$ values varied seasonally by 2‰ to 3‰, whereas $\delta^{15}\text{N}$ values varied by upwards of 6‰. This variability obviously needs to be considered when using isoscapes to track movement of animals through different habitats, particularly where animals may be selectively using different habitats during different times of the year.

Diadromous isoscapes—Quantifying movements of fishes between marine and freshwater environments has proved to be particularly amenable to ecogeochemistry approaches. Significant compositional differences between freshwater and ocean water generate distinctive isoscape gradients across the two systems. Stable carbon and oxygen isotopes provide perhaps the best tracer of diadromous movements, as spatial and temporal variability of freshwater end-members are generally higher than the relevant seawater end-members. Both $\delta^{13}\text{C}_{\text{DIC}}$ and $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ are lower in almost all freshwater systems compared to the coastal ocean (Kerr et al. 2007; Walther and Thorrold 2008). Moreover, as mentioned earlier, salinity is generally linearly correlated with $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ and therefore may allow for more subtle reconstructions of estuarine habitat use beyond a binary distinction between marine and freshwater habitats. Interestingly, Kerr et al. (2007) found that $\delta^{13}\text{C}_{\text{DIC}}$ was both tightly correlated with salinity and showed less seasonal and interannual variability than $\delta^{18}\text{O}_{\text{H}_2\text{O}}$ in a Chesapeake Bay tributary. Based on a high correlation between $\delta^{13}\text{C}_{\text{DIC}}$ and otolith $\delta^{13}\text{C}$

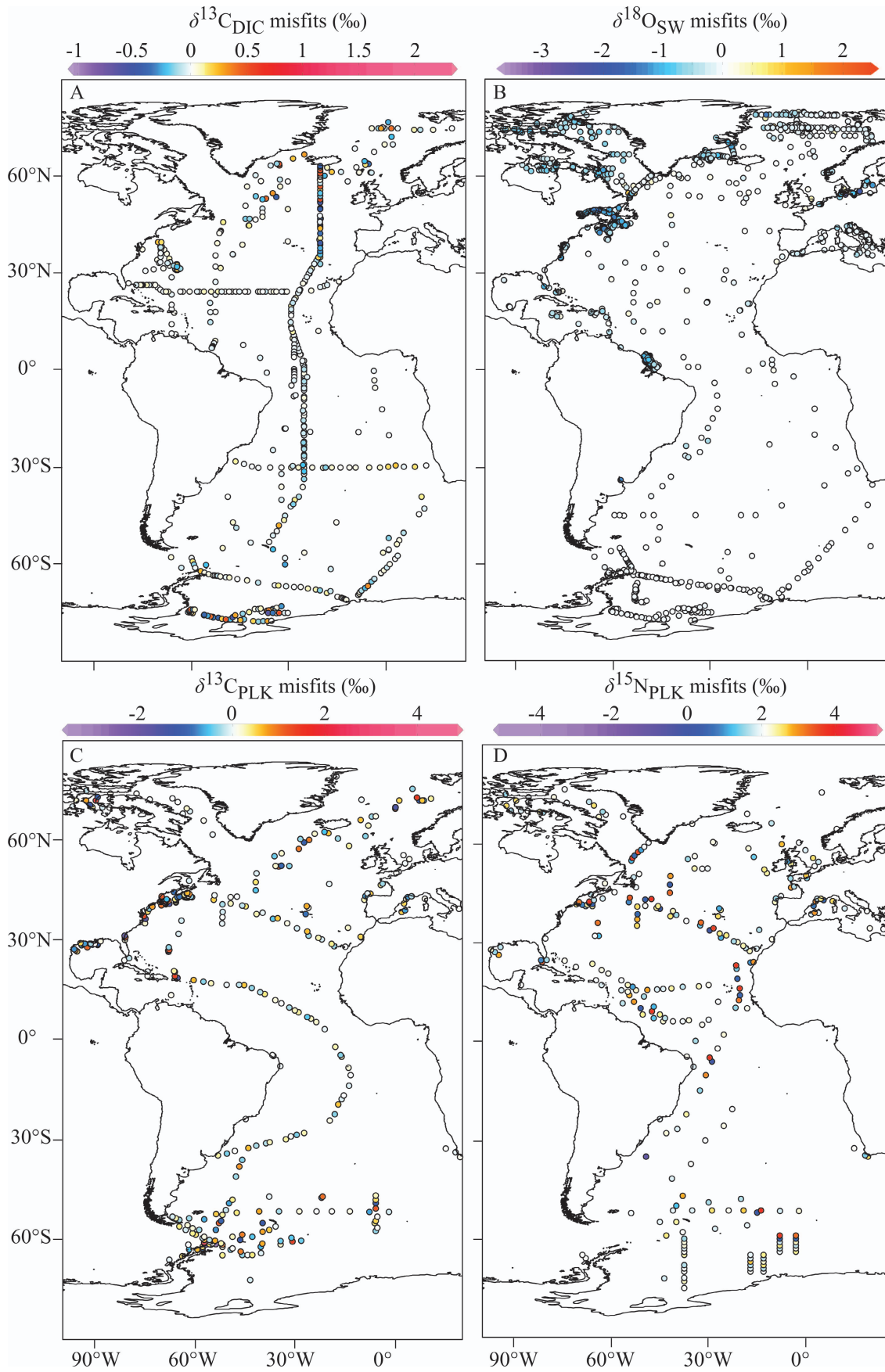
was a better tracer of habitat use as a function of salinity for fish populations, at least in the Patuxent River.

Several elemental ratios also differ significantly among freshwater and ocean waters. Notably, the concentrations of those elements in calcified tissues reflect dissolved concentrations of the elements in the ambient environment (Bath et al. 2000; Elsdon and Gillanders 2004; Dorval et al. 2005). Strontium (Sr) remains the most widely used element to track diadromous migrations (Elsdon et al. 2008). The size of the oceanic reservoirs of Sr and calcium (Ca), along with residence times of millions of years, results in relatively invariant seawater Sr:Ca ratios (8.5 mmol mol⁻¹; De Villiers 1999), and similarly invariant ⁸⁷Sr:⁸⁶Sr ratios of 0.70198 (Ando et al. 2010). Alternatively, freshwater values show significant geographic and temporal variability, with Sr:Ca ratios ranging from 0.27 to 19.18 mmol mol⁻¹ (Brown and Severin 2009). Similarly, ⁸⁷Sr:⁸⁶Sr ratios reflect bedrock values of watersheds and typically vary from ~ 0.704 in basaltic drainages to at least 0.75 in older highly radiogenic granites (Barnett-Johnson et al. 2010; Muhlfeld et al. 2012). It remains, therefore, necessary to quantify Sr:Ca and ⁸⁷Sr:⁸⁶Sr ratios in freshwater end-members in the systems of interest. Nonetheless, profiles of Sr:Ca and ⁸⁷Sr:⁸⁶Sr across archival tissues, including fish otoliths and scales, have often revealed unambiguous evidence of fish movement between freshwater and marine habitats (Tzeng and Tsai 1994; Limburg 2001; McCulloch et al. 2005).

Dissolved barium (Ba) concentrations also often differ significantly between freshwater and coastal marine waters. In seawater, Ba typically follows a nutrient-like distributions with relatively high concentrations in riverine and coastal areas compared to slope and oceanic waters (Shen and Sanford 1990). Freshwater dissolved Ba concentrations vary by nearly an order of magnitude globally around a worldwide riverine average of 0.10 μmol L⁻¹ (Gaillardet et al. 2003). Conversely, open-ocean surface values are typically 0.01 to 0.02 μmol L⁻¹, increasing to 0.03 μmol L⁻¹ and 0.09 μmol L⁻¹ at 3 km depth in the North Atlantic and deep North Pacific, respectively (Bruland and Lohan 2004). Therefore, episodic upwelling of the relatively high Ba concentrations found in colder, nutrient-rich deep waters can also be a significant source of Ba variability to the ocean surface waters (Lea et al. 1989; Kingsford et al. 2009). Similarly, episodic coastal flooding events may also significantly increase dissolved Ba levels in coastal waters over relatively short time scales (Alibert et al. 2003). While Ba:Ca and Ba:Sr ratios have been used to infer diadromous movements in at least one species (McCulloch et al. 2005), interpretation of Ba data is more difficult than

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Fig. 1. (A) Dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$) isoscape of seawater ($n = 2507$) from the upper 100 m of the Atlantic Ocean. (B) Oxygen ($\delta^{18}\text{O}_{\text{SW}}$) isoscape of seawater ($n = 6004$) from the upper 100 m of the Atlantic Ocean and Mediterranean Sea. (C) Zooplankton organic carbon ($\delta^{13}\text{C}_{\text{PLK}}$) isoscape ($n = 546$) from the upper 150 m of the Atlantic Ocean and Mediterranean Sea. (D) Zooplankton organic nitrogen ($\delta^{15}\text{N}_{\text{PLK}}$) isoscape ($n = 365$) from the upper 150 m of the Atlantic Ocean and Mediterranean Sea. Contour plots were generated in Ocean Data View (Schlitzer 2002) from a meta-analysis of published data (regional breakdown and references in Tables 1 and 2). Black dots indicate sample locations.



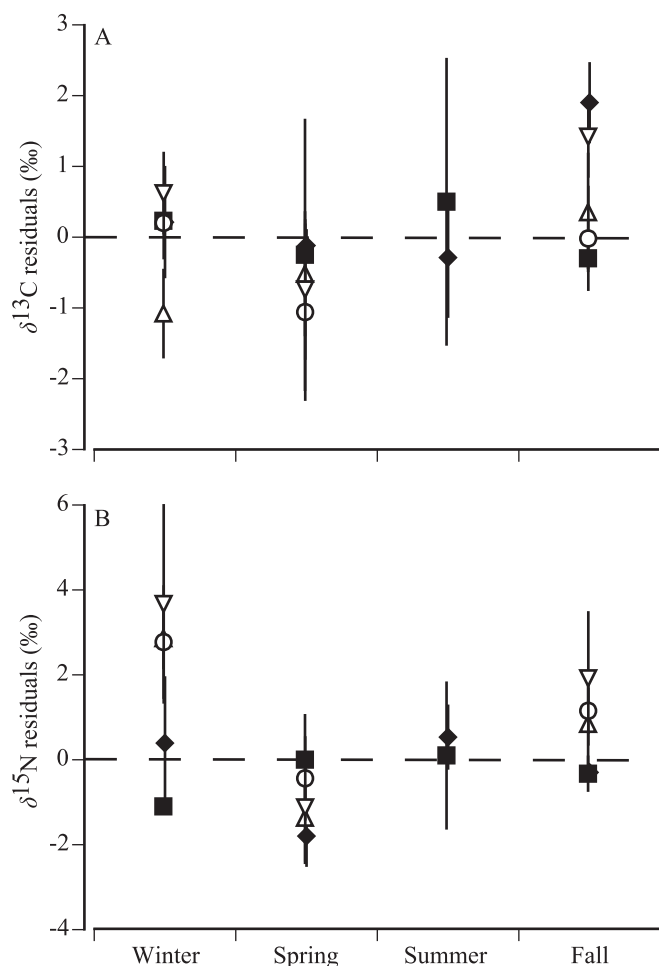


Fig. 3. Seasonal variability (residuals from the mean) in zooplankton (A) $\delta^{13}\text{C}$ values and (B) $\delta^{15}\text{N}$ values from the Northwest Atlantic Ocean (filled symbols; Lysiak 2009) and Northeast Atlantic Ocean (open symbols; Kurten et al. 2012). Different symbols represent different sites within a region.

for Sr because of the confounding influence of these short-term temporal variations in dissolved Ba concentrations.

While Sr and Ba are typically the most commonly used trace elements, there are a number of other elements, including magnesium (Mg), potassium (K), manganese (Mn), copper (Cu), zinc (Zn), and lead (Pb) that have been used to examine habitat use and movement patterns between fresh and marine environs (Thorrold et al. 1998a; Milton and Chenery 2001). Variations in several of these other trace elements (both the isotope values and element-to-calcium ratios) can reflect natural, watershed

variability and anthropogenic point sources. In the large Fly River, Papua New Guinea, water contaminated by a nearby copper mine can have mean total dissolved copper concentrations reach $20 \mu\text{g L}^{-1}$ at the confluence of the Ok Tedi and Fly Rivers 800 km from the coast and remain as high as $8 \mu\text{g L}^{-1}$ 400 km downstream (Storey and Figa 1998). Geffen et al. (1998) showed that the uptake of mercury and lead into fish otoliths was related to water concentrations of these metals.

Applications

In its most basic sense, ecological connectivity represents the movement of individuals between spatially distinct locations (Harrison and Bjorndal 2006). Animals travel among habitats over daily, seasonal, and ontogenetic time scales, which play an important role in the ecology of individuals and populations, as well as the resilience of ecosystem structure and functioning. Here, we illustrate the use of ecogeochemistry to address three components of connectivity: dispersal and natal homing, functional connectivity, and migratory connectivity. We define these terms as follows to avoid any confusion. Dispersal is the intergenerational spread of propagules away from their natal location, whereas natal homing represents the return of individuals to their place of birth after moving away from the place that they were spawned. Functional connectivity is the movement of individuals among spatially separated habitats resulting from interactions between behavioral processes and seascape configuration. Finally, migratory connectivity refers to movement of individuals between locations due to shifts in some key resource, such as food availability or breeding requirements, often on seasonal time scales.

Natal origins—Theoretical studies suggest that the proportion of pelagic larvae retained within or transported among geographically separated subpopulations is a critical determinant of processes that drive local and meta-population dynamics of marine species (Cowen and Sponaugle 2009). Tracking larval dispersal in marine fishes is challenging because many marine species are highly fecund, producing millions of tiny offspring that are difficult to tag without introducing significant handling effects. In addition, the high mortality rate of early life history stages makes the probability of recovering tagged individuals extremely low. Dealing with these limitations over the potentially large spatial and temporal scales at which these linkages occur makes the use of conventional mark–recapture techniques daunting (Thorrold et al. 2002).

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Fig. 2. (A) Gridded misfits for the dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$) isoscape ($n = 2507$) from the upper 100 m of the Atlantic Ocean (Fig. 1A). Mean gridded misfits = 0.02‰ , root mean square = 0.29‰ . (B) Gridded misfits for the oxygen ($\delta^{18}\text{O}_{\text{SW}}$) isoscape ($n = 6004$) from the upper 100 m of the Atlantic Ocean and Mediterranean Sea (Fig. 1B). Mean gridded misfits = 0.2‰ , root mean square = 1.14‰ . (C) Gridded misfits for the zooplankton organic carbon ($\delta^{13}\text{C}_{\text{PLK}}$) isoscape ($n = 546$) from the upper 150 m of the Atlantic Ocean and Mediterranean Sea (Fig. 1C). Mean gridded misfit = 0.01‰ , root mean square = 0.89‰ . (D) Gridded misfits for the zooplankton organic nitrogen ($\delta^{15}\text{N}_{\text{PLK}}$) isoscape ($n = 365$) from the upper 150 m of the Atlantic Ocean and Mediterranean Sea (Fig. 1D). Mean gridded misfits = 0.01‰ , root mean square = 0.43‰ . All gridded misfits were calculated in Ocean Data View (Schlitzer 2002).

A number of studies have employed ecogeochemistry as a natural tracer technique to track larval dispersal and natal homing (Elsdon et al. 2008).

Swearer et al. (1999) used growth histories and trace element profiles from bluehead wrasse (*Thalassoma bifasciatum*) otoliths as archival recorders of potential dispersal pathways. The authors hypothesized that larvae retained in the nutrient-rich, productive coastal water masses around St. Croix would have faster growth rates and larger size at settlement than individuals dispersing to St. Croix from nutrient-poor, open-ocean waters. In addition, the larvae retained around St. Croix would also have high concentrations of particle-reactive trace elements (particularly lead [Pb]) in their otoliths, reflecting the locally elevated trace element concentrations relative to oceanic waters. The authors found that a high proportion of larvae recruiting to reefs on the leeward side of St. Croix, particularly in the summer, were large, fast-growing individuals with high Pb concentrations in their otoliths that, together, were characteristic of local retention around St. Croix. Conversely, fall recruitment events on the windward side of the island were composed primarily of small, slow-growing individuals whose otoliths had a threefold lower Pb concentration, characteristic of dispersal from nutrient-depleted offshore environs.

Thorrold et al. (1998b, 2001) used elemental ratios and stable carbon and oxygen isotopes in otoliths to examine natal homing in weakfish (*Cynoscion regalis*). During its annual migration along the east coast of the United States, *C. regalis* moves from overwintering grounds south and offshore of Cape Hatteras to spawning locations in estuaries throughout the species' range (Florida to Maine). The authors found that geochemical values in otoliths of juvenile weakfish varied significantly among five estuaries along the east coast of the United States. Using these estuarine-specific signatures, Thorrold et al. (2001) showed high levels of natal homing in spawning weakfish (60% to 81%), with straying largely confined to locations adjacent to natal estuaries. These findings were in contrast to earlier population genetics work on *C. regalis* that showed little genetic structuring throughout the region.

More recently, ecogeochemistry approaches have been used to identify natal origins of ocean-phase anadromous fish (Walther and Thorrold 2010) and to locate marine feeding grounds of anadromous fish caught upon returning to natal rivers to spawn (MacKenzie et al. 2011). Walther and coworkers initially identified unique geochemical signatures in otoliths of young-of-the-year American shad (*Alosa sapidissima*) from a total of 20 rivers along the east coast of the United States (Walther and Thorrold 2008). They then used river-specific values in $\delta^{18}\text{O}$, $^{87}\text{Sr} : ^{86}\text{Sr}$, $\text{Sr} : \text{Ca}$, and $\text{Ba} : \text{Ca}$ in the core region of adult otoliths to determine natal origins of ocean-phase subadults collected in the Gulf of Maine (Walther and Thorrold 2010). Almost all of the fish were assigned to one of only two rivers, suggesting that shad did not mix extensively during ocean residency. Rather, immature fish from river populations appear to exhibit diverse migratory behaviors and therefore are likely to encounter variable ocean conditions and predators while resident in coastal oceans. MacKenzie and

colleagues studied the inverse problem of identifying marine feeding grounds of Atlantic salmon (*Salmo salar*) from collections of adults returning to spawn in natal rivers after 3 to 5 yr of ocean residency. MacKenzie et al. (2011) found that fish returning to different rivers around the U.K. over an 18 yr period had consistently distinct $\delta^{13}\text{C}$ values in scale material deposited during ocean residency. Based on a correlation between sea surface temperature and scale $\delta^{13}\text{C}$ values, they inferred that fish from the different rivers must have been spatially segregated on marine feeding grounds in the North Atlantic. Conventional tagging studies had been unable to resolve questions of the location of ocean residency despite a million salmon tagged since the 1950s in English and Welsh rivers (MacKenzie et al. 2011).

Functional connectivity—Marine seascapes are complex mosaics of patchily distributed habitats, including coastal wetlands, nearshore habitats, and offshore systems that are linked through fish movement. Recently, attention has been directed at the issue of preserving critical seascape functions as well as habitat types, with particular emphasis on functional connectivity (McCook et al. 2009). Initially developed in landscape ecology, functional connectivity is an emergent property of species–seascape interactions and is a particularly useful concept for assessing functional linkages among juvenile nursery habitats and coral reefs using ecogeochemistry.

Fry et al. (1999) used a bulk stable isotope approach to identify the importance of juvenile nursery habitats in shallow seagrass meadows and mangrove-lined bays to pink shrimp (*Farfantepenaeus duorarum*) caught offshore in the Tortugas and Sanibel fisheries. Shrimp from seven seagrass meadows had $\delta^{13}\text{C}$ values (−15‰ to −9‰) that were distinct from those collected in 12 mangrove-lined bays (−29‰ to −18‰). Approximately 60% of juvenile individuals captured in the offshore fisheries had similar signatures to the offshore residents. The other 40% of juvenile shrimp were classified as recent immigrants, most of which showed seagrass values with only a few showing mangrove values. These results supported the hypothesis that the major spring peak of pink shrimp recruitment into the South Florida offshore fisheries is fueled by ontogenetic migration from seagrass meadows.

Nakamura et al. (2008) used a similar bulk muscle $\delta^{13}\text{C}$ approach to infer black-tail snapper (*Lutjanus fulvus*) movement from coastal mangroves to coral reefs around Ishigaki Island, Japan. The authors identified distinct mangrove (−23‰ to −17‰) and coral reef (−16‰ to −8‰) habitat signatures using local prey and congeneric resident fish, mangrove red snapper (*Lutjanus argentimaculatus*) and humpback red snapper (*Lutjanus gibbus*), respectively. The majority of small *L. fulvus* (88%) on coral reefs had muscle $\delta^{13}\text{C}$ values indicative of residence in the mangrove habitat, suggesting recent immigration from a coastal wetland nursery. Due to the fast turnover rate of muscle tissue, those juvenile nursery habitat signatures transitioned quickly to local reef signatures. As a result, it was difficult to distinguish individuals that were lifetime reef residents from those that may have arrived from a

coastal wetland nursery sufficiently beyond the half-life of the tissue turnover rate.

To overcome the challenges of tissues with fast turnover rates, some researchers have used accretionary tissues, including fish otoliths, that provide a chronological record that is metabolically inert post-deposition. Mateo et al. (2010) used bulk $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis, coupled with elemental profiles, to estimate post-settlement movement of French grunts (*Haemulon flavolineatum*) and schoolmaster snapper (*Lutjanus apodus*) from coastal mangrove lagoons and seagrass beds to coral reefs around two Caribbean Islands. In this instance, the authors classified adult fish collected on offshore coral reefs to either the mangrove or seagrass nursery habitat based on the geochemistry of the core region of otoliths that corresponded to the time period when the fish were resident in juvenile habitats. Between 40% and 68% of French grunt subadults collected from fore-reef stations in St. Croix, and 70% and 74% in Puerto Rico spent their juvenile period in mangrove nurseries. By contrast, nearly 100% of schoolmaster on both islands resided as juveniles in mangrove habitats.

Targeting the juvenile core of otoliths, which preserves an isotopic record of juvenile habitat residence, avoids the potential problem of tissue turnover obscuring the juvenile habitat signature in adult muscle tissue. However, McMahon et al. (2011b) showed that it is not always possible to distinguish residence in mangrove and seagrass nursery habitats using bulk otolith stable isotope analysis (SIA). Conventional bulk otolith and muscle SIA and essential amino acid (AA) SIA were conducted on snapper collected from seagrass beds, mangroves, and coral reefs in the Red Sea, Caribbean Sea, and Pacific coast of Panama. The authors found that while bulk stable isotope values in otoliths showed regional differences, it was not always possible to distinguish nursery residence on local scales. Essential AA $\delta^{13}\text{C}$ values in otoliths, on the other hand, varied as a function of habitat type and provided a better tracer of residence in different juvenile nursery habitats than conventional bulk otolith SIA alone.

Migration connectivity—Several studies have taken advantage of large-scale (thousands of kilometers) geographic variation in carbon, nitrogen, and oxygen to track the ocean basin-scale migration of large pelagic animals, including cetaceans, pinnipeds, teleost fishes, and marine birds. Schell et al. (1989) and Best and Schell (1996) exploited the large high-latitude $\delta^{13}\text{C}_{\text{POM}}$ gradients in the North Pacific Ocean and Southern Ocean, respectively, to track annual migration patterns of mysticete whales. Both studies showed that baleen $\delta^{13}\text{C}$ varied seasonally, corresponding to geographic variations in the $\delta^{13}\text{C}_{\text{PLK}}$ of prey organisms consumed along the annual migratory route between wintering and summering grounds. Cyclical $\delta^{15}\text{N}$ patterns in baleen growth plates were consistent with an annual migratory starvation and recovery cycle. Killingley (1980) took a unique approach to track California gray whale (*Eschrichtius robustus*) migrations from the Arctic Pacific in spring and summer to Baja California, Mexico, in winter. This study used $\delta^{18}\text{O}$ analysis of growth bands from the epizoic barnacle (*Cryptolepas rhachianecti*) that encrust

gray whales as a proxy for local water $\delta^{18}\text{O}_{\text{SW}}$ values in which the whale resided during the time of barnacle growth band formation. Killingley compared the expected barnacle $\delta^{18}\text{O}$ values, calculated from regional salinity– $\delta^{18}\text{O}_{\text{SW}}$ relationships and temperature along the known migration route, to the actual $\delta^{18}\text{O}$ values of barnacles collected from a gray whale in San Ignacio Lagoon. Modeled and observed $\delta^{18}\text{O}$ values agreed well, indicating that latitudinal gradients in $\delta^{18}\text{O}_{\text{SW}}$ were accurately reflected in the barnacle growth bands, thus serving as a tracer of migration pathways.

Newsome et al. (2007) used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of archaeological seal bones to examine foraging patterns and population distributions of northern fur seals (*Callorhinus ursinus*) on the eastern Pacific Ocean. Northern fur seals are a common pinniped species in archaeological sites from southern California to the Aleutian Islands, yet today they breed almost exclusively on offshore islands at high latitudes. Prehistoric populations of adult female northern fur seals had significantly lower $\delta^{13}\text{C}$ values than harbor seals (*Phoca vitulina*), a nonmigratory species that feeds nearshore. Consistently low $\delta^{13}\text{C}$ values in fur seals likely represent feeding in deep, offshore waters. The prehistoric adult female northern fur seals clustered into three latitudinal foraging groups based upon their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values: a southern group (California) with high isotope values, a northern group (eastern Aleutian, Gulf of Alaska, and Pacific Northwest) with intermediate values, and a western Aleutian group with very low isotope values. These data also confirmed that prehistoric northern fur seals from California were not immigrants from northern waters but instead were year-round residents.

Mendes et al. (2007) used a similar approach with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of the teeth of sperm whales (*Physeter macrocephalus*) in the Northeastern Atlantic to examine ontogenetic shifts in movement and trophic ecology. Stable isotope profiles showed a trend of decreasing $\delta^{13}\text{C}$ and increasing $\delta^{15}\text{N}$ with age, punctuated by marked declines in $\delta^{13}\text{C}$ values around 9 to 10 yr and again around 20 yr for many individuals. These authors attributed the first marked decline to male segregation from natal groups in low latitudes following the onset of puberty between 4 and 15 yr and the gradual movement poleward into ^{13}C -depleted temperate waters. The second decline around age 20 likely reflected movement into further ^{13}C -depleted, productive high latitudes to facilitate the spurt of accelerated growth rate observed around that age. Interestingly, the periodic migrations back to low-latitude breeding grounds were not reflected in the $\delta^{13}\text{C}$ profiles, most likely due to the short residence time at low latitude relative to the time spent in high-latitude feeding grounds. The observed increase in $\delta^{15}\text{N}$ with age is likely to be caused by an ontogenetic shift in trophic level coupled with movement from low latitudes with a low $\delta^{15}\text{N}_{\text{Base}}$ to high latitudes with a correspondingly high $\delta^{15}\text{N}_{\text{Base}}$.

Trophic and geographic stable isotope structure—Eco-geochemistry has been employed, in some form or another, for many years to examine migration or trophic dynamics in the marine environment, primarily using bulk tissue

SIA (Peterson and Fry 1987; Hobson 1999; Post 2002). However, with conventional bulk SIA it can be difficult to tease apart differences in consumer stable isotope values due to movement through habitats with different baseline stable isotope values from those due to shifts in trophic position (Post 2002). This challenge is particularly true for highly migratory species with life histories characterized by large-scale movements and variable or shifting diets (Estrada et al. 2005; Kerr et al. 2006; Lorrain et al. 2009).

Recent advances in compound-specific SIA of individual biological compounds, including AAs and fatty acids (Meier-Augenstein 1999; Sessions 2006), have opened the door for more complex studies of connectivity and trophic dynamics than was possible with conventional mark-recapture and feeding observation techniques (Popp et al. 2007; Lorrain et al. 2009; McMahon et al. 2011b). Modest $\delta^{13}\text{C}$ fractionation between diet and bulk tissue often reflects relatively large trophic fractionation ($\delta^{13}\text{C}$) for many nonessential AAs and little to no fractionation for all essential AAs (Hare et al. 1991; Jim et al. 2006; McMahon et al. 2010). Although plants and bacteria can synthesize the essential AAs de novo, most animals have lost the necessary enzymatic pathways to synthesize these AAs at a rate sufficient for normal growth and must incorporate them directly from their diet (Borman et al. 1946; Reeds 2000). As a result, $\delta^{13}\text{C}$ fractionation of essential AAs is typically near 0‰. Consumer essential AA $\delta^{13}\text{C}$ values represent the isotopic fingerprints of $\delta^{13}\text{C}$ values at the base of the food web in which the animal is feeding and therefore provides a promising tool to track animal movement through isotopically distinct food webs.

Moderate increases in bulk $\delta^{15}\text{N}$ with trophic position reflect an averaging of large increases in the $\delta^{15}\text{N}$ of some AAs, termed trophic AAs, and little or no change in others, referred to as source AAs (McClelland and Montoya 2002; Chikaraishi et al. 2007). Trophic AAs, such as alanine, aspartic acid, glutamic acid, isoleucine, leucine, proline, and valine, can either be synthesized by animals or undergo significant transamination and deamination reactions, resulting in larger $\delta^{15}\text{N}$ fractionation between tissue and diet upwards of 7‰. Fractionation of trophic AAs represents a more robust indicator of changes in trophic level than bulk SIA (McClelland and Montoya 2002; Chikaraishi et al. 2007). Conversely, source AAs are those that animals cannot synthesize themselves, and must incorporate directly from their diet. These AAs, including glycine, phenylalanine, serine, and threonine, exhibit little to no trophic fractionation and provide a fingerprint of $\delta^{15}\text{N}_{\text{Base}}$. Compound-specific SIA makes use of the differences in fractionation of trophic and source AAs to provide an internally indexed indicator of trophic position that normalizes for $\delta^{15}\text{N}_{\text{Base}}$. In addition, source AA $\delta^{15}\text{N}$ values can act as a valuable tool to track animal movements across isotopically distinct marine environments, for example, from coastal to oceanic waters or from tropical to high latitudes.

Compound-specific SIA provides a complementary approach to traditional bulk stable isotope techniques for tracking animal migrations in the marine environment, and in many instances, provide more in-depth information

about habitat use and movement patterns. Stable isotope analyses of AAs and fatty acids have previously been used to examine detailed information about diet (Fantle et al. 1999; Popp et al. 2007; Chikaraishi et al. 2009), the sources of complex mixtures of organic matter (Uhle et al. 1997; McCarthy et al. 2004), and more recently, habitat use and movement patterns (Lorrain et al. 2009; McMahon et al. 2011a). The ability to assess both the $\delta^{15}\text{N}_{\text{Base}}$ isotope signature as well as trophic position from a single analysis avoids one of the biggest confounding variables of bulk SIA. Compound-specific SIA therefore represents a powerful tool for future ecogeochemistry applications and clearly warrants greater attention from the ecological community.

Ecogeochemistry relies, in large part, on the presence of isoscapes that represent spatiotemporal composites of the chemical, physical, and biological processes structuring marine ecosystems. The isoscapes we presented in this review revealed a great deal more geographic variation in key elements than was previously appreciated. Advances in statistical tools have allowed for more accurate assignments to populations or specific habitats by combining isotope and other data types, including conventional tagging and population genetics, in a Bayesian framework (Smith and Campana 2010; Van Wilgenburg and Hobson 2011; Chabot et al. 2012). However, the ecogeochemistry approach is not without its own limitations and inherent challenges. If animals reside in geochemically indistinguishable habitats, or move through habitats faster than the local signature can be recorded, then the ecogeochemistry approach may underestimate habitat use or fail to fully resolve movement patterns. Therefore, to enhance the utility of isoscapes, we need continued field collections for SIA, both in space and time. The development of time-explicit isoscapes is particularly important in light of the growing effects of climate change and ocean acidification on the biological, chemical, and physical processes of the world's oceans (Bowen 2010). The effects of climate change on the biology (e.g., temperature effects on productivity and species composition and distribution), chemistry (e.g., hypoxic effects on denitrification) and hydrography (e.g., climate effects on evaporation rates and circulation) will potentially have far-reaching effects on baseline isoscapes, both spatially and temporally. Given the logistical challenges of generating extensive spatial and temporal coverage of observational data, the development of robust isoscapes would be greatly improved with a more mechanistic understanding of what establishes and maintains isotope structure. This will likely require developing process-based, coupled biogeochemical-physical ocean models to reconstruct baseline marine isoscapes (Schmittner et al. 2008; Somes et al. 2010). Enhanced knowledge of isotopic routing and fractionation factors, particularly of individual compound classes, is also necessary to fully realize the potential of ocean ecogeochemistry.

Finally, we were struck by the results from a recent review that found > 40% of published studies analyzing $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ were conducted in marine ecosystems (Boecklen et al. 2011). Despite these efforts, we have not yet fulfilled the promise of SIA in ocean ecosystems. An ecogeochemistry approach, based on the documentation of

isoscapes and the use of compound-specific SIA to distinguish movements through isoscapes and changes in diet, provides a powerful framework to significantly advance the field over the next decade.

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