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Multiple regression models of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for fish populations in the eastern Gulf of Mexico

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ABSTRACT

Multiple regression models were created to explain spatial and temporal variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish populations on the West Florida Shelf (eastern Gulf of Mexico, USA). Extensive trawl surveys from three time periods were used to acquire muscle samples from seven groundfish species. Isotopic variation ($\delta^{13}\text{C}_{\text{var}}$ and $\delta^{15}\text{N}_{\text{var}}$) was calculated as the deviation from the isotopic mean of each fish species. Static spatial data and dynamic water quality parameters were used to create models predicting $\delta^{13}\text{C}_{\text{var}}$ and $\delta^{15}\text{N}_{\text{var}}$ in three fish species that were caught in the summers of 2009 and 2010. Additional data sets were then used to determine the accuracy of the models for predicting isotopic variation (1) in a different time period (fall 2010) and (2) among four entirely different fish species that were collected during summer 2009. The $\delta^{15}\text{N}_{\text{var}}$ model was relatively stable and could be applied to different time periods and species with similar accuracy (mean absolute errors 0.31–0.33‰). The $\delta^{13}\text{C}_{\text{var}}$ model had a lower predictive capability and mean absolute errors ranged from 0.42 to 0.48‰. $\delta^{15}\text{N}$ trends are likely linked to gradients in nitrogen fixation and Mississippi River influence on the West Florida Shelf, while $\delta^{13}\text{C}$ trends may be linked to changes in algal species, photosynthetic fractionation, and abundance of benthic vs. planktonic basal resources. These models of isotopic variability may be useful for future stable isotope investigations of trophic level, basal resource use, and animal migration on the West Florida Shelf.

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1. Introduction

Isoscapes are contour maps that depict geographic variability in stable isotopes. They are useful in isotope-based studies of diet, trophic level, or animal migration (Cherel and Hobson, 2007; Hobson et al., 2010; West et al., 2010). Isoscapes can be created empirically by interpolating between measured data points, or by creating process-oriented models using variables that correlate with, or result in, isotopic fractionation or source shifts (Bowen and Revenaugh, 2003; Graham et al., 2010; West et al., 2010). Because they may incorporate location-specific data, process-based models can be more accurate predictors of isotopic values than spatial interpolation among data points (Bowen and Revenaugh, 2003). Process-based models may use static variables, such as the calculation of mean $\delta^{18}\text{O}$ in precipitation based upon latitude and altitude (Bowen and Wilkinson, 2002), or temporally dynamic variables, such as the calculation of marine organic matter $\delta^{13}\text{C}$ values based upon CO_2 concentration and phytoplankton growth rate (Hofmann et al., 2000).

1.1. Isotopic baselines on continental shelves

Spatial isotopic gradients in marine consumers are dependent on the isotopic signatures of primary producers (Graham et al., 2010; Nerot et al., 2012). The $\delta^{15}\text{N}$ signatures of marine primary producers are influenced by nutrient source, fractionation during biological processes, and the degree to which primary productivity decreases available nutrient supplies (Kendall et al., 2001; Sigman and Casciotti, 2001; Graham et al., 2010). Marine $\delta^{15}\text{N}$ spatial gradients are often linked to transitions from eutrophic to oligotrophic waters (Casey and Post, 2011; Nerot et al., 2012; Radabaugh et al., 2013). Nitrogen fixation by diazotrophs such as the cyanobacterium *Trichodesmium* exhibit minimal fractionation from atmospheric N_2 , resulting in fixed $\delta^{15}\text{N}$ values close to 0‰ (Carpenter et al., 1997; Graham et al., 2010). Higher $\delta^{15}\text{N}$ values in the range of 5–9‰ can result from nutrients and POM in terrestrial runoff, particularly if fluvial inputs include sewage or manure (Kendall et al., 2001; Mayer et al., 2002). As a result, $\delta^{15}\text{N}$ values are generally higher in eutrophic coastal waters and lower in the oligotrophic open ocean (Casey and Post, 2011; Nerot et al., 2012).

$\delta^{13}\text{C}$ values of marine primary producers are influenced by the isotopic signature of aqueous dissolved inorganic carbon (DIC) and the magnitude of photosynthetic fractionation (Maberly et al., 1992; Hofmann et al., 2000). Photosynthetic fractionation (ϵ_p) is

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the selective fixation of ^{12}C over ^{13}C during photosynthesis, causing primary producers to have lower $\delta^{13}\text{C}$ signatures relative to aqueous CO_2 . The magnitude of ϵ_p is greater in high aqueous CO_2 concentrations, high light intensities, during slow growth rates, and for cells with a small surface area-to-volume ratio (Thompson and Calvert, 1995; Popp et al., 1998; Rost et al., 2002; Radabaugh et al., 2014).

On continental shelves, the $\delta^{13}\text{C}$ baseline is generally higher in shallow, nearshore regions (Fry, 1988; Hobson et al., 1994; Cherel and Hobson, 2007; Graham et al., 2010; Nerot et al., 2012; Radabaugh et al., 2013). While these higher $\delta^{13}\text{C}$ values in shallow waters may be due to lower ϵ_p , they also may be reflecting the isotopic signature of benthic primary production. Phytoplankton and benthic algae are the two main basal resources (primary producers) in continental shelf ecosystems (Okey and Mahmoudi, 2002; MacIntyre et al., 1996; Rooney et al., 2006). Globally, $\delta^{13}\text{C}$ values of marine benthic algae are $\sim 5\%$ higher than phytoplankton (France, 1995; Doi et al., 2010), providing an endogenous isotopic tracer for determining the relative contributions of planktonic and benthic basal resources to the biomass of consumers (Hobson et al., 1994; Cherel and Hobson, 2007).

Knowledge of spatial variation in baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values is necessary in order to avoid inaccurately attributing natural spatial isotopic variation to changes in basal resource use or trophic level. However, the creation of empirical isoscapes based upon repetitive sampling is both costly and time consuming. Previous studies have modeled marine isotopic variation through correlations with variables such as temperature, salinity, CO_2 concentration, and depth (Hofmann et al., 2000; Jennings and Warr, 2003; Barnes et al., 2009). Even though these models are based on long-term averages of environmental parameters, they still have significant predictive power that can explain isotopic variation at higher trophic levels (Jennings and Warr, 2003; Barnes et al., 2009).

The study presented here focuses on the use of water-quality parameters derived from satellite data to determine if dynamic parameters have a stronger predictive capability for isotopic values compared to static parameters. Remote sensing offers both wide spatial coverage and high temporal and spatial resolutions, which may facilitate detection of temporally dynamic spatial isotopic patterns and aid in understanding their underlying causes. The objective of this study was to produce dynamic models of spatial isotopic variation of fish populations on the West Florida Shelf. These models could be used to study the driving forces behind isotopic variation and be applied to future stable isotope studies on the West Florida Shelf.

2. Methods

2.1. Study area

Samples for isotopic analysis were collected on the West Florida Shelf (WFS) in the eastern Gulf of Mexico (Fig. 1). The broad, gently sloping continental shelf has a predominantly sandy bottom with $\sim 35\%$ hard bottom (Parker et al., 1983; Okey and Mahmoudi, 2002). The northwestern portion of the sampled region consists of eutrophic and mesotrophic waters associated with the Mississippi River and Mobile Bay watersheds (Rabalais et al., 1996; Del Castillo et al., 2001). Portions of the Mississippi River plume may be carried south along the WFS in the Gulf of Mexico loop current (Del Castillo et al., 2001; Hu et al., 2005). Along the coast of peninsular Florida, the WFS transitions to an oligotrophic system, with diazotrophs such as *Trichodesmium* spp. providing an important source of fixed nitrogen (Macko et al., 1984; Lenos et al., 2001; Mulholland et al., 2006; Holl et al., 2007).

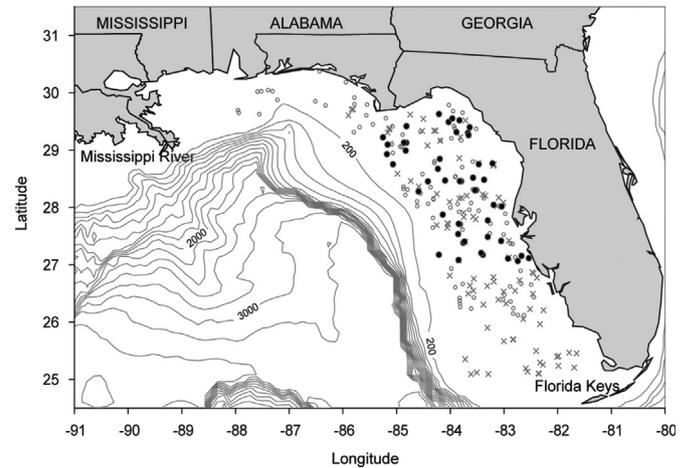


Fig. 1. Locations of sample collection on the West Florida Shelf during three time periods. Open circles are trawling sites from summer 2009, crosses are from summer 2010, and filled circles are from fall 2010. Isobaths are shown at 200 m intervals.

2.2. Sample collection

A comprehensive account of the sampling procedure is provided in Radabaugh et al. (2013). Briefly, samples were collected during research cruises for the Southeast Area Monitoring and Assessment Program (SEAMAP), a state/federal program designed to collect fisheries independent monitoring data (<http://sero.nmfs.noaa.gov/grants/seamap.htm>). Samples were collected from three SEAMAP cruises: 10–30 July 2009, 27 June–14 July 2010, and 16 October–12 November 2010. These cruises are hereafter referred to as summer 2009, summer 2010, and fall 2010.

Seven common, widely distributed fish species were selected as targets for investigation: *Calamus proridens* (littlehead porgy), *Diplectrum formosum* (sand perch), *Haemulon aurolineatum* (tomtate), *Haemulon plumieri* (white grunt), *Lagodon rhomboides* (pinfish), *Syacium papillosum* (dusky flounder), and *Synodus foetens* (inshore lizardfish). All species were collected during summer 2009. In summer and fall 2010, only *C. proridens*, *S. papillosum*, and *S. foetens* were collected. While at sea, standard lengths were recorded and a lateral muscle sample was collected midway between the dorsal and caudal fin and frozen. Samples of benthic algae were obtained from the stomachs of the variegated sea urchin, *Lytechinus variegatus*. A bucket of surface water was prefiltered through a 125 μm filter to remove most zooplankton. This water was then filtered through pre-combusted GF/F filters using a peristaltic pump at 10 psi; the filtered samples of particulate organic matter (POM) were frozen. POM and benthic algae samples were acidified to remove inorganic carbon. The acidification procedure used to remove calcium carbonate from sea urchin stomach contents did not significantly alter algal $\delta^{15}\text{N}$ [see Radabaugh et al. (2013) for additional details].

Isotopic analyses were performed on an elemental analyzer (Carlo-Erba NA2500 Series II) coupled to a continuous-flow isotopic ratio mass spectrometer (ThermoFinnigan Delta+XL) following the procedure in Radabaugh et al. (2013). Analytical precision, obtained by replicate measurements of NIST 1570a spinach leaves, was $0.08 \pm 0.19\%$ for $\delta^{15}\text{N}$ and $-27.28 \pm 0.21\%$ for $\delta^{13}\text{C}$ (average standard deviation of $n=307$ replicates). Lipid correction was not necessary as the C:N ratios of all fish muscle samples were below 3.5, thus lipid content was below 5% (Post et al., 2007). A length correction for ontogenetic shifts in trophic level was applied to each fish species if there was a significant relationship between the standard lengths of the fish and isotopic values (i.e., the correction was applied if the linear regression slope p was

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