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Stable Isotope Analysis of Fish, Invertebrates, and Particulate Organic Matter in the Sacramento-San Joaquin River Delta (California, USA)

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

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in

Evolution, Ecology, and Organismal Biology

by

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Dedication

To Mom and Dad
Qapla'!

ABSTRACT OF THE DISSERTATION

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Doctor of Philosophy, Evolution, Ecology, and Organismal Biology
University of California, Riverside, September 2021
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Freshwater systems are irreplaceable natural resources, and they are imperiled globally by both anthropogenic and natural pressures. The Sacramento-San Joaquin river delta (SSJD) in California is among the most heavily human impacted river systems. The SSJD drains the western slope of the Sierra Nevada mountains and serves as a hub for California's agricultural and municipal water distribution system. Pervasive geomorphological and hydrological alteration have created a novel distribution of water and habitat in the SSJD. Here, I use stable isotope analysis of fatty acids and amino acids to investigate the sources of organic matter available to consumers in the SSJD. Moreover, I elucidate the basal sources of organic matter supporting fish of conservation interest, such as the Chinook salmon (*Oncorhynchus tshawytscha*).

My results confirm the importance of algae for fish in the SSJD. However, I demonstrate that inputs of organic matter derived from fungi, bacteria, and higher plants may be important as well. In Chinook salmon, I show that juveniles rearing in off-channel habitats maintained higher muscular concentrations of fatty acids. In total, my results suggest that availability of off-channel, and floodplain, habitats is important to fish in the SSJD.

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Introduction

Background

Freshwater habitats are among the most economically and ecologically significant ecosystems globally. Rivers, in particular, provide a home to habitat-endemic species, serve as the media for a non-trivial portion of global biogeochemical cycling, connect inland systems with each other and the marine environment, and are exploited for municipal, recreational, and agricultural uses. One of the most heavily altered freshwater systems is the Sacramento-San Joaquin river delta (SSJD) in California, USA. Historically, this river delta drained the western slope of the Sierra Nevada mountain range and would have inundated vast wetlands and floodplains in CA's central valley and provided rearing grounds and habitat for native species. Concurrent with CA's growth as an economic and agricultural powerhouse, the degree of habitat alteration in the SSJD has also increased. Generally, my work is concerned with how differences in river conditions (e.g. discharge, water temperature), and habitat types (e.g. altered channel versus restored floodplain), interact to affect species of socioeconomic interest, such as Chinook salmon (*Oncorhynchus tshawytscha*).

Species evolve through time to optimize fitness under the conditions presenting selective pressures. Thus, alterations to the distribution of, and characteristics within, freshwater systems influence the fitness of the species within them. These changes in fitness can be positive or negative for the species

in question. However, widespread alterations in the distribution of freshwater species across multiple habitat types associated with changes in water chemistry, watercourse geomorphology, and the spatiotemporal distribution of freshwaters suggest undesirable ecological outcomes for anadromous fishes, such as salmon, and floodplain-dependent fish, such as Delta Smelt (*Hypomesus transpacificus*), to be the norm. In addition to constituting the basal resources supporting consumer communities, the composition and quantity of organic matter (OM) supplied to aquatic ecosystems has implications for food web structure and ecosystem functioning (e.g. terrestrial organic carbon export to marine systems).

Analyses of stable isotope compositions of nutrients and OM are powerful tools owing to the integration of isotopic signals from the contributing sources and biogeochemical processes that formed the analyte. In other words, consumers and producers reflect the isotopic composition of the resources they assimilate. By measuring and comparing the isotopic compositions of OM in environmental constituents, and applying a priori assumptions about likely patterns of resource utilization, estimations of resource utilization and OM source prevalence can be made. Stable isotope techniques are already used to characterize and track the sources of nutrients and OM in major rivers and floodplains and smaller stream systems. In some instances, however, overprinting and turnover of isotopic signatures during transport, as well as

inadequate source differentiation, can complicate the interpretation of isotopic data stemming from analysis of bulk OM. Confounding factors, such as overprinting and source homogeneity, are a challenge when studying riverine habitats with dynamic patterns of nutrient availability and cycling as well as consumer resource availability through space and time.

Research Questions

Three primary research questions are addressed herein, and are as follows:

1) Does the elemental and isotopic composition of POM vary appreciably on shorter time scales than it has been previously studied? If so, what environmental variables are most associated with these variations? (Chapter 1: POM)

Significance: Conceptual and numerical models for riverine ecosystems have historically assumed the elemental and stable isotope composition of POM, as a proxy for POM's biochemical composition, to vary predictably as a function of differences in the primary OM sources to the POM pool. Demonstrating increased variability in POM composition as a function of in situ environmental variables, on small spatiotemporal scales (weekly, < 10km), suggests that forthcoming models for riverine

productivity need to incorporate finer scale variations in the composition of available OM and the role it plays in ecosystem functioning.

2) Which basal sources of protein are important for supporting fish? (Chapter 2: Amino Acids)

Significance: Recalcitrant OM, typically non-nutritive terrestrial residues, can be pervasive in large river systems. However, the role that proteinaceous components of riverine OM play in supporting higher trophic levels is likely outsized. Characterizing differences that arise in the stable isotope composition of amino acids in POM between habitat types provides a framework to assess not only bulk differences in the type or OM available, but also potentially to trace sources of assimilated OM in consumer species of interest, such as the chinook salmon.

3) How does rearing in different habitats (e.g. river channel versus wetland) influence fish fatty acid nutrition? (Chapter 3: Fatty Acids)

Significance: Heterotrophic pathways may be important vectors for OM into higher-level consumers in habitats where detrital contributions are large or where phytoplankton inputs are low. Future conservation efforts could be influenced by an increased understanding of the role that more cryptic basal carbon sources (e.g., methane derived carbon) play in

supporting top-level consumers, relative to conventional (e.g. phytoplankton) pathways. Isotopic analysis of specific, and energetically valuable, biomolecules (i.e. fatty acids) constitutes a means to directly link basal sources of organic carbon to consumer biomass. However, the role that metabolism and dietary variability play in shaping observed patterns in the stable isotope composition and abundance of fatty acids in consumer tissues is poorly constrained in natural populations. This uncertainty underpins the importance of studies like mine, which in addition to their ecological interpretations, also provide context to interpret future results.

Chapter 1

Dynamic River Processes Drive Variability in Particulate Organic Matter Over Fine Spatiotemporal Scales

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Abstract

We sampled freshwater suspended particulate organic matter (POM) to determine its carbon and nitrogen stable isotope composition and collected co-located water chemistry data in California's Sacramento - San Joaquin Delta from sites on the Mokelumne and Cosumnes rivers. A 10 km^2 area was sampled across 12 sites and divided among three habitat types (i.e., riverine, slackwater/slough, and off-channel), 34 times between November, 2016 and July, 2017. Here, we describe the variability in water quality and POM variables, and assess factors associated with that variability using dimensional reduction and linear modeling within the context of our habitat types.

The stable isotope composition of freshwater POM and water chemistry variables differed significantly across small areas (< 10 km) and short time frames (weekly). Hydrological connectivity amongst sites was found to be an important factor in the isotopic and elemental composition of POM. During periods of low hydrological connectivity, *in situ* dynamics were strongly associated with differentiation of POM in different habitats. Discharge (16-433 m^3/s) and water temperature (8-30° C) were the variables most associated with variations in the composition of POM. Slackwater sites showed the greatest variability in POM composition, which may be symptomatic of longer water residence times, increased cycling rates of nutrients and organic matter, or a combination of the two.

Variability in POM stable isotope composition demonstrates that caution should be exercised when interpreting analyses that assume a static POM stable isotope composition based on two-end member mixing. Unconstrained variability in space or time could confound interpretations of models and data. Moving forward, conceptual and numerical models for river ecosystems that emphasize temporally heterogeneous lateral exchange amongst habitat patches should be prioritized when considering restoration efforts and monitoring outcomes.

Introduction

The composition and quantity of particulate organic matter (POM) supplied to aquatic ecosystems has implications for food web structure and ecosystem functioning (e.g. terrestrial organic carbon (OC) export to marine systems) (J. J. Cole et al., 2007; Koehler, Wachenfeldt, Kothawala, & Tranvik, 2012; Yamashita, McCallister, Koch, Gonsior, & Jaffé, 2015). Additionally, river conditions (e.g. discharge and water temperature) and water chemistry influence the capacity of river ecosystems to process imported, or to produce exportable, POM. The composition of POM, at any given place and time, reflects upstream land-use practices and geomorphology, as well as local water chemistry, river conditions, and community composition. To date, however, few studies have examined compositional variability of POM at fine spatiotemporal scales. The variability, and potential uncertainty, of POM characteristics makes it difficult to determine the significance or contribution of POM and its constituents to riverine ecosystem function.

POM is typically comprised of varying proportions of degraded plant biomass, entrained soil aggregates, and autochthonous organic matter (i.e. phytoplankton, microalgae, and bacteria) (Kendall, Silva, & Kelly, 2001; Liénart et al., 2016; Ngugi, Oyoo-Okoth, Gichuki, Gatune, & Mwangi-Kinyanjui, 2016). In freshwater systems, basal sources of organic matter supporting secondary production center around the relative importance of both terrestrial carbon

subsidies and autochthonous production (Brett et al., 2017). Contributions of OM from autochthonous and terrestrial sources can have diverse impacts on ecosystems, owing to variability in the nutritional quality and recalcitrance of OM from each source. Terrestrially-derived OC supports ecosystem metabolism by providing microbes with organic matter for respiration, but algal carbon more readily propagates into higher trophic levels (Mitrovic & Baldwin, 2016; Sobczak et al., 2005; Taipale et al., 2016). Biomarker analysis and compound specific stable isotope analysis have been used to show preferential incorporation of autochthonous OM into consumers (Taipale et al., 2014; Thorp & Bowes, 2016). The higher nutritional quality, e.g. fatty acid content (Brett & Müller-Navarra, 1997; Torres-Ruiz, Wehr, & Perrone, 2007) and low C:N ratio biomolecules like proteins (Müller-Solger, Jassby, & Müller-Navarra, 2002), in autochthonous basal resources relative to terrestrial organic matter enhances its incorporation by consumers.

Connectivity of floodplain and other off-channel habitats with the main river channel has been shown to influence nutrient transformation, carbon cycling, and autochthonous organic matter production (Ahearn, Viers, Mount, & Dahlgren, 2006; S. K. Hamilton & Lewis, 1987; Junk & Wantzen, 2004; Pearson, Pizzuto, & Vargas, 2016; Preiner, Drozdowski, Schagerl, Schiemer, & Hein, 2008; Sheibley, Ahearn, & Dahlgren, 2006; Welti et al., 2012). Anthropogenic bank and channel alterations are globally pervasive, resulting in changes to

hydrographs and connectivity between main channel and off-channel habitats (Hupp, Pierce, & Noe, 2009; Moyle & Mount, 2007). These physical alterations have changed lateral and longitudinal biogeochemical cycling patterns, habitat availability and biodiversity, often with negative results (Burgess, Pine, & Walsh, 2012; Inamine et al., 2010; Poff & Zimmerman, 2009; Poff, Olden, Merritt, & Pepin, 2007). Reconnecting rivers with their floodplains and other off-channel habitats as well as approximating historic natural flow regimes are important facets of river restoration efforts (Funk et al., 2019; Hein et al., 2016; Paillex, Dolédec, Castella, & Mérigoux, 2009; Poff & Zimmerman, 2009; Rood et al., 2005). Results from engineered, natural, and modelled floodplain reconnections have been positive with respect to restored ecological communities and reduced human flood risk (Burgess et al., 2012; Guida, Swanson, Remo, & Kiss, 2015; Hein, Reckendorfer, Thorp, & Schiemer, 2005; Paillex, Dolédec, Castella, Mérigoux, & Aldridge, 2012; Pander, Mueller, & Geist, 2015; Stoffels, Clarke, Rehwinkel, & McCarthy, 2014).

Reconnected floodplains and inundated polders, low lying lands usually protected from inundation by dikes or levees, have reduced water velocities, allow increased water residence times, and have an increased photic proportion of the water column relative to channel habitat. These changes to river conditions are conducive to algal growth and increase the potential for the proliferation of algae in off-channel sites to subsidize local and downstream secondary

production (Jassby & Cloern, 2000; Opperman, 2012; Opperman, Luster, McKenney, Roberts, & Meadows, 2010). It is hypothesized that increasing the proportion of floodplain and off-channel habitats will increase habitat availability and the nutritional quality of the POM pool available for secondary production, which could in turn support the growth of native fish populations (Jassby & Cloern, 2000; Jeffres, Opperman, & Moyle, 2008; Katz et al., 2017; Opperman, 2012; Opperman et al., 2010; Stoffels et al., 2014).

Stable isotope composition of POM can be a powerful tool for the characterization of organic matter owing to the integration of isotopic signals from biogeochemical processes. Differences in the stable isotope composition of POM can be interpreted as differences in the nutrient or OM regime at a given location (Kendall, Elliott, & Wankel, 2007). In some instances, however, overprinting and turnover of isotopic signatures during transport, as well as inadequate source differentiation, can complicate the interpretation of isotopic data (Cloern, Canuel, & Harris, 2002). That said, isotopic and elemental compositions of POM are frequently measured as background variables in riverine studies. However, the interpretation of POM composition has often stopped at linear mixing models rather than delving into the complexity that POM isotope composition holds.

We started with the simple hypothesis that the isotopic composition of POM in our river system would vary longitudinally, and perhaps linearly, with terrestrial influence declining downstream, in favor of autochthonous production.

To test this hypothesis, our strategy was to pair carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope compositions of POM to co-located water chemistry on and around a site slated for floodplain restoration in 2020. Specifically, we examined the relationships between stable isotopes in POM, water chemistry, and river conditions, in a system characterized by a high degree of spatiotemporal variability in abiotic variables (e.g. water residence time, water temperature, river discharge). Although we began our analyses using simple linear models, we then related our stable isotope and in situ water chemistry data, collected over an extended time period (≈ 9 months), using multivariate statistics to closely scrutinize POM dynamics.

Methods

Study Site

Widely recognized as one of North America's most invaded and human impacted ecosystems, the Sacramento-San Joaquin River delta (the Delta) has been heavily altered over the past 150 years (Lund, Hanak, Fleenor, & Howitt, 2007). Habitat alteration, introductions of invasive species (e.g., filter feeders such as clams), flow alterations, and increased water diversions for human use (Cloern et al., 2016; Jassby, Cloern, & Cole, 2002; Tockner & Stanford, 2002) have altered the composition and quantity of POM within the Delta for almost a century. Concurrent with the physical and chemical changes to Delta habitats,

populations of native fish species have declined as well (Mac Nally et al., 2010; Moyle, Katz, & Quiñones, 2011; Sommer et al., 2007). Implicated in these declines are multiple and often confounding drivers, not limited to decreases in the nutritional quality and quantity of POM available to fuel secondary production (Bennett & Moyle, 1996; Feyrer, Herbold, Matern, & Moyle, 2003; Jassby, 2008; Sommer et al., 2007).

The McCormack-Williamson Tract (MWT) located near the confluence of the Mokelumne and Cosumnes rivers has been highlighted as one of the priority restoration opportunities within the Delta and has been the subject of other research (Beagle, Whipple, & Grossinger, 2013; Brown & Pasternack, 2004; Florsheim, Mount, Hammersmark, Fleenor, & Schladow, 2008; Moyle et al., 2012; Young, 2017). The Cosumnes River has the distinction of being the only large, unregulated river on the western slope of the Sierra Nevada Mountains. As such, the Cosumnes maintains a mostly natural flow regime, with changes in river condition, e.g. discharge and stage, occurring mostly as a result of interplay between meteorological and antecedent conditions in the watershed. Additionally, the lack of dams on the Cosumnes also results in a natural sediment regime (Wohl et al., 2015). The natural variability in hydrologic conditions coupled with an unaltered sediment regime on the Cosumnes is hypothesized to be important for driving geomorphological processes on connected floodplains (Florsheim & Mount, 2002; 2003). Conversely, the Mokelumne River, a primary

tributary to the Delta is highly regulated with an altered flow regime and limited sediment budget (Ahearn, Sheibley, & Dahlgren, 2005). The floodplains of the Cosumnes River near its confluence with the Mokelumne River have been the focus of process based restoration efforts over the past two decades (Swenson, Whitener, & Eaton, 2003). The variability in hydrologic conditions, an unaltered sediment regime, and floodplain habitat reconnection have resulted in enhanced aquatic ecosystem productivity in the Cosumnes watershed (Jeffres et al., 2008; Moyle et al., 2012). Restoration work at the MWT is an effort to expand previously successful upstream actions to tidally influenced regions of the Delta.

Decreasing human flood risk and increasing direct metrics of native species success (e.g. population or body condition data) in the Delta is the ultimate goal of these restoration activities. However, positive ecological outcomes from process-based restoration efforts are underwritten by the biogeochemical changes affected by those efforts. Therefore, our data are invaluable for contextualizing future changes in the biogeochemistry of the MWT as restoration efforts proceed. Conclusions based on finer spatial-scale data (< 10 km^2 extent), like ours, focusing closely on a river reach and its associated peripheral waterways (e.g. slackwater and floodplain habitats) may not apply universally, although reducing the spatial extent of our study substantially alleviated logistical concerns associated with intense sampling. Conversely, this finely spatiotemporally resolved data lends itself perfectly to examination of the *in*

situ dynamics of water quality and POM. Here we demonstrate coupling of elemental and isotopic information on POM, with water chemistry and environmental data to explore variability in POM composition and the factors affecting it.

The MWT (38.253° N -121.284° W) is a 6.7 km^2 levee-ringed island, or polder, situated in the northeast Delta with farmlands at or below sea level (Figure 1.1). The surrounding riverine habitats are a mix of river channels, backwater sloughs, and managed canals. Flows around MWT are dominated by unregulated flow from the Cosumnes River and managed releases from Camanche Dam into the Mokelumne River. During summer, Sacramento River water enters the study site through the Delta Cross Channel (Figure 1.1). Due to its position near the inland extent of the tidal prism, tidal cycles also influence the movement of waters surrounding the MWT, particularly during periods of low outflows and high tides. The MWT is bordered on the west by Snodgrass Slough, which flows south from the Stone Lakes Wildlife Refuge and connects to the Mokelumne River at the southern tip of the MWT. The Delta Cross Channel diverts Sacramento River water via Snodgrass Slough into the Mokelumne River to offset salinity intrusion into the Delta during low flow periods and ensure ongoing delivery of freshwater to Central Valley Water Project and State Water Project pumping facilities in the southern Delta (US Bureau of Reclamation, 2017).

Nearly three months into our sampling period, the levee on the southeastern side of MWT failed on February 11, 2017, resulting in a flooded interior of the island. An emergency breach was excavated in a southwestern section of levee to relieve interior levee pressure and prevent further levee collapses. The levee failure created an off-channel flow-through habitat, similar to the proposed restored state, that persisted until levees were repaired and the island was reclaimed in May 2017. The temporary creation of off-channel habitat was a unique opportunity to examine the spatiotemporal dynamics associated with polder restoration as MWT and other similar locations have been identified as potential locations to restore freshwater and wetland habitats throughout the region (Young, 2017).

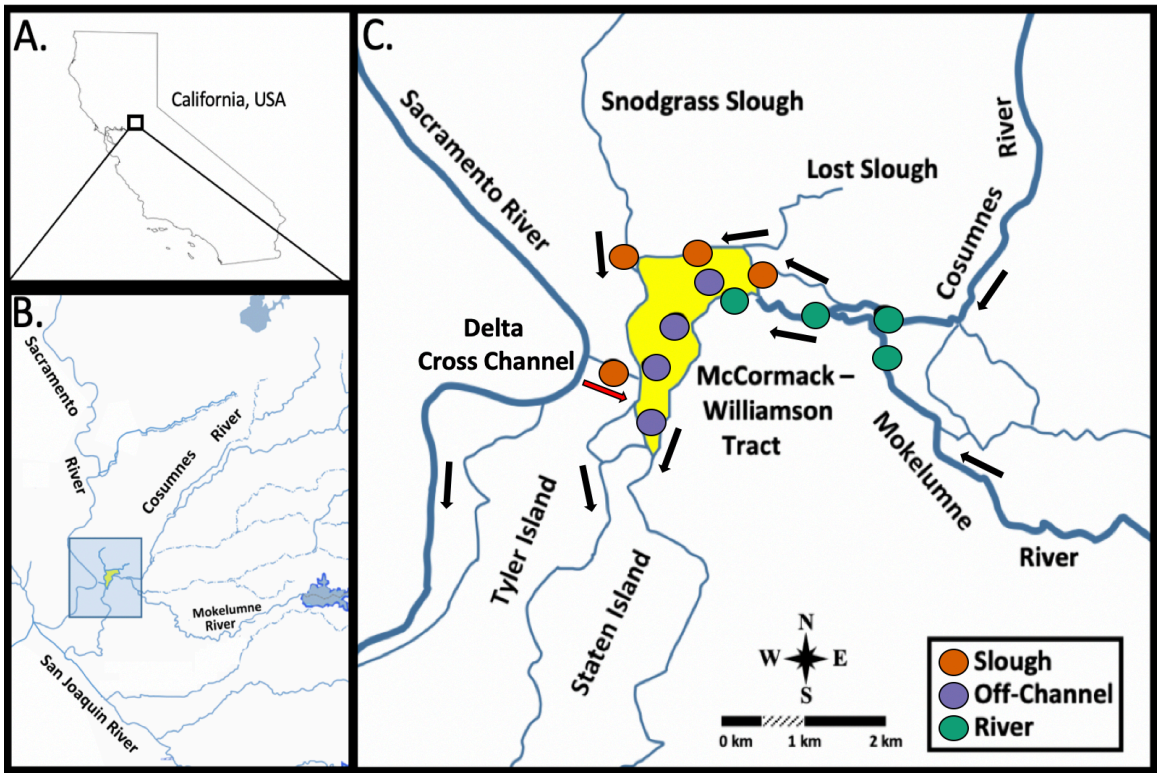


Figure 1.1. Maps showing study area. Panel A: California, USA. Panel B: Expanded image of Sacramento-San Joaquin River Delta. Panel C: Expanded view of highlighted region in panel B, McCormack-Williamson Tract and surrounding area with sample stations labeled by habitat type. Yellow area demarcates arrow of inundation on the MWT during the flood period. Black arrows adjacent to waterways indicate direction of flow, while the red arrow near the Delta Cross Channel indicates conditional flow based on seasonal gate operations.

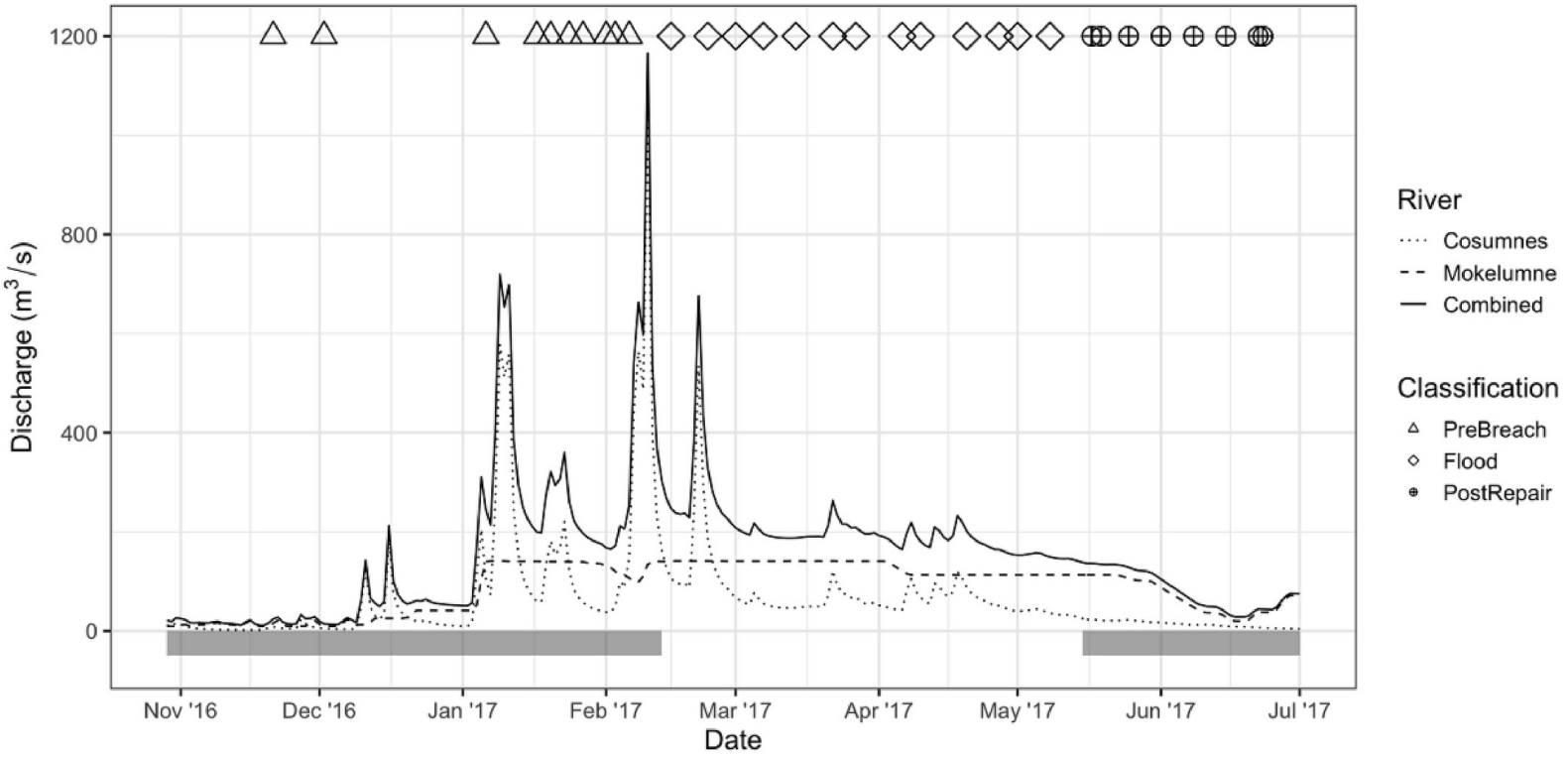
Sampling Design

We conducted our sampling in three distinct habitat types (Figure 1.1; river, slough, and off-channel) across three time periods (Figure 1.2; pre-flood, flood, and post-repair). Riverine sites were located along the Mokelumne and Cosumnes Rivers, and they generally exhibited higher water velocities and increased depth relative to off-channel and slough sites. Slough sites were

typically characterized by lower velocities, longer water residence times, and high plant abundances, (mainly invasive water hyacinth *Eichhornia crassipes*) relative to other site types. The off-channel sites were in the shallow open-water habitat created by the flooding of the MWT.

The delineation of the three time periods was based on environmental conditions, namely the presence of the compromised levee which allowed ongoing flooding of the MWT. Pre-flood samples were taken during November-February when water temperatures and solar inputs were relatively low and large winter storms elicited large peaks in the hydrograph that swelled river channels; the flooded period samples were collected during February-May as temperatures and solar inputs increased and off-channel inundated areas were expansive; post-repair period samples were taken in May-June during the warmest, sunniest, and the lowest discharge phase of our sampling. Therefore, our 12 sampling stations and 34 sampling days were divided into a 2:3:2 matrix of spatiotemporal bins representing the pre-breach, flood, and post-repair periods crossed with our three habitat types during periods of inundation (Table 1.1).

Figure 1.2. Hydrograph for the MWT sampling during water year 2017. Mokelumne and Cosumnes discharge data collected from gages at Camanche Dam (DWR CDEC) and Michigan Bar (USGS 11335000), respectively. Sampling dates labeled by time period above with time period shifts indicated by shaded bar along x-axis.



Variable	Min - Mean - Max	Time Period	Riverine	Slough	Off-Channel
Sample Size (n)	-	Pre-Breach	39	38	49
		Flood	51	39	
		Post-Repair	29	32	
Water Temperature (°C)	7.9 - 14.5 - 30.2	Pre-Breach	9.9±1.2	10.1±1.5	15±2.7
		Flood	12.1±1.8	16.1±2.6	
		Post-Repair	18.5±3.9	22.8±3.6	
Chlorophyll-a (μg/L)	0.53 - 2.7 - 22.8	Pre-Breach	1.9±1	4±3.4	2.1±1.2
		Flood	1.5±0.7	2.6±2	
		Post-Repair	1.1±0.4	6.2±5.1	
Turbidity (FNU)	1.3 - 17.4 - 272.4	Pre-Breach	24.5±34.2	33.2±48.9	19.5±32
		Flood	14.5±18.5	8.5±7	
		Post-Repair	8.5±2.9	9.8±7	
Dissolved Oxygen Saturation (%)	43.6 - 90.9 - 135.4	Pre-Breach	90.2±5.9	77.6±10	99±10.7
		Flood	92.1±7.4	91±14.6	
		Post-Repair	90.2±6.3	93.1±13.1	
Specific Conductance (mS/cm)	0.04 - 0.09 - 0.35	Pre-Breach	0.08±0.03	0.13±0.4	0.07±0.01
		Flood	0.07±0.02	0.12±0.05	
		Post-Repair	0.06±0.02	0.09±0.01	
Total Dissolved Solids (mg/L)	24.7 - 56.3 - 227.4	Pre-Breach	49.9±17.2	86±23.6	44.8±5.8
		Flood	45.2±13.4	77.5±33	
		Post-Repair	37.3±12.8	55.5±9	
Salinity (ppt)	0.02 - 0.04 - 0.17	Pre-Breach	0.04±0.01	0.06±0.02	0.03±0.004
		Flood	0.03±0.01	0.06±0.02	
		Post-Repair	0.03±0.01	0.04±0.01	
pH	6.4 - 7.2 - 8.5	Pre-Breach	7.1±0.2	7.0±0.2	7.3±0.2
		Flood	7.3±0.2	7.3±0.3	
		Post-Repair	7.2±0.3	7.2±0.2	

Table 1.1. Summary of sonde water quality sampling (mean±sd) for each time period and site type from the McCormack – Williamson tract, Sacramento County, California between December 2016 and June 2017.

Water Quality Data

In situ water quality measurements were made using a YSI EXO2 multiparameter sonde (Xylem Inc.; New York, USA), equipped with sensors for

pH, conductivity/turbidity, chlorophyll-a, dissolved oxygen (DO mg/L), and temperature. The sonde was calibrated monthly and instrumental error is assumed to be <1%. In the case of chlorophyll-a, resolution is 0.1 μg/L. DO-percent saturation, specific conductance, total dissolved solids, and salinity were estimated from *in situ* water quality measurements. Sampling was conducted aboard a 5 m Jon boat, in transects surrounding POM sampling locations, at speeds less than 10 km/hr with the sonde suspended from the gunwale at a depth of 0.4 m. We avoided sampling waters disturbed by the boat's movement. Water quality measurements taken within 25 m of POM sample were averaged to create paired POM-water quality data. All measurements were made between the hours of 0900 and 1530 PST and collected in 5 s intervals.

POM Sampling

Grab samples of water (1L) were collected approximately 10 cm below the surface and filtered on site through pre-combusted 25 mm GF/F filters, 0.7 μm pore size (GE Healthcare; Buckinghamshire, UK) using a hand pump. Filters were stored separately in organic-free aluminum foil, and transported to the lab for isotopic analysis. At the lab, GF/F filters were immediately dried overnight at 50°C and subsequently stored at -20°C.

Laboratory Analysis

For isotopic analysis, half of each filter was stripped of extraneous glass fiber and packed into a tin capsule (Cloern et al., 2002). Low C:N ratios of preliminary samples and no visible effervescence upon reaction of a subset of samples with 1N HCl (n=10) confirmed the lack of inorganic carbon in our samples. Consequently, our samples were not acidified to avoid unpredictable alteration of nitrogen isotopic ratios (Schlacher & Connolly, 2014). Carbon and nitrogen isotopic analyses were conducted at the University of California Merced Stable Isotope Laboratory using a continuous flow setup comprised of a Costech 4010 elemental combustion system with a zero-blank auto-sampler connected to a Delta V-Plus isotope ratio mass spectrometer via a Conflo-IV open split interface (Thermo-Fisher; Bremen, DE). Measurements of $\delta^{13}C$ and $\delta^{15}N$ were done on single samples, with standards placed throughout each run. Results are reported in standard delta notation relative to the respective standards for carbon and nitrogen, Vienna PeeDee Belemnite and atmospheric N2. In-house standards used for validation were: Acetanelide ($\delta^{13}C$: -27.86‰; $\delta^{15}N$: -0.75‰), EM Soil ($\delta^{13}C$: -27.6‰; $\delta^{15}N$: -1.7‰), and Peach Leaf ($\delta^{13}C$: -25.99‰; $\delta^{15}N$: 1.98‰). Across all runs, Acetanilide (n=62) and Peach Leaf (n=44) yielded standard material variations ≤ 0.3 and 0.1 ‰ (1 σ) for nitrogen and carbon respectively, while EM Soil (n=44) varied ≤ 0.5 and 0.1 ‰ (1 σ) for nitrogen and carbon, respectively. C:N ratios were calculated based on the known C/N content

of the acetanilide standard (71.09 %C; 10.36 %N). The C:N ratios reported herein are atomic ratios.

Statistical Analysis

All statistical analyses were performed in R, with the vegan and lm.beta packages. We selected the variables in our dataset that were most relevant to the composition of POM at our sites – [chlorophyll-a], Turbidity, C:N ratio, $\delta^{13}C$ and $\delta^{15}N$ – for principal component analysis (PCA). This technique has the advantage of reducing the dimensionality of data, effectively combining correlated variables, and potentially revealing a syndrome of correlations within a large dataset that may be obscure to bivariate analysis. PCA is sensitive to differences in the scale of variables. Therefore, data were transformed using Tukey's Ladder of Power transformation to approximate normality, which was then followed by z-transformation to normalize the scale of variables before PCA. We applied perMANOVA on the POM variables to identify significant differences in POM composition between sample groups (habitat type, time period) and validate observed differences in principal component space. We tested for the effect of time period and habitat type on centroid location separately, considering each factor fixed. Permutations were held at 999 and Euclidean distance metrics were used throughout. In some cases, perMANOVA was implemented to test whether significant differences existed between single variables amongst groups.

This test behaves similarly to one-way ANOVA, yet is nonparametric (Anderson, 2001).

Following group-wise estimation of POM samples multivariate centroid distances (using PERMDISP2 procedure in vegan), we performed one-way ANOVA to determine if group dispersion varied; we considered the habitat type or time period fixed factors and tested for an effect on the centroid distance in multivariate space (Anderson, 2006). We used Euclidean distances, therefore this procedure is a multivariate analogue for Levene's test. Here we determined whether significant perMANOVA results could be attributed to true differences in POM characteristics (i.e. multivariate centroid location), or were an artifact of differences in group dispersions. When ANOVA results were significant, indicating at least one group had significantly different multivariate dispersion, Tukey's Honest Significant Difference (HSD) test was applied to determine which groups (habitat type, time period) differed, and how. Bonferroni corrections were used to constrain elevated Type I error rates for hypothesis testing.

We investigated relationships between environmental conditions and POM composition using partial Mantel tests. This test compared Euclidean dissimilarity matrices, constructed from POM and z-transformed environmental variables, to determine whether samples taken under dissimilar environmental conditions also had dissimilar POM compositions. The analysis was iteratively repeated on every possible combination of variables to identify the environmental variable(s) with

the dissimilarities most strongly correlated to POM compositional dissimilarities. We conditioned for temporal autocorrelation in our partial Mantel tests by using Euclidean distances between sampling dates.

The above analyses highlight the presence of differences in POM composition but do not describe the direction of associations between environmental variables and POM composition. We explored the directionality of relationships between environmental variables (e.g. water temperature, Cosumnes discharge, Mokelumne discharge, combined discharge, salinity, pH) and POM characteristics (chlorophyll-a concentrations, turbidity, C:N ratio, $\delta^{13}C$ and $\delta^{15}N$), as indicated by PCA eigenvalues, using stepwise multiple regression. We selected the best model for each principal component, as estimated by Akaike Information Criterion (AIC) score. Variance inflation factors were < 1.6 for all variables in the two models we tested, so we dismissed multicollinearity as a confounding factor. Model residuals were checked for normality using the Shapiro-Wilk test ($P < 0.05$), and assumptions of homoscedasticity were assessed graphically (Appendices 1.1 & 1.2).

We also used the non-parametric Kendall's rank coefficient test to characterize bivariate relationships. Lastly, we applied a criterion to roughly classify POM samples: C:N ratios in freshwater POM that were less than 8 are diagnostic of dominance by heterotrophic microbes or microalgae, whereas C:N

ratios greater than 15 are categorized as being dominated by a mix of terrestrial plant and macrophyte inputs (Kendall et al., 2001).

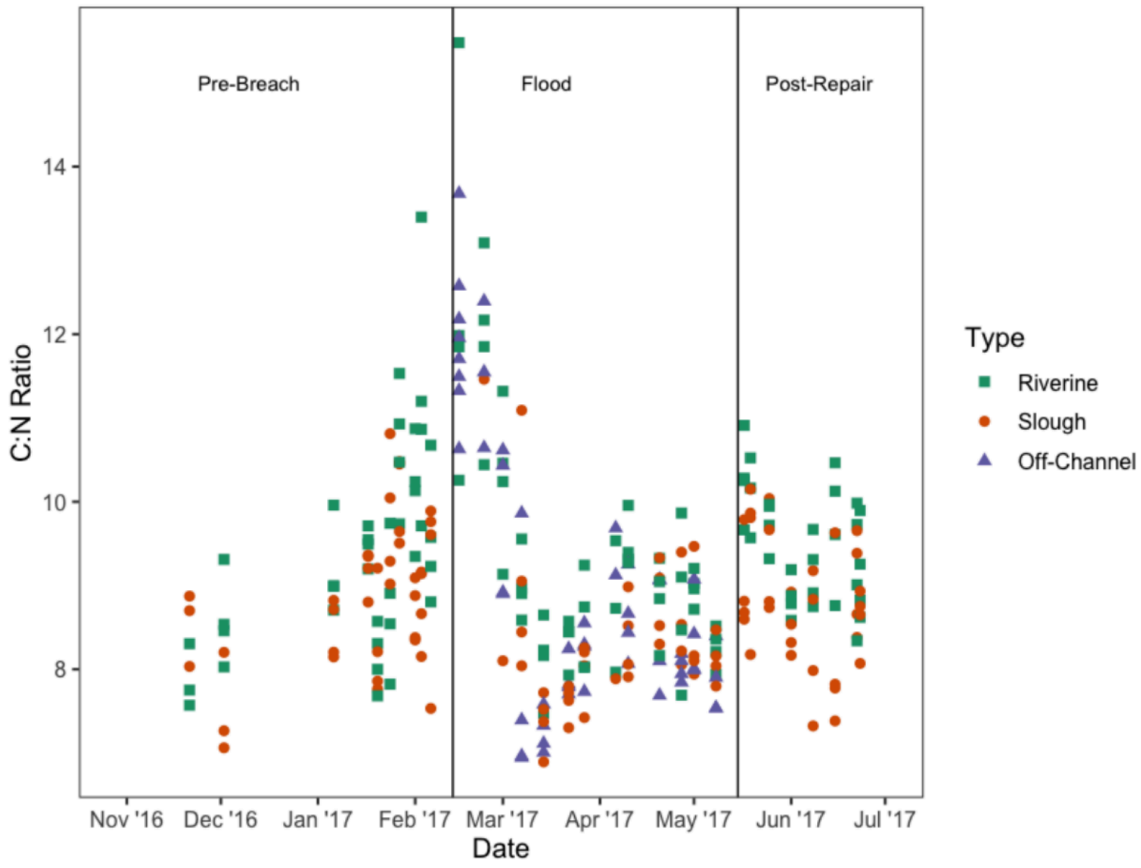


Figure 1.3. C:N ratios in POM samples through time at different habitat types. Notice the spike at all site types near the start of February, followed by a steep decline in both slough and off-channel sites. n=283.

Results

General POM Characteristics

We observed varying degrees of dominance by allochthonous and autochthonous OM throughout our sampling. The majority of POM samples had

C:N ratios between 8 and 15 suggesting contributions from both terrestrial and phytoplanktonic or microbial sources (Figure 1.3; Table 1.2). C:N ratios < 8, suggesting a primarily phytoplanktonic or microbial source, were measured in 18% of all POM samples; 36% of off-channel samples had C:N ratios < 8. In contrast, only 8% of riverine and 21% of slough samples had C:N ratios < 8. In all, 50% of the samples with a C:N ratio < 8 were collected during the flooded period. A clear spike in C:N ratios at all habitat types was observed at the end of the pre-flood period and start of the flood period (Figure 1.3).

Table 1.2. Summary of particular organic matter isotopic and elemental data (mean±sd) for each time period and site type for samples collected from the McCormack – Williamson tract, Sacramento County, California between December 2016 and June 2017.

Variable	C:N Ratio			δ^{15}N (‰)			δ^{13}C (‰)		
Period	Pre-Breach	Flood	Post-Repair	Pre-Breach	Flood	Post-Repair	Pre-Breach	Flood	Post-Repair
Riverine	9.4±1.2	9.4±1.5	8.8±0.7	4.0±1.5	6.1±1.4	6.3±1.8	-27.6±0.7	-28±1.2	-28.7±1.1
Slough	8.9±0.9	8.3±0.9	8.7±0.8	4.5±1.6	7.2±1.8	7.4±2.1	-29.2±2.4	-30.7±2.1	-31.5±1.5
Off-Channel		8.9±1.5			5.5±1.7			-29.2±1.3	

POM composition in our system was the result of an interplay between delivered from upstream and the composition attained after environmentally-mediated in situ processes had acted upon the pool of delivered POM. The $\delta^{15}N$ in POM (Figure 1.4; Appendix 1.3) was positively correlated with water temperature and increased throughout the sampling period. The $\delta^{13}C$ (Figure 1.5) and the C:N ratio (Figure 1.3) did not show a directional shift throughout our sampling, but the C:N ratio was weakly negatively correlated to temperature. Univariate perMANOVA revealed that turbidity was the only variable that did not contribute to differentiation among site types within a time period (Table 1.3). The $\delta^{13}C$, the C:N ratio, and chlorophyll-a concentrations on the other hand, were often significantly different across time periods and habitat types (Table 1.1 & 1.2).

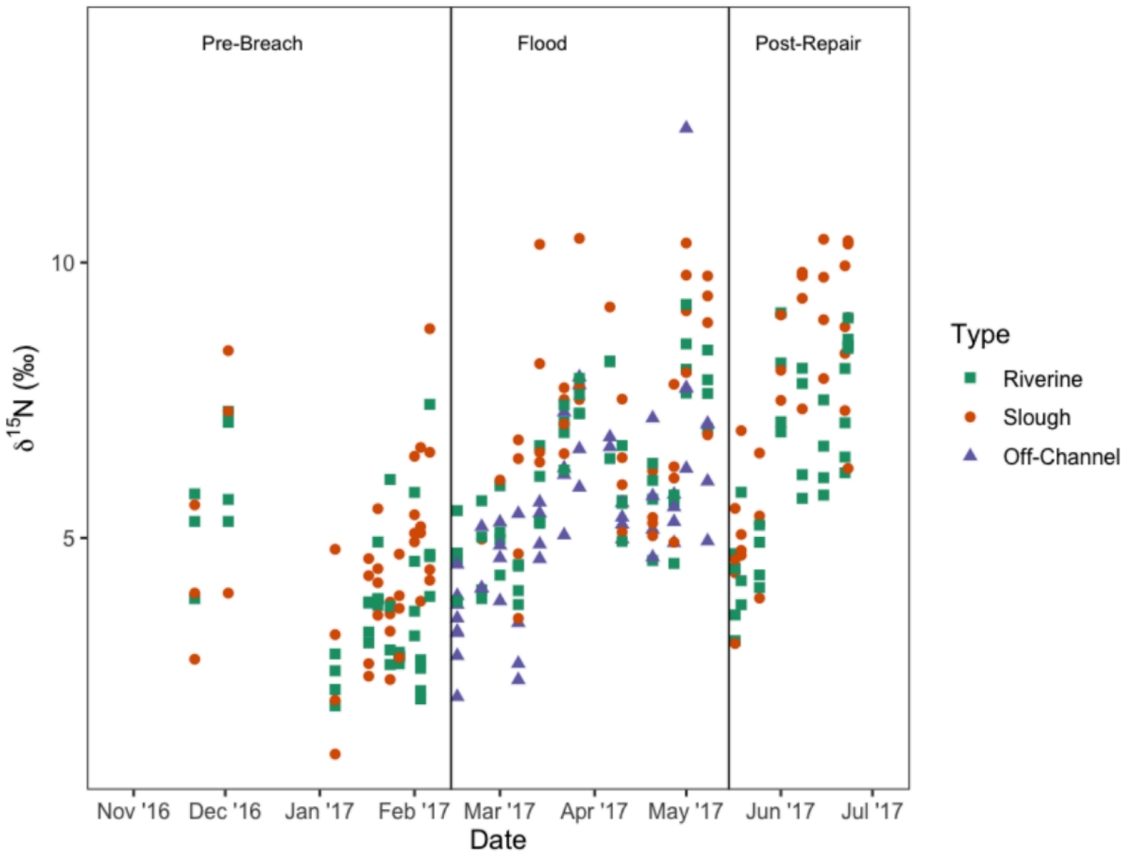


Figure 1.4. Nitrogen isotope ratios of POM through time. A clear upward trend is evident through sampling accompanied by simultaneous jagged dips at all site types in April and May. Different symbols show different habitat types (n=283).

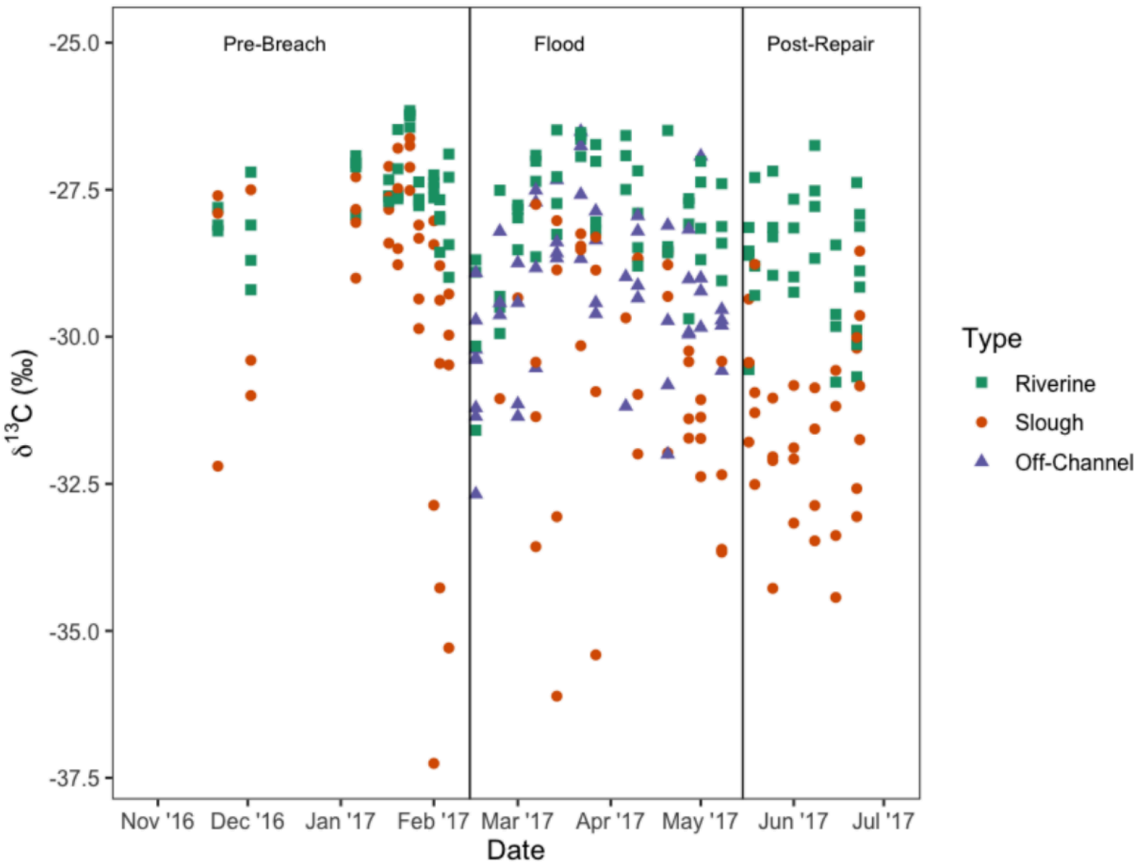


Figure 1.5. Carbon isotope compositions of POM through time. Different symbols show different habitat types (n=283).

Table 1.3. Univariate comparison of variables between habitat types, during the flooded period, using perMANOVA. Bonferroni correction for multiple comparisons (p = 0.003) were applied and habitat type was considered a fixed factor.

Variable	Riverine-Slough	Riverine-Off Channel	Slough-Off Channel
$\delta^{13}C$ (‰)	pseudo-$F_{1, 88}$ = 66.1; R^2=0.43; *P < 0.003*	pseudo-$F_{1, 97}$ = 27.1; R^2=0.22; *P < 0.003*	pseudo-$F_{1, 85}$ = 17.3; R^2= 0.17; *P < 0.003*
$\delta^{15}N$ (‰)	N.S.	N.S.	pseudo-$F_{1, 85}$ = 18.7; R^2= 0.18; *P < 0.003*
C:N Ratio	pseudo-$F_{1, 88}$ = 14.1; R^2=0.14; *P < 0.003*	N.S.	N.S.
Turbidity	N.S.	N.S.	N.S.
[Chlorophyll-a]	pseudo-$F_{1, 88}$ = 13.9; R^2=0.14; *P < 0.003*	N.S.	N.S.

Riverine POM

Overall, C:N ratios at riverine sites were low, but were uncorrelated with the chlorophyll-a concentration. During the pre-flood period, we identified a positive correlation between $\delta^{13}C$ and the chlorophyll-a concentration (Appendix 1.4). As higher flows persisted through January into February, $\delta^{13}C$ generally decreased moving into the flood period.

During the flood period, $\delta^{15}N$ values were more positive than during the pre-flood period. Chlorophyll-a concentration was positively correlated with discharge. However, the C:N ratio, the concentration of chlorophyll-a, and dissolved oxygen percent saturation were not correlated. The C:N ratio was positively correlated with turbidity (Appendix 1.4).

After levee repair, discharge decreased abruptly owing to reductions in dam releases on the Mokelumne and natural decreases in Cosumnes River discharge (Figure 1.2). During this period, the C:N ratio of POM decreased, while $\delta^{15}N$, $\delta^{13}C$, and chlorophyll-a concentration increased. However, chlorophyll-a concentration was not significantly correlated with $\delta^{15}N$, $\delta^{13}C$, discharge, or the C:N ratio (Appendix 1.4).

Slough POM

We observed low percent saturation of dissolved oxygen with no correlation with chlorophyll-a concentrations in slough sites during the pre-flood

period (Appendix 1.5). This period was characterized by low connectivity between slough and river sites and high macrophyte abundances, mainly the floating plant *Eichhornia crassipes*. As with riverine sites, the C:N ratio of POM from slough sites was routinely low (C:N < 10). In contrast to riverine sites, during the flood period we observed exceptionally negative $\delta^{13}C$ values, < -35‰, at slough sites (Figure 1.4). In fact, the slough samples showed the greatest variation in $\delta^{13}C$, in addition to having higher $\delta^{15}N$ than other site types. During the flood period we observed the greatest connectivity between our, generally lentic, slough sites and the river channels.

During the post-repair period when reduced discharge created slackwater conditions at the slough sites, we observed the highest chlorophyll-a concentrations, dissolved oxygen saturation values, and a relatively invariant C:N ratio. The $\delta^{13}C$ values measured at slough stations during the post-repair period were, on average, the lowest $\delta^{13}C$ values measured in our study (Table 1.2). However, while the mean was low, we no longer observed any extremely negative $\delta^{13}C$ values, < -35‰.

Off-Channel POM

Off-channel POM was compositionally different from the riverine POM delivered to that habitat through the levee breach. Reconnected off-channel habitat was differentiated from riverine habitat by the isotopic composition of

POM, as well as by the correlations amongst variables. We determined that at off-channel sites, chlorophyll-a concentrations were significantly correlated with discharge and turbidity (Appendix 1.6). Percent saturation of dissolved oxygen was greater off-channel than in the river, but was not correlated with the concentration of chlorophyll-a. The only POM variable that was significantly different from the river during the flood period was $\delta^{13}C$ (Table 1.3). Nonetheless, chlorophyll-a concentrations at off-channel sites were generally intermediate to those at the river and slough sites (Appendix 1.3).

Multivariate Analyses

The first two axes of the PCA of POM characteristics (i.e. turbidity, C:N ratio, [chlorophyll-a], $\delta^{13}C$, and $\delta^{15}N$) generated eigenvectors that explained 69.3% of the total variation and revealed spatiotemporal differences (Figure 1.6 & 1.7; Appendix 1.7). Principal component 1 (PC1) explained 40% of the variability in the data and was most heavily loaded by the $\delta^{15}N$ and turbidity. Principal component 2 (PC2) explained 29% of the variability in the data and was most heavily loaded by the chlorophyll-a concentration and $\delta^{13}C$. When all variables and samples were considered together, perMANOVA on POM composition (i.e. C:N ratio, $\delta^{13}C$, $\delta^{15}N$, Turbidity, and [chlorophyll-a]) revealed a significant main effect of sampling period on multivariate centroid location for riverine [pseudo-F2, 116 = 4.7, $P < 0.01$] and slough [pseudo-F2, 106 = 8.4, $P < 0.01$] samples. A

significant main effect of sampling period [pseudo-F2, 274 = 10.5, $P < 0.001$] was still present when all samples were considered together (Appendix 1.8). A significant difference in centroid location between site types was found between riverine and slough sites only during the post-repair period [pseudo-F1, 59 = 11.6, $P < 0.01$] (Table 1.4).

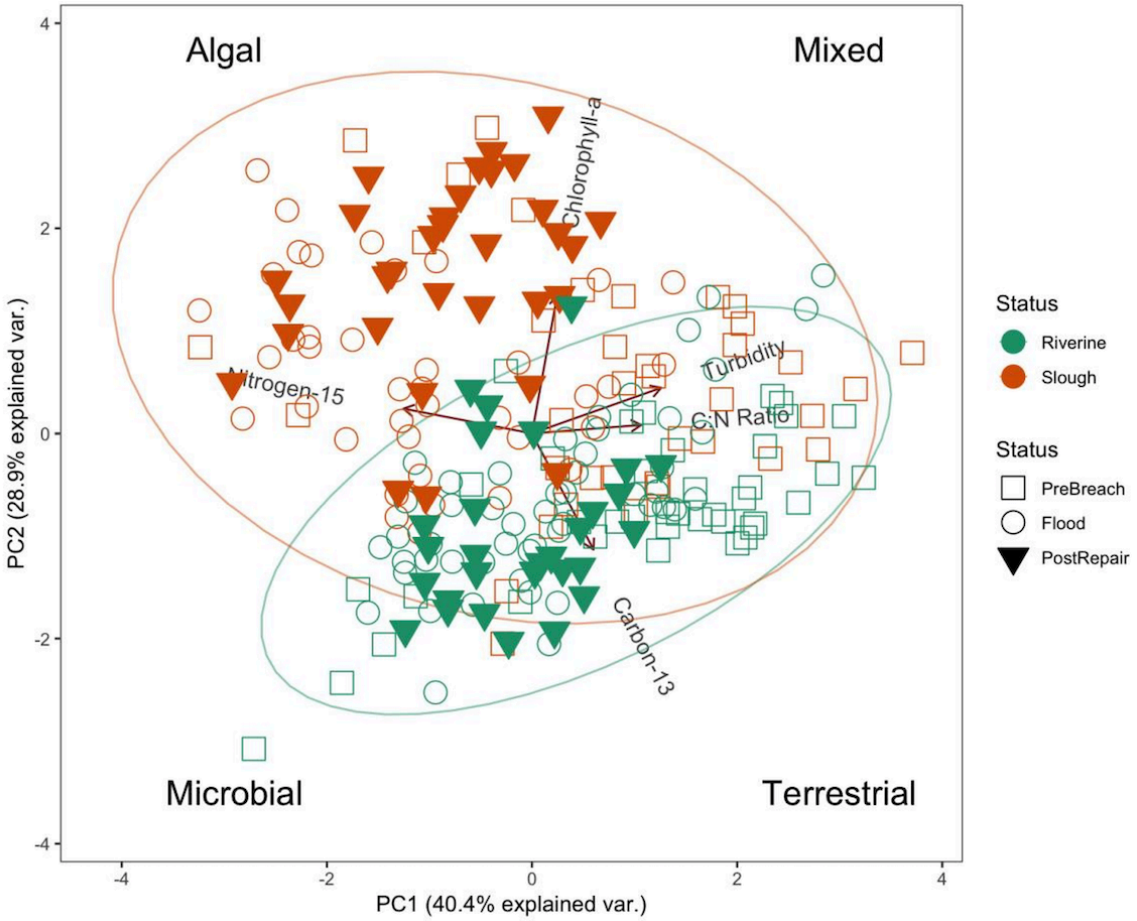


Figure 1.6. Principal component analysis of POM characteristics from all habitat types and sampling days. Principal components 1 and 2 are shown on the X and Y axes, respectively, and different habitat types are shown in different colors. Annotations indicate hypothetical positions for OM sources potentially contributing to our POM. The 'mixed' area is populated by POM samples without a clear, seemingly-dominant, source. 95% confidence intervals are drawn as ellipses (n=276).

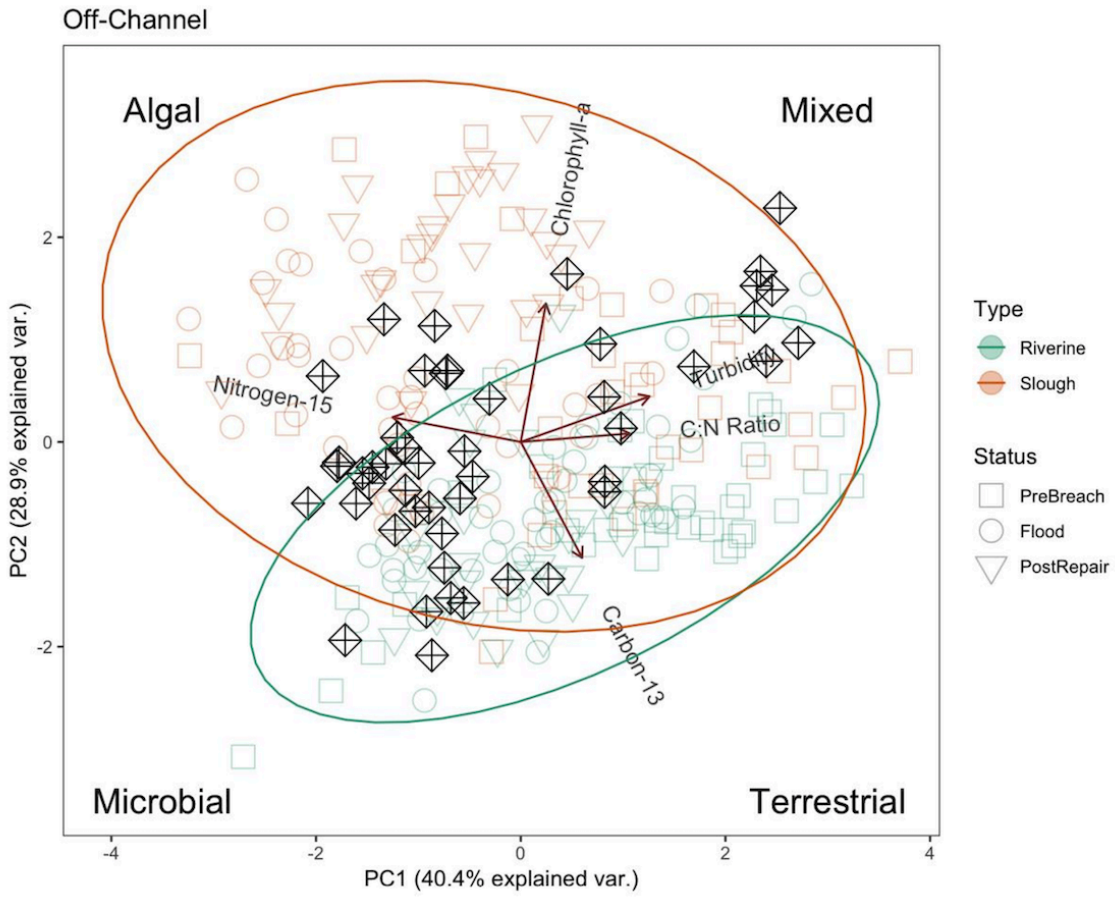


Figure 1.7. Principal component analysis of off-channel POM characteristics over 95% confidence ellipses for slough and riverine POM. Off-channel POM populates both ellipses, incorporating characteristics of both riverine and slough POM. Annotations indicate hypothetical positions for OM sources potentially contributing to our POM. The 'mixed' area is populated by POM samples without a clear, seemingly-dominant, source.

Table 1.4. Results of perMANOVA testing for an effect of habitat type on centroid location, within a given time period; habitat type was considered a fixed factor. A significant result indicates that the true position of the multivariate centroid for two different habitat types was significantly different within a given time period, and significance was assessed at $P < 0.01$.

Pre-Flood		River	Slough	
	River	-	N.S.	
	Slough	N.S.	-	
Flood		**River**	**Slough**	**Off-Channel**
	River	-	N.S.	N.S.
	Slough	N.S.	-	N.S.
	Off-Channel	N.S.	N.S.	-
Post-Repair		**River**	**Slough**	
	River	-	pseudo-$F_{1, 59} = 11.6$ *P < 0.01*	
	Slough	pseudo-$F_{1, 59} = 11.6$; *P <0.01*	-	

Only during the post-repair period did multivariate dispersion of POM characteristics differ significantly between habitat types [ANOVA: $F_{1, 59} = 7.5$, $P < 0.01$]; specifically, we observed significantly increased dispersion at slough ($M = 7.1 \pm 5.6$) sites relative to riverine ($M = 3.4 \pm 1.2$) sites during this period [Tukey HSD: Slough - Riverine = 3.7 ± 2.2, $P < 0.01$]. When considering the effect of time period, pairwise comparisons following ANOVA [$F_{2, 274} = 7.1$, $P < 0.01$] indicated that pre-breach ($M = 25.7 \pm 33.4$) multivariate dispersion was significantly greater than dispersion during the flood ($M = 12.2 \pm 19.2$; [Tukey HSD: Pre-Breach – Flood = 13.5 ± 6.0, $P < 0.01$]), and post-repair ($M = 6.0 \pm 4.7$; [Tukey HSD: Pre-Breach – Post-Repair = 19.7 ± 9.0, $P < 0.01$]) periods. Flood and post-repair POM parameter dispersions, however, were not significantly different from each other.

Partial mantel tests showed that the model with the highest correlation included Cosumnes River discharge and water temperature (Mantel rho: 0.47, $p = 0.001$, permutations = 999). Multiple regression of PC1 yielded a significant model including Cosumnes discharge, water temperature, pH, and salinity (Table 1.5). This result shows that increases in Cosumnes discharge, and decreased water temperature, pH, and salinity were associated with increases in turbidity, and C:N ratio with more negative $\delta^{15}N$ values. Multiple regression of PC2 also yielded a significant model including water temperature, salinity, combined Cosumnes/Mokelumne discharge and pH (Table 1.5). pH changed very little over

the course of our sampling, however, it was correlated with other variables. These results demonstrate that decreased water temperature, salinity, and combined Cosumnes/Mokelumne discharge were associated with reduced chlorophyll-a concentrations and more positive $\delta^{13}C$.

Variable	Model 1 (PC1)		Significance (p <)	Model 2 (PC2)		Significance (p <)
	Coefficient (β)	Std. Error		Coefficient (β)	Std. Error	
Total Discharge	-	-	-	0.41	2.1E-05	0.001
Water Temperature	-0.3	1.5E-02	0.001	0.65	1.4E-02	0.001
pH	-0.23	2.5E-01	0.001	0.65	2.1E-01	0.1
Salinity	-0.12	3.4E+00	0.01	0.49	2.8E+00	0.001
Cosumnes Discharge	0.43	3.2E-05	0.001	-	-	-
	Residual Standard Error	1.019		Residual Standard Error	0.86	
	Adjusted R^2	0.49		Adjusted R^2	0.48	

Table 1.5. Description of models yielded from stepwise regression of POM characteristics on environmental variables. Shown here are standardized regression coefficients (β) calculated from the significant model for PC1 [$F_{4, 271} = 65.94$; $P < 0.001$] and for PC2 [$F_{4, 271} = 65.25$; $P < 0.001$].

Discussion

POM Composition through Space and Time

Our results reveal higher isotopic variability in POM over smaller areas and shorter time frames than previously published studies. We achieved this novel finding by sampling diverse and dynamic habitats at the confluence of two rivers with contrasting hydrology. Because off-channel habitats are non-trivial components of river systems globally, their role needs to be fully understood to construct accurate models of OM dynamics in river systems. Our results support conceptual and numerical models that integrate temporally heterogeneous exchange between habitat types as an important facet of fully understanding ecosystem functioning, particularly in river-floodplain systems which are especially dynamic with regards to lateral exchange between the channel and off-channel habitats.

During our study, POM was not comprised of varying mixes of compositionally static terrestrial and autochthonous sources. Had mixing of static sources been the primary mechanism for formulating the POM sampled throughout our study, we would have observed consistent relationships among variables. It is also possible that alteration of POM, particularly by microbes, quickly and unpredictably overprints and obscures signatures from sources that may have had relatively uniform elemental and isotopic compositions (e.g. terrestrial plant matter). Caution should be exercised when attempting to apply or

extrapolate isotope source mixing models involving POM in systems where river condition and the potential for lateral exchange between habitats varies greatly. Although linear models provide some understanding of POM composition as it relates to hydrological variables, not until we used multivariate analyses did we see the more complex patterns in our data. For example, connectivity amongst sites was an important determinant of POM composition. POM transported from upstream sometimes resulted in a common POM composition amongst different sampling locations, particularly during high-flow periods characterized by increased connectivity between sites. In contrast, during periods of low hydrological connectivity, differentiation of POM in different habitats was driven by in situ processes. Accordingly, we found the greatest variation in POM composition in slackwater habitats where connectivity was routinely low, residence time was long, and disturbance limited.

The components comprising POM varied throughout our sampling period with terrestrial plant particles always comprising a portion of riverine POM along with algal biomass (Figure 1.6). The negative relationship between the C:N ratio and δ^{15}N coupled with consistently low C:N ratios, sometimes in the absence of significant chlorophyll-a concentrations, indicates that non-photosynthetic microbial biomass on plant particles might have contributed significant OM as well (Angradi, 1994; Macko & Estep, 1984). Conversely, the unexplained covariance of δ^{15}N amongst site types throughout our entire sampling period

suggests that δ^{15}N of POM was partially mediated by a factor that was universal among sites, such as a widespread nutrient subsidy or environmental constraints on nutrient cycling (Thibodeau, Hélie, & Lehmann, 2013). Persistent inputs of nitrogen such as that bound in allochthonous OM or entrained in runoff and during high flow events would also result in the negative correlation between discharge and δ^{15}N that we observed (Table 1.5). The negative correlations between δ^{15}N and turbidity support this idea as well. Similarly, this correlation could also result from the dilution of POM in pools having ^{15}N-enriched POM with POM that is relatively ^{15}N-depleted from incoming water (Ock & Takemon, 2013). Multiple plausible explanations when interpreting data like these make compound specific isotope and biomarker analyses promising methods to apply in the future to further understand the spatiotemporal dynamics of riverine POM composition and the role it plays in supporting secondary production.

While in situ dynamics were important, the presence of POM transported from upstream was ubiquitous throughout our study site particularly during periods that were characterized by increased connectivity between sites (i.e. high discharge). In support of this finding, our models show that POM centroid location was generally invariable as a function of site type within a single time period. Conversely, the movement of the multivariate centroid of all POM throughout time is presumably influenced by the drastically different meteorological and river conditions experienced throughout our sampling.

Presumably, the importance of terrestrial inputs is greatest during periods of high precipitation (November – April for our study site), while the prevalence of autochthonous production increases when water temperatures and solar inputs increase (May – October) (Harmelin-Vivien, Dierking, Bănaru, Fontaine, & Arlhac, 2010; Wantzen, de Arruda Machado, Voss, Boriss, & Junk, 2002).

The composition of POM was significantly influenced by variability in habitat and environmental conditions. Increased multivariate dispersion at slough sites may be symptomatic of longer residence times of water, increased cycling rates of nutrients and organic matter, or a combination of the two. Our results for carbon isotopes are consistent with previous work showing variability in POM $\delta^{13}C$ values and water age being associated with increased autochthonous organic matter (Hein, Baranyi, Herndl, Wanek, & Schiemer, 2003). The role of slackwater areas, such as our slough sites, as important habitats for nutrient cycling and production of OM which can support riverine food webs has been previously established (Hein et al., 2005). Conversely, the increased dispersion during the build-up to the flood period seems unrelated to changes in autochthonous production. Increased aquatic-terrestrial OM exchange in the winter, due to flooding, is the apparent reason for increased multivariate dispersion during that period.

The variation in the stable isotopic composition of POM we observed in our < $10km^2$ scale study is comparable to that found in continental scale studies

of the stable isotope composition of POM in North America (Kendall et al., 2001; Onstad, Canfield, Quay, & Hedges, 2000), Russia (Lobbes, Fitznar, & Kattner, 2000; Rachold & Hubberten, 1999), and New Zealand (Pingram, Collier, Hamilton, Hicks, & David, 2012). POM composition did not, however, vary randomly at our smaller scale. In addition to the univariate variability observed, we found similar correlations among elemental and isotopic composition of POM and hydrologic characteristics (i.e. streamflow and turbidity), as Kendall et al. (2001), although on a finer scale.

Implications for Management and Restoration

Consistent with ideas presented by (Jassby & Cloern, 2000), we documented that after achieving connectivity with the river, off-channel habitats supported significant autochthonous productivity, as POM sampled off-channel differentiated from the riverine sourced POM. Water quality and POM composition variables, respectively, were rarely consistent among off-channel stations, which highlights the spatial heterogeneity that can arise in poorly mixed floodplain habitats. We observed increases in the concentration of chlorophyll-a at most off-channel stations during flow pulses, which we have attributed to turbulent mixing of antecedent floodplain water of varying water age back into inflowing waters. Mean concentrations were, however, similar to those observed in other studies of off-channel sites located in the Delta and during hydrologic

connection (Ahearn et al., 2006; Lehman, Sommer, & Rivard, 2008; Schemel, Sommer, Müller-Solger, & Harrell, 2004).

Excluding periods of increased flow, we did not find significant increases in chlorophyll-a concentration in off-channel sites. Off-channel zooplankton abundances may have suppressed measured chlorophyll-a concentrations by exerting top-down control on planktonic autotrophs. Increased zooplankton biomass in off-channel sites has been positively correlated with water residence time, thereby exerting non-trivial grazing pressure (Baranyi, Hein, Holarek, Keckeis, & Schiemer, 2002; Keckeis et al., 2003). In turn, off-channel invertebrate communities can serve as high quality food for the growth and development of fishes (Jeffres et al., 2008). The productivity of this newly inundated site at MWT may be partially driven by terrestrial nutrient subsidies that would decline over time. The potential role and significance of these subsidies warrants further exploration and highlights the importance of understanding the outcomes and efficacy of future restoration actions.

Hydrology and water quality are vitally important in determining POM composition and in turn, the base of the aquatic food web. Cosumnes River discharge and local water temperature were positively correlated with Euclidean distances between POM variables, demonstrating the importance of discharge and water temperature variability in establishing spatiotemporal heterogeneity in POM composition. Following rain events, spikes in discharge were caused by

increased flow from the Cosumnes River, which lacks upstream regulating dams, emphasizing the ecological significance of unregulated river systems. The Delta, and other similar ecosystems, may be best served by a more natural flow regime incorporating multiple peaks in discharge throughout winter and spring. Access to floodplains also reduces water velocity and increases residence time which should increase the potential for autochthonous OM production and nutrient cycling (Schiemer, Keckeis, Reckendorfer, & Winkler, 2001).

Our results highlight the dynamic nature of POM composition in this river system and provide context to interpret data from similar systems. In dynamic tidally-influenced systems, the nitrogen and carbon stable isotope compositions of POM have the capacity to vary on finer spatiotemporal scales than have been previously reported. This new knowledge of previously uncharacterized spatiotemporal variability has implications for freshwater science, such as the spatial and temporal distribution of future data collection efforts and the interpretation of POM data aimed at quantifying ecosystem productivity and trophic structure. Particular care should be taken in ecosystems, such as river-floodplain sites, that are characterized by a high degree of spatiotemporal variability in habitat availability and connectivity. If higher spatiotemporal resolution is not logistically feasible, more complex size (e.g. fine vs. coarse POM) and class (e.g. living vs. detrital) fractionations of POM could also provide scientifically valuable insights (Delong & Thorp, 2006).

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Works Cited

Ahearn, D. S., Sheibley, R. W., & Dahlgren, R. A. (2005). Effects of river regulation on water quality in the lower Mokelumne River, California. *River Research and Applications*, 21(6), 651–670. http://doi.org/10.1002/rra.853

Ahearn, D. S., Viers, J. H., Mount, J. F., & Dahlgren, R. A. (2006). Priming the productivity pump: flood pulse driven trends in suspended algal biomass distribution across a restored floodplain. *Freshwater Biology*, 51(8), 1417–1433. http://doi.org/10.1111/j.1365-2427.2006.01580.x

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 32–46.

Anderson, M. J. (2006). Distance-Based Tests for Homogeneity of Multivariate Dispersions. *Biometrics*, 62(1), 245–253. http://doi.org/10.1111/j.1541-0420.2005.00440.x

Angradi, T. R. (1994). Trophic Linkages in the Lower Colorado River: Multiple Stable Isotope Evidence. *Journal of the North American Benthological Society,* 13(4), 479–495. http://doi.org/10.2307/1467845

Baranyi, C., Hein, T., Holarek, C., Keckeis, S., & Schiemer, F. (2002). Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. *Freshwater Biology*, (47), 1–10.

Beagle, J. R., Whipple, A. A., & Grossinger, R. M. (2013). Landscape Patterns and Processes of the McCormack-Williamson Tract and Surrounding Area: A framework for restoring a resilient and functional landscape (pp. 1–42).

Bennett, W. A., & Moyle, P. B. (1996). Where Have All the Fishes Gone? Interactive Factors Producing Fish Declines in the Sacramento-San Joaquin Estuary. In J. T. Hollibaugh (Ed.), (pp. 519–542). Presented at the 75th Annual: Pacific DivisionAmerican Association for the Advancement of Science, San Francisco, CA.

Brett, M. T., & Müller-Navarra, D. C. (1997). The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshwater Biology,* 38, 483–499.

Brett, M. T., Bunn, S. E., Chandra, S., Galloway, A. W. E., Guo, F., Kainz, M. J., et al. (2017). How important are terrestrial organic carbon inputs for

secondary production in freshwater ecosystems? *Freshwater Biology,* 12(8), 67–21. http://doi.org/10.1111/fwb.12909

Brown, K. J., & Pasternack, G. B. (2004). The geomorphic dynamics and environmental history of an upper deltaic floodplain tract in the Sacramento–San Joaquin Delta, California, USA. *Earth Surface Processes and Landforms,* 29(10), 1235–1258. http://doi.org/10.1002/esp.1088

Burgess, O. T., Pine, W. E., III, & Walsh, S. J. (2012). Importance of Floodplain Connectivity to Fish Populations in the Apalachicola River, Florida. *River Research and Applications*, 29(6), 718–733. http://doi.org/10.1002/rra.2567

Cloern, J. E., Canuel, E. A., & Harris, D. (2002). Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. *Limnology and Oceanography*, 47(3), 713–729. http://doi.org/10.4319/lo.2002.47.3.0713

Cloern, J. E., Robinson, A., Grenier, L., Grossinger, R. M., Boyer, K., Burau, J. R., et al. (2016). Primary Production in the Delta: Then and Now. *San Francisco Estuary and Watershed Science*, 14(3). http://doi.org/10.15447/sfews.2016v14iss3art1

Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G., et al. (2007). Plumbing the Global Carbon Cycle: Integrating Inland Waters into the Terrestrial Carbon Budget. *Ecosystems*, 10(1), 172–185. http://doi.org/10.1007/s10021-006-9013-8

Delong, M. D., & Thorp, J. H. (2006). Significance of instream autotrophs in trophic dynamics of the Upper Mississippi River. *Oecologia*, 147, 76–85. http://doi.org/10.1007/s00442-005-0241-y

Feyrer, F., Herbold, B., Matern, S. A., & Moyle, P. B. (2003). Dietary shifts in a stressed fish assemblage: Consequences of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes*, 67(3), 277–288. http://doi.org/10.1023/A:1025839132274

Florsheim, J. L., & Mount, J. F. (2002). Restoration of floodplain topography by sand-splay complex formation in response to intentional levee breaches, Lower Cosumnes River, California. Geomorphology, 44, 67–94.

Florsheim, J. L., & Mount, J. F. (2003). Changes in lowland floodplain sedimentation processes: pre-disturbance to post-rehabilitation, Cosumnes River, CA. *Geomorphology*, 56(3-4), 305–323. http://doi.org/10.1016/S0169-555X(03)00158-2

Florsheim, J. L., Mount, J. F., Hammersmark, C., Fleenor, W. E., & Schladow, G. S. (2008). Geomorphic Influence on Flood Hazards in a Lowland Fluvial-Tidal Transitional Area, Central Valley, California. *Natural Hazards Review*, 9(3), 116–124. http://doi.org/10.1061/(ASCE)1527-6988(2008)9:3(116)

Funk, A., Martínez-López, J., Borgwardt, F., Trauner, D., Bagstad, K. J., Balbi, S., et al. (2019). Identification of conservation and restoration priority areas in the Danube River based on the multi-functionality of river-floodplain systems. *Science of the Total Environment*, 654, 763–777. http://doi.org/10.1016/j.scitotenv.2018.10.322

Guida, R. J., Swanson, T. L., Remo, J. W. F., & Kiss, T. (2015). Strategic floodplain reconnection for the Lower Tisza River, Hungary: Opportunities for flood-height reduction and floodplain-wetland reconnection. *Journal of Hydrology*, 521(C), 274–285. http://doi.org/10.1016/j.jhydrol.2014.11.080

Hamilton, S. K., & Lewis, W. M., Jr. (1987). Causes of Seasonality in the Chemistry of a Lake on the Orinoco River floodplain, Venezuala. *Limnology and Oceanography*, 32(6), 1277–1290.

Harmelin-Vivien, M., Dierking, J., Bănaru, D., Fontaine, M. F., & Arlhac, D. (2010). Seasonal variation in stable C and N isotope ratios of the Rhone River inputs to the Mediterranean Sea (2004–2005). *Biogeochemistry,* (100), 139–150. http://doi.org/10.1007/s10533-010-9411-z

Hein, T., Baranyi, C., Herndl, G. J., Wanek, W., & Schiemer, F. (2003). Allochthonous and autochthonous particulate organic matter in floodplains of the River Danube: Importance of..., *Freshwater Biology,* (48), 220–232.

Hein, T., Reckendorfer, W., Thorp, J. H., & Schiemer, F. (2005). The role of slackwater areas for biogeochemical processes in rehabilitated river corridors: examples from the Danube. *Large Rivers,* 15(1-4), 425–442.

Hein, T., Schwarz, U., Habersack, H., Nichersu, I., Preiner, S., Willby, N., & Weigelhofer, G. (2016). Current status and restoration options for

floodplains along the Danube River. *Science of the Total Environment*, 543, 778–790. http://doi.org/10.1016/j.scitotenv.2015.09.073

Hupp, C. R., Pierce, A. R., & Noe, G. B. (2009). Floodplain Geomorphic Processes and Environmental Impacts of Human Alteration Along Coastal Plain Rivers, USA. *Wetlands,* 29(2), 413–429.

Inamine, M., Punyamurthula, S., Bonakdar, H., Mahnke, S., Millet, R., & Dell, P. (2010). California's Levee Evaluation Program. Presented at the US Society of Dams Conference, Sacramento, CA.

Jassby, A. D. (2008). Phytoplankton in the Upper San Francisco Estuary: Recent Biomass Trends, Their Causes, and Their Trophic Significance. *San Francisco Estuary and Watershed Science*, 6(1 SN -).

Jassby, A. D., & Cloern, J. E. (2000). Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). *Aquatic Conservation: Marine and Freshwater Ecosystems*, 10(5), 323–352. http://doi.org/10.1002/1099

Jassby, A. D., Cloern, J. E., & Cole, B. E. (2002). Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem. *Limnology and Oceanography*, 47(3), 698–712. http://doi.org/10.4319/lo.2002.47.3.0698

Jeffres, C. A., Opperman, J. J., & Moyle, P. B. (2008). Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environmental Biology of Fishes*, 83(4), 449–458. http://doi.org/10.1007/s10641-008-9367-1

Junk, W. J., & Wantzen, K. M. (2004). The Flood Pulse Concept: New Aspects, Approaches and Applications—An Update, 1–25.

Katz, J. V. E., Jeffres, C., Conrad, J. L., Sommer, T. R., Martinez, J., Brumbaugh, S., et al. (2017). Floodplain farm fields provide novel rearing habitat for Chinook salmon. *PloS One*, 12(6). http://doi.org/10.1371/journal.pone.0177409

Keckeis, S., Baranyi, C., Hein, T., Holarek, C., Riedler, P., & Schiemer, F. (2003). The significance of zooplankton grazing in a floodplain system of the River Danube. J*ournal of Plankton Research*, 25(3), 243–253.

Kendall, C., Elliott, E. M., & Wankel, S. D. (2007). Tracing Anthropogenic Inputs of Nitrogen to Ecosystems. In R. H. Michener & K. Lajtha (Eds.), Stable Isotopes in Ecology and Environmental Science (Second, pp. 375–449). Oxford, UK.

Kendall, C., Silva, S. R., & Kelly, V. J. (2001). Carbon and nitrogen isotopic compositions of particulate organic matter in four large river systems across the United States. *Hydrological Processes*, 15(7), 1301–1346. http://doi.org/10.1002/hyp.216

Koehler, B., Wachenfeldt, von, E., Kothawala, D., & Tranvik, L. J. (2012). Reactivity continuum of dissolved organic carbon decomposition in lake water. *Journal of Geophysical Research: Biogeosciences*, 117, G01024. http://doi.org/10.1029/2011JG001793

Lehman, P. W., Sommer, T. R., & Rivard, L. (2008). The influence of floodplain habitat on the quantity and quality of riverine phytoplankton carbon produced during the flood season in San Francisco Estuary. *Aquatic Ecology*, 42, 363–378. http://doi.org/10.1007/s10452-007-9102-6

Liénart, C., Susperregui, N., Rouaud, V., Cavalheiro, J., David, V., Del Amo, Y., et al. (2016). Dynamics of particulate organic matter in a coastal system characterized by the occurrence of marine mucilage – A stable isotope study. *Journal of Sea Research,* 116(C), 12–22. http://doi.org/10.1016/j.seares.2016.08.001

Lobbes, J. M., Fitznar, H. P., & Kattner, G. (2000). Biogeochemical Characteristics of Dissolved and Particulate Organic Matter in Russian Rivers Entering the Arctic Ocean. *Geochimica Et Cosmochimica Acta*, 64(17), 2973–2983.

Lund, J. R., Hanak, E., Fleenor, W. E., & Howitt, R. E. (2007). Envisioning futures for the Sacramento-San Joaquin delta. Public Policy Institute of CA.

Mac Nally, R., Thomson, J. R., Kimmerer, W. J., Feyrer, F., Newman, K. B., Sih, A., et al. (2010). Analysis of pelagic species decline in the upper San Francisco Estuary using multivariate autoregressive modeling (MAR). *Ecological Applications*, 20(5), 1417–1430. http://doi.org/10.1890/09-1724.1

Macko, S. A., & Estep, M. L. F. (1984). Microbial alteration of stable nitrogen and carbon isotopic compositions of organic matter. *Organic Geochemistry*, 6, 787–790.

Mitrovic, S. M., & Baldwin, D. S. (2016). Allochthonous dissolved organic carbon in river, lake and coastal systems: transport, function and ecological role. *Marine and Freshwater Research*, 67, 5–9. http://doi.org/10.1071/MFv67n9_ED

Moyle, P. B., & Mount, J. F. (2007). Homogenous rivers, homogenous faunas. *PNAS*, 104(14), 5711–5712.

Moyle, P. B., Bennett, W. A., Durand, J. R., Fleenor, W. E., Gray, B., Hanak, E., et al. (2012). Where the Wild Things Aren't: Making the Delta a Better Place for Native Species (pp. 1–55). *Public Policy Institute of California.*

Moyle, P. B., Katz, J. V. E., & Quiñones, R. M. (2011). Rapid decline of California's native inland fishes: A status assessment. *Biological Conservation*, 144, 2414–2423. http://doi.org/10.1016/j.biocon.2011.06.002

Müller-Solger, A. B., Jassby, A. D., & Müller-Navarra, D. C. (2002). Nutritional quality of food resources for zooplankton (Daphnia) in a tidal freshwater system (Sacramento-San Joaquin River Delta). Limnology and *Oceanography*, 47(5), 1468–1476. http://doi.org/10.4319/lo.2002.47.5.1468

Ngugi, C. C., Oyoo-Okoth, E., Gichuki, J., Gatune, C., & Mwangi-Kinyanjui, J. (2016). Fingerprints of upstream catchment land use in suspended particulate organic matter (SPOM) at the river discharge sites in Lake Victoria (Kenya): insights from element, stable isotope and lipid biomarker analysis. *Aquatic Sciences*, 79(1), 73–87. http://doi.org/10.1007/s00027-016-0480-5

Ock, G., & Takemon, Y. (2013). Effect of reservoir-derived plankton released from dams on particulate organic matter composition in a tailwater river (Uji River, Japan): source partitioning using stable isotopes of carbon and nitrogen. *Ecohydrology*, 21, n/a–n/a. http://doi.org/10.1002/eco.1448

Onstad, G. D., Canfield, D. E., Quay, P. D., & Hedges, J. I. (2000). Sources of Particulate Organic Matter in Rivers from the Continental USA: Lignin

phenol and Stable Carbon Isotope Compositions. *Geochimica Et Cosmochimica Acta*, 64(20), 3539–3546.

Opperman, J. J. (2012). A Conceptual Model for Floodplains in the Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science*, 10(3). http://doi.org/10.15447/sfews.2012v10iss3art4

Opperman, J. J., Luster, R. A., McKenney, B. A., Roberts, M., & Meadows, A. W. (2010). Ecologically Functional Floodplains: Connectivity, Flow Regime, and Scale. *Journal of the American Water Resources Association*, 46(2), 211–226. http://doi.org/10.1111/j.1752-1688.2010.00426.x

Paillex, A., Dolédec, S., Castella, E., & Mérigoux, S. (2009). Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. *Journal of Applied Ecology*, 46(1), 250–258. http://doi.org/10.1111/j.1365-2664.2008.01593.x

Paillex, A., Dolédec, S., Castella, E., Mérigoux, S., & Aldridge, D. C. (2012). Functional diversity in a large river floodplain: anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity. *Journal of Applied Ecology*, 50(1), 97–106. http://doi.org/10.1111/1365-2664.12018

Pander, J., Mueller, M., & Geist, J. (2015). Succession of fish diversity after reconnecting a large floodplain to the upper Danube River. *Ecological Engineering*, 75, 41–50. http://doi.org/10.1016/j.ecoleng.2014.11.011

Pearson, A. J., Pizzuto, J. E., & Vargas, R. (2016). Influence of run of river dams on floodplain sediments and carbon dynamics. *Geoderma*, 272(C), 51–63. http://doi.org/10.1016/j.geoderma.2016.02.029

Pingram, M. A., Collier, K. J., Hamilton, D. P., Hicks, B. J., & David, B. O. (2012). Spatial and temporal patterns of carbon flow in a temperate, large river food web. *Hydrobiologi*a, 729(1), 107–131. http://doi.org/10.1007/s10750-012-1408-2

Poff, N. L., & Zimmerman, J. K. H. (2009). Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, 55, 194–205. http://doi.org/10.1111/j.1365-2427.2009.02272.x

Poff, N. L., Olden, J. D., Merritt, D. M., & Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences*, 104(14), 5732–5737.

Preiner, S., Drozdowski, I., Schagerl, M., Schiemer, F., & Hein, T. (2008). The significance of side-arm connectivity for carbon dynamics of the River Danube, Austria. *Freshwater Biology*, 53, 238–252. http://doi.org/10.1111/j.1365-2427.2007.01888.x

Rachold, V., & Hubberten, H. W. (1999). Carbon Isotope Composition of Particulate Organic Material in East Siberian Rivers. In R. E. Aalto, H. Kassens, H. A. Bauch, I. A. Dmitrenko, H. Eicken, H. W. Hubberten, et al. (Eds.), Land-Ocean Systems in the Siberian Arctic (pp. 223–238). Springer-Verlag.

Rood, S. B., Samuelson, G. M., Braatne, J. H., Gourley, C. R., Hughes, F. M., & Mahoney, J. M. (2005). Managing river flows to restore floodplain forests. *Frontiers in Ecology and the Environment*, 3(4), 193–201.

Schemel, L. E., Sommer, T. R., Müller-Solger, A. B., & Harrell, W. C. (2004). Hydrologic variability, water chemistry, and phytoplankton biomass in a large floodplain of the Sacramento River, CA, U.S.A. *Hydrobiologia*, 513, 129–139.

Schiemer, F., Keckeis, S., Reckendorfer, W., & Winkler, G. (2001). The “inshore retention concept” and its significance for large rivers. *Large Rivers*, 12(2), 509–516.

Schlacher, T. A., & Connolly, R. M. (2014). Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: a review and synthesis. *Methods in Ecology and Evolution*, 5(6), 541–550. http://doi.org/10.1111/2041-210X.12183

Sheibley, R. W., Ahearn, D. S., & Dahlgren, R. A. (2006). Nitrate loss from a restored floodplain in the Lower Cosumnes River, California. *Hydrobiologia*, 571(1), 261–272. http://doi.org/10.1007/s10750-006-0249-2

Sobczak, W. V., Cloern, J. E., Jassby, A. D., Cole, B. E., Schraga, T. S., & Arnsberg, A. (2005). Detritus fuels ecosystem metabolism but not metazoan food webs in San Francisco estuary's freshwater delta. *Estuarie*s, 28(1), 124–137. http://doi.org/10.1007/BF02732759

Sommer, T. R., Armor, C., Baxter, R. D., Breuer, R., Brown, L. R., Chotkowski, M., et al. (2007). The Collapse of Pelagic Fishes in the Upper San Francisco Estuary. *Fisheries*, 32(6), 270–277. http://doi.org/10.1577/1548-8446(2007)32

Stoffels, R. J., Clarke, K. R., Rehwinkel, R. A., & McCarthy, B. J. (2014). Response of a floodplain fish community to river-floodplain connectivity: natural versus managed reconnection. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(2), 236–245. http://doi.org/10.1139/cjfas-2013-0042

Swenson, R. O., Whitener, K., & Eaton, M. (2003). Restoring floods on floodplains: riparian and floodplain restoration at the Cosumnes River Preserve. *California Riparian Systems*.

Taipale, S. J., Brett, M. T., Hahn, M. W., Martin-Creuzburg, D., Yeung, S., Hiltunen, M., et al. (2014). Differing Daphnia magna assimilation efficiencies for terrestrial, bacterial, and algal carbon and fatty acids. *Ecology*, 95(2), 563–576.

Taipale, S. J., Galloway, A. W. E., Aalto, S. L., Kahilainen, K. K., Strandberg, U., & Kankaala, P. (2016). Terrestrial carbohydrates support freshwater zooplankton during phytoplankton deficiency. *Nature*, 1–15. http://doi.org/10.1038/srep30897

Thibodeau, B., Hélie, J.-F., & Lehmann, M. F. (2013). Variations of the nitrate isotopic composition in the St. Lawrence River caused by seasonal changes in atmospheric nitrogen inputs. *Biogeochemistry*, (115), 287–298. http://doi.org/10.1007/s10533-013-9834-4

Thorp, J. H., & Bowes, R. E. (2016). Carbon Sources in Riverine Food Webs: New Evidence from Amino Acid Isotope Techniques. *Ecosystems,* 20, 1029–1041. http://doi.org/10.1007/s10021-016-0091-y

Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: present state and future trends. *Environmental Conservation*, 29(03), 1–23. http://doi.org/10.1017/S037689290200022X

Torres-Ruiz, M., Wehr, J. D., & Perrone, A. A. (2007). Trophic relations in a stream food web: importance of fatty acids for macroinvertebrate consumers. *Journal of the North American Benthological Society*, 26(3), 509–522. http://doi.org/10.1899/06-070.1

US Bureau of Reclamation. (2017). Delta Cross Channel Fact Sheet (pp. 1–2). Mid-Pacific Region Public Affairs.

Wantzen, K. M., de Arruda Machado, F., Voss, M., Boriss, H., & Junk, W. J. (2002). Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. *Aquatic Sciences - Research Across Boundaries*, (64), 239–251.

Welti, N., Bondar-Kunze, E., Mair, M., Bonin, P., Wanek, W., Pinay, G., & Hein, T. (2012). Mimicking floodplain reconnection and disconnection using 15N mesocosm incubations. *Biogeosciences*, 9(11), 4263–4278. http://doi.org/10.5194/bg-9-4263-2012

Wohl, E., Bledsoe, B. P., Jacobson, R. B., Poff, N. L., Rathburn, S. L., Walters, D. M., & Wilcox, A. C. (2015). The Natural Sediment Regime in Rivers: Broadening the Foundation for Ecosystem Management. *BioScience*, 65(4), 358–371. http://doi.org/10.1093/biosci/biv002

Yamashita, Y., McCallister, S. L., Koch, B. P., Gonsior, M., & Jaffé, R. (2015). Dynamics of dissolved organic matter in fjord ecosystems: Contributions of terrestrial dissolved organic matter in the deep layer. *Estuarine, Coastal and Shelf Science*, 159(C), 37–49. http://doi.org/10.1016/j.ecss.2015.03.024

Young, A. (2017). McCormack Williamson Tract Project Aims to Protect People and Wildlife. Retrieved from: http://resources.ca.gov/ecorestore/2019/01/mccormack-williamson-tract-project-aims-to-protect-people-and-wildlife/

Chapter 2

Dietary Sources of Amino Acids in Fish from the Cosumnes River: Evidence from Compound Specific Isotope Analysis

Bobby J. Nakamoto

Introduction

Estuaries globally are some of the most degraded and imperiled ecosystems (Lotze et al. 2008). The Sacramento-San Joaquin River Delta (SSJD) is one of the most geomorphologically, ecologically, and hydrodynamically altered and managed system on the planet. Unfortunately, the ecology of native fish in the SSJD is intertwined with the human-impacted hydrology and geomorphology, to the detriment of the fish (Kiernan & Moyle, 2012; Moyle, 1995; Moyle et al., 2016; Moyle & Mount, 2007). Losses of important intertidal wetlands, and other off-channel habitats (i.e. floodplains), exacerbated by exotic species invasions, have resulted in ongoing declines in native fish populations (T. R. Sommer et al., 2007).

A native fish of conservation concern is the Chinook salmon (*Oncorhynchus tshawytscha*). Chinook salmon are an economically, and culturally, significant fish species; however, populations are dwindling and significantly bolstered by hatchery operations (Moyle et al. 2011). Anadromous Chinook salmon migrate inland from the ocean, through the SSJD, to spawn. After emergence, wild juveniles rear in freshwater habitats whilst emigrating downstream, passing through estuary habitat towards the ocean. Ideally, this out-migration coincides with the seasonal activation of floodplain habitat which provides productive rearing habitat for the juveniles (T. R. Sommer et al., 2001, 2005). The resources assimilated during this period are important to early

growth, which is a good predictor of successful recruitment to adulthood (Unwin et al. 1997, McCormick et al. 1998). Chinook salmon, have life histories adapted to exploitation of high primary productivity during seasonal floodplain activation (Moyle et al., 2007). Although, detrital food web subsidies might also potentiate significant growth in some individuals (Jeffres et al., 2020).

Phytoplankton are thought to be the most important basal resource for fish in the SSJD, mostly due to their high nutritional content (e.g. highly unsaturated fatty acids). Allochthonous and detrital carbon is thought to have lower assimilation efficiency than algae, and can contain toxic components. Therefore, reductions in phytoplankton productivity in the SSJD are implicated in the demise of native fishes. In contrast to this idea, estimates for phytoplankton production in the delta have trended upwards even during periods when fish populations have continued to decline (Jassby, 2008; Jassby et al., 2002). Furthermore, phytoplankton productivity was historically a relatively small part of the delta's annual production (Cloern et al., 2016). It seems alternatives to phytoplankton, such as emergent macrophytes, are already utilized widely in some habitats (e.g. tidal wetlands) that would have been more abundant in the historical SSJD (Cloern et al., 2016; Grimaldo et al., 2009; E. R. Howe & Simenstad, 2011; Sobczak et al., 2005; Young et al., 2020). The extent to which these resources might be exploited by seasonal SSJD users, such as Chinook, is unknown. Year-

round resident fish might interact with these alternative basal carbon sources more frequently due to the ephemerality of high pelagic production in the SSJD.

The characteristics of available organic matter (OM) in the SSJD are spatiotemporally heterogeneous. As most top consumers are mobile, they are theoretically capable of accessing a wide array of OM. In general, fish feed at a higher trophic level than invertebrate communities, despite the presence of plant matter in fish gut contents. Thus, invertebrates link fish to their basal carbon sources. Invertebrates also more commonly exhibit reliance on a single basal carbon source than fish, which presumably have easier access to a wider range of resources (Young et al., 2020). Invertebrates are relatively immobile, have less plastic foraging capabilities, and are impacted by local biophysical and hydrological conditions; these factors limit invertebrate diet to an accessible subset of local resources. By feeding on a small array of invertebrates, fish might assimilate OM from multiple basal carbon sources. Presumption of low assimilation efficiency for amorphous vegetative material gives invertebrates, and other fish, precedence in consideration as a significant source of nutrition when identified in fish stomach contents. Whether or not inconspicuous components of the vegetation found in fish gut contents (i.e. fungal or microbial biomass) might contribute significantly is not fully resolved. Furthermore, these same inconspicuous components might contribute to the nutrition of lower trophic level invertebrates also.

The most important resource for consumers seems to be environment dependent in the SSJD. Open water habitats tend towards significant pelagic production (i.e. phytoplankton) while consumers in habitats with high macrophyte abundance, naturally, are exposed to increased inputs from those plants (Lehman et al., 2008; Schroeter et al., 2015; Young et al., 2020). Overlaying the balance between differing basal carbon sources is the role that heterotrophic recycling of those sources (i.e. detrital food webs) might play in providing OM to invertebrates and fish (Jeffres et al., 2020). Increased understanding of the sources of nutrition for fish in SSJD is necessary to help natural resource managers and conservation practitioners prioritize and implement successful management actions.

Approach

While the dietary habits of some organisms can be described readily—observationally, most organisms have diets that are more difficult to accurately describe. Characterizing diet, and nutrition, can be complicated by an inability to make long term observations in the wild, to discover cryptic prey, or to disentangle the nutritional significance of multiple dietary items (Newsome et al., 2007, 2010).

Two of the most common methods applied to study diet are bulk stable isotope analysis of carbon and nitrogen (BSIA) and gut-content analysis (GCA).

BSIA works because consumers assimilating carbon and nitrogen from dietary items have isotopic compositions resembling that of their diet with well described trophic fractionation. Trophic structure can be elucidated by comparing the isotopic compositions of consumers and potential food sources. However, the relationship can be noisy, because dietary items are not always isotopically differentiated enough to apply mixing models, and specific information about the source of biomolecules is not obtained.

Gut content analysis, on the other hand, has the benefit of providing unequivocal evidence that a particular dietary item was consumed the date the fish was captured. Unfortunately, GCA is labor intensive and can overestimate the importance of less nutritive, but common or conspicuous dietary items, while underestimating the significance of less prominent, but nutritionally dense, food sources (e.g. microbes). Individual success can be reduced, even if sufficient foods to meet energetic needs are consumed, if sufficient amounts of diet-essential biomolecules are not consumed.

It is useful, here, to establish a distinction between an organism's nutrition and its diet. The diet could be considered the sum total of items consumed by an organism. Nutrition, on the other hand, is concerned with the role that dietary items play in supplying the specific vitamins, minerals, and macromolecules an organism needs to survive and grow. At the most basic level, lipids, carbohydrates, and proteins categorize the macromolecules comprising all

dietary items. Consumers, by definition, are required to seek out foods that meet their nutritional requirements of these macromolecules in order to survive and reproduce. After consumption, OM can either be excreted, metabolized, or assimilated into biomass without alteration.

The transfer of unaltered biomolecules between trophic levels is known as routing (O'Brien et al., 2002). Routing results in a traceable, and nutritionally significant link between consumers and dietary items. Furthermore, unaltered biomolecules may be routed directly through multiple trophic levels (Chikaraishi et al., 2011). The continued unaltered transfer of these biomolecules during trophic transfers not only links adjacent trophic links (predator -> prey) but also allows for the linking of top predators with the basal sources supporting them when they are separated by multiple trophic levels. To meet demand, however, routing is more necessary for some biomolecules than others (Newsome et al., 2014).

In general, consumers are unable to synthesize a subset of biomolecules that are indispensable to cell function *de novo*. These biomolecules are usually termed, diet- essential (essential, or indispensable). Alternatively, they can be synthesized, but not in sufficient amounts to meet demand or only if a certain precursor is provided in the diet as well (i.e. "conditionally essential"). For most animals, certain amino acids are essential (EAA). For optimal growth and reproduction these EAA must be present in the diet or supplied by microbiota in

the gut. The inability of higher organisms (e.g. fish) to synthesize some amino acids necessitates that their entire pool of these compounds derives from routed biomolecules produced at lower trophic levels, or gut microbiota (Newsome et al., 2020).

An emerging tool used to characterize the source of amino acids comprising consumer tissues, and thus consumer diet, is compound specific isotope analysis of amino acids (CSIA-AA). CSIA-AA provides more specific information than BSIA by determining the isotope composition of individual molecules rather than entire tissues. The utility of CSIA-AA in characterizing the significance of possible basal protein sources to consumers derives from two phenomena: 1) the potential for routing of unaltered amino acids (AA) between trophic levels and, 2) taxonomic differences in metabolism driving, so-called, "AA-Fingerprints." AA-fingerprinting generally refers to measuring and exploiting of the diagnostic patterns of isotope fractionation associated with varying metabolism across/within different taxonomic groups.

Scott et al. (2006) found that CSIA-AA could elucidate variations in microbial metabolism when the carbon isotope composition of amino acids in microbial cultures was analyzed with discriminant function analysis. The key of this methodology is the use of supervised machine learning techniques to analyze the patterns and differences in amino acid carbon isotopes (AA-δ^{13}C) amongst groups. Larsen et al. (2009) applied this concept in a natural system to

differentiate basal sources of carbon to consumers (e.g., Plant, Fungal, Bacterial), as well as corroborate known insect diets through a comparison of $\delta^{13}C$ of AA in dietary items with those in consumers. Since then, this methodology has been applied to a diverse array of questions involving carbon sources supporting consumers in riverine (Bowes & Thorp, 2015; Thorp & Bowes, 2016), mangrove (Larsen et al., 2012) and marine and coastal systems (Larsen et al., 2015; McMahon et al., 2016; Smith et al., 2018), as well as aquaculture authentication (Wang et al., 2018) and arctic invertebrate nutrition (Larsen et al., 2016). Usually, linear discriminant analysis (LDA) is used to generate classification functions based on AA-$\delta^{13}C$.

Objectives

Here, we present results from bulk and compound specific isotope analysis of juvenile Chinook salmon, as well as other co-located consumers, in the SSJD. We also present data on particulate organic matter and sources of primary production collected from the same region to contextualize our results from consumers. We then compare our data to prior CSIA-AA measurements using LDA and an open-access Bayesian mixing model (FRUITS; (Fernandes et al., 2014)) in order to estimate the importance of different basal carbon sources to fish, in turn, assessing whether multiple pathways operate together to fuel secondary production or if a single basal source dominates.

Methods

Fish

Our samples come from the same region in the SSJD, however, they were collected and analyzed as part of separate sampling efforts (Appendix 2.1a and b). Cosumnes (2016) fish were captured by fyke netting floodplain habitat in the Cosumnes river watershed during Winter of water year 2016. McCormack-Williamson Tract (MWT; 2017) fish samples were collected after being stranded in off-channel habitat. Inundation of the MWT was the result of a levee failure and stranding occurred after the subsequent repair of the levee during the 2017 water year. MWT is a short distance (10 km) downstream from the Cosumnes site. Cosumnes (2018) fish were captured via fyke netting in the same area that Cosumnes (2016) fish were captured, during water year 2018.

Only a subset of Chinook salmon analyzed for this study came from field sampling of wild individuals. All wild salmon analyzed in this study were out-migrating juveniles captured via fyke netting on inundated floodplains within the Cosumnes river watershed (CA, USA). We also received a subset of tissue samples (Delta, 2019) from experimentally enclosed Chinook juveniles sourced from a hatchery (Jeffres et al. in prep). The experimentally enclosed individuals' tissues were sampled after having been incubated in different, natural, habitats as part of a study on juvenile salmonid growth in the SSJD. These experimental individuals were enclosed in SSJD habitats for 45 days to allow their diet and

tissues to approach steady state before being sacrificed. Fish tissue samples were collected as dorsal muscle tissue. In all cases, tissue samples were stored frozen until lyophilization and analysis.

Species	FL (mm)	n	Origin
Chinook	79.4 ± 9.4	5	Cosumnes, 2016
Striped Bass	267	1	Cosumnes, 2016
Chinook	68 ± 11.8	16	Cosumnes, 2018
Chinook	NA	10	Delta, 2019
Bluegill	97.5 ± 8.1	4	MWT, 2017
Bullhead	202.7 ± 12.5	3	MWT, 2017
Crappie	112, 114	2	MWT, 2017

Table 2.1. Description of fish analyzed in this study. Body size data was not collected for the subset of Delta, 2019 fish analyzed. However, they were similar in size to individuals sampled prior.

Plankton and Invertebrates

Planktonic organisms for isotope analysis were collected from the same sites as fish using tows of 5 minutes each. A 0.3 m. diameter 50-μM. mesh plankton net was deployed stationary in the current within 1 meter of the surface. Upon collection, samples were concentrated into 250 mL Teflon bottles using DI water for transport and storage. Samples were stored frozen.

In the lab, invertebrates were identified to the lowest taxonomic level possible using relevant keys and phytoplankton cells were separated for isotope analysis with the aid of a dissecting microscope (Thorp & Covich, 2010). To obtain sufficient biomass for isotope analysis, individual organisms were pooled. When possible, taxa were pooled by sampling event for analysis. However, for

small organisms this was only possible for common taxa with high abundance during sampling, i.e. cladocera and copepoda. Often, invertebrates collected from a single tow were pooled and analyzed together as zooplankton. After separation, invertebrate samples were freeze-dried before preparation for isotope analysis.

Particulate Organic Matter and Producers

Archived POM samples collected from the MWT were used in this study (Nakamoto et al. 2020). Briefly, surface waters were passed through precombusted 0.2-μM pore size glass fiber filters until the filter reached impermeability. Extraneous glass fiber was removed and filters containing POM were dried at 50°C overnight, and stored frozen in precombusted aluminum foil. To ensure adequate material for AA analysis, multiple (4) filters were pooled for each analysis (Appendix 2.2a, b, and c).

Samples of primary producers and organic litter were taken by hand in the field, rinsed with DI water, and transported to the lab in Whirl-Pak bags, or Falcon tubes. All higher plant and algae samples were collected near MWT in water year 2017. Primary producer samples were dried at 50°C overnight, and ground to powder using a mortar and pestle.

Bulk Isotope Analysis

Dried samples were weighed into tin boats for stable isotope analysis. Carbon and nitrogen isotopic analyses were conducted at the University of California Merced Stable Isotope Laboratory using a continuous flow setup comprised of a Costech 4010 elemental analyzer with a zero-blank auto-sampler connected to a Delta V-Plus isotope ratio mass spectrometer via a Conflo-IV open split interface (Thermo-Fisher Scientific; Waltham, MA, USA). Measurements of $\delta^{13}C$ and $\delta^{15}N$ were done on single samples with standards placed throughout each run. Results are reported in standard delta notation relative to the international standards for carbon and nitrogen, Vienna PeeDee Belemnite and atmospheric N_2. In-house standards used for validation were: Acetanelide ($\delta^{13}C$: -27.86‰; $\delta^{15}N$: -0.75‰), EM Soil ($\delta^{13}C$: -27.6‰; $\delta^{15}N$: -1.7‰), and Peach Leaf ($\delta^{13}C$: -25.99‰; $\delta^{15}N$: 1.98‰). C:N ratios were calculated based on the known C/N content of the acetanilide standard (71.09 %C; 10.36 %N) and are reported as atomic ratios. Within run precision for standard materials is ≤ 0.5 and 0.1 ‰ (1 σ) for nitrogen and carbon, respectively.

Amino Acid Analysis

Lyophilized samples of consumer and producer tissue, or oven-dried POM filters were hydrolyzed in 6N HCl at 110°C for 20 hrs. Free amino acids were then reacted with acidified 2-isopropanol, followed by esterification with N-trifluoracetic

acid anhydride to produce their N-trifluoroacetate/isopropyl ester derivatives (Silfer et al. 1991). Amino acid derivatives were analyzed in triplicate for $\delta^{13}C$ on a Thermo Scientific Delta V Plus IRMS interfaced to a Trace 1310 gas chromatograph via Isolink II and Conflo IV interfaces (Thermo-Fisher Scientific; Waltham, MA, USA) in the EDGE Stable Isotope Lab, UC Riverside (2017, 2018, 2019 samples) and UC Merced (2016 samples). Amino acids were separated on a BPX-5 GC column (SGE Analytical; Ringwood, Victoria, Australia) with a 0.32 mm ID and a film thickness of 1μm. The injector was held at 250°C and operated in Split/Splitless mode. Splitless time was 1 minute for injections. The oven was 50°C and held for 2 minutes during injection. After 2 minutes, a ramp rate of 15°C/min was applied until the oven reached 125°C, after which the ramp rate was decreased to 3°C/min until 160°C. The ramp rate was then increased again to 4°C/min until 190°C. Then the ramp rate increased again to 6°C/min until it reached 275°C. A final ramp of 15°C/min increased oven temperature to 320°C before cooling. Combustion of separated AA derivatives to CO_2 for $\delta^{13}C$ analysis was carried out in a nickel-lined ceramic reactor operated at 1000°C. Amino acid working standard materials (Sigma-Aldrich; St. Louis, MO) of known isotopic composition were derivatized and analyzed alongside samples to monitor reproducibility and correct for the inclusion of derivative atoms in our analyte molecules. $\delta^{13}C$ values of standard materials were measured with a Costech 4010 Elemental Analyzer (Valencia, CA, USA) interfaced to a Delta V Plus IRMS. True

amino acid $\delta^{13}C$ values were calculated using the following equation: $\delta^n X_{Sample} = (\delta^n X_{DSam} - \delta^n X_{DStd} + \delta^n X_{MStd} * p_{Std}) / p_{Std}$. Where $\delta^n X_{DSam}$ is the value of the derivatized sample, $\delta^n X_{DStd}$ is the value of the derivatized standard, $\delta^n X_{MStd}$ is the value of the standard-underivatized, and p_{Std} is the proportion of atoms in the derivative molecule that derive from the precursor amino acid. The isotope ratio of Alanine (Ala), Glycine (Gly), Threonine (Thr), Serine (Ser), Valine (Val), Leucine (Leu), Isoleucine (Ile), Proline (Pro), Aspartic Acid/Aspartate (Asx), Glutamic Acid/Glutamate (Glx), Phenylalanine (Phe), and Lysine (Lys) were measured with this method. Within run standard deviations for standard materials ranged from 0.46 for Ala, Gly, and Thr up to 0.73 for Ile (n=78).

Published Values

Literature values used to construct our LDA model were obtained from prior publications of $\delta^{13}C$ analysis of amino acids (Appendix 2.3). These values were originally published with taxonomic information of varying detail. We recoded the taxonomic complexity to four classes to facilitate interpretation in our system: Algae, Bacteria, Fungi, and Plants. In total, we used previously published $\delta^{13}C$ values for eight amino acids (Ala, Gly, Glx, Asx, Phe, Val, Leu, Ile) (Larsen 2012, Larsen 2009, Larsen 2013, Thorp 2016). Some publications report $\delta^{13}C$ values for AA not listed here, however, we narrowed our data

selection to result in a reference dataset with no gaps or incomplete rows to minimize imputation.

LDA Model

Amino acid $\delta^{13}C$ values were z-scaled, grouping the AA within each sample, prior to LDA to obviate differences in $\delta^{13}C$ derived from differences in local inorganic carbon isotope values (e.g., differing baseline) and to more closely assess patterns across individuals. To ensure that our datasets (i.e., literature values and data from this study) would be normalized/standardized to a comparable cellular metabolite pool we excluded Thr, Ser, Lys, and Pro before LDA analysis. LDA model construction was done in two steps: exploratory model parameterization, and final model construction and validation. In all cases, we used the *lda* function from the MASS package to generate discriminant functions which could estimate source class as a function of amino acid $\delta^{13}C$. In practice, these discriminant functions are linear functions of AA values that maximize intergroup variance, and minimize intra-group variance. A stepwise approach was used to identify the combination of variables most effective at differentiating our source groups (Algae, Bacteria, Fungi, Plants). That is to say, a separate model for each combination of predictor variables ($\delta^{13}C$-AA) was constructed. This model was trained using only the previously published $\delta^{13}C$-AA and the accompanying information on taxonomy. The array of models generated in this

fashion were compared using leave-one-out (LOO) cross-validation; the model was iteratively trained, excluding a single data point each time, and the models ability to correctly identify the class membership of the excluded point was measured. Data are not replaced, so the model was iterated N times and each sample was left out once. A model with 90% leave-one-out validation accuracy correctly identified the class of 90% of 'left-out' samples. The variables (AA) used in the model with the highest validation accuracy were retained.

After the most effective combination of variables was determined, the final model was trained using that same combination of variables, but incorporating the entire dataset. We then projected our standardized $\delta^{13}C$ values from producers, consumers, and POM into our linear discriminant space to estimate source class membership (Algae, Bacteria, Fungi, Plants) for our consumers, producers, and POM based on their $\delta^{13}C$-AA. Significance of group differences were assessed using MANOVA (Pillai-Bartlett Trace).

Statistical Analysis

All statistical analyses were performed in R (R Core Team, 2019). Normality of variables was checked through visual inspection of Q-Q plots. Data from each isotope, for groups from bulk data (i.e. fish, invertebrates, macrophytes) were checked individually. Amino acids were checked individually, as well. Before LDA, we tested for homoscedasticity in AA-$\delta^{13}C$ among groups

using the Fligner-Killeen test. Welch's *t*-test, two-tailed, was used to compare group means except when a paired *t*-test was used. Observations were paired by collection date and location, when possible. Correlation was measured using Pearson's product moment correlation coefficient. Significance was assessed at $p < 0.05$ throughout.

Source Proportion Estimates

In order to provide an estimate of the proportion of the AA pool from each source (Algae, Bacteria, Fungi, or Plants) we used an open source Bayesian mixing model: FRUITS ("Food Reconstruction Using Isotopic Transferred Signals") (Fernandes et al., 2014). We used the mean and standard deviation of AA in our overall source groups (Algae, Bacteria, Fungi, Plants) as source values and their uncertainty, respectively. For samples measured in this study, we used the mean and measurement uncertainty (standard deviation of our triplicate measurement). We used FRUITS to compare mean-centered AA-δ^{13}C data from consumers and POM to that in source groups. As with LDA, we considered the full set of AA for normalization, but only compared the AA identified by the LDA model (i.e. Gly, Ile, Leu, Phe, Val) in FRUITS. FRUITS compares these two sets of values and calculates credible interval estimates for the proportion of the AA pool coming from each source.

Posterior probabilities of source membership for our consumer and POM samples generated by our LDA could also be considered point estimates for the proportional contributions from potential sources (Fox et al., 2019; Smith et al., 2018) Our posterior probabilities for class membership were used to constrain simple priors for the individuals analyzed by the FRUITS mixing model. We provided the prior information that the AA source with the greatest posterior probability in LDA classification for that individual, was likely to contribute the greatest proportion of considered AA's, in that individual. The model was updated through 5000 steps, for burn in, before 10000 sampled updates. Results from the model were collected as credible interval estimates of contributions of individual sources to specific consumer and POM samples.

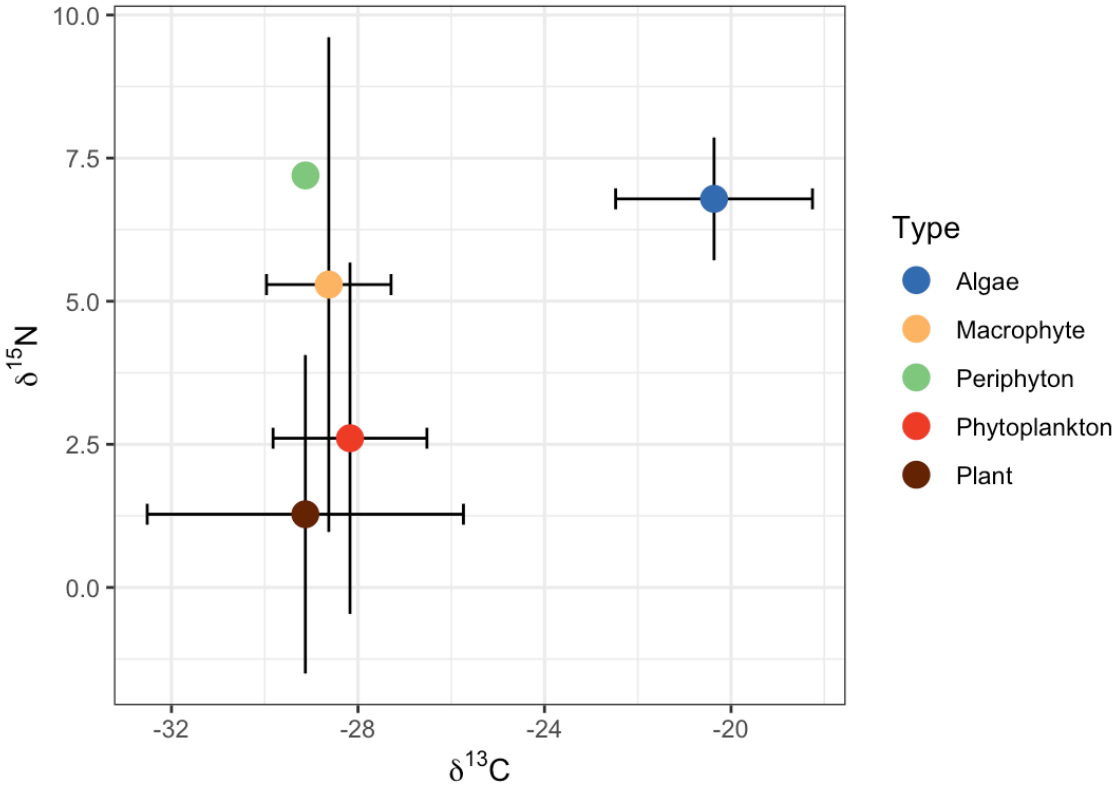

Figure 2.1. Bulk carbon and nitrogen isotope composition of primary producers collected in the Sacramento-San Joaquin Delta (CA, USA).

Results

Bulk Carbon and Nitrogen Isotopes

The measured primary producers' nitrogen and carbon stable isotope composition varied widely from -4.2‰ to 16.9‰ and -33.8‰ to -13.9‰, respectively (Figure 2.1). Phytoplankton samples had $\delta^{13}C$ ranging -33.7‰ and -24.6‰, and $\delta^{15}N$ between -4.2‰ and 12.6‰ (n = 71). There was no significant

negative correlation between the C:N ratio and $\delta^{13}C$ once outliers with high C:N (> 150) were excluded. The macrophytes (n = 17) measured had $\delta^{13}C$ between -31.3‰ and -25.6‰ and $\delta^{15}N$ between -2.7‰ and 17‰. Algae (n=3) had $\delta^{13}C$ between -22.7‰ and -18.6‰ and $\delta^{15}N$ ranging 5.6‰ to 7.8‰. Terrestrial plants (n = 56) had $\delta^{13}C$ ranging -33.8‰ to -13.9‰, and $\delta^{15}N$ between -2.5‰ and 10‰. In general, the distribution of isotope compositions in phytoplankton ($\delta^{13}C$ = -28.2 ± 1.6‰; $\delta^{15}N$ = 2.6 ± 3.1‰), macrophytes ($\delta^{13}C$ = -28.6 ± 1.3‰; $\delta^{15}N$ = 5.3 ± 4.3‰), and terrestrial plants ($\delta^{13}C$ = -29.1 ± 3.4‰; $\delta^{15}N$ = 1.3 ± 2.9‰) overlapped significantly, while attached algae ($\delta^{13}C$ = -20.4 ± 2.1‰; $\delta^{15}N$ = 6.8 ± 1.1‰) were differentiated by higher $\delta^{13}C$.

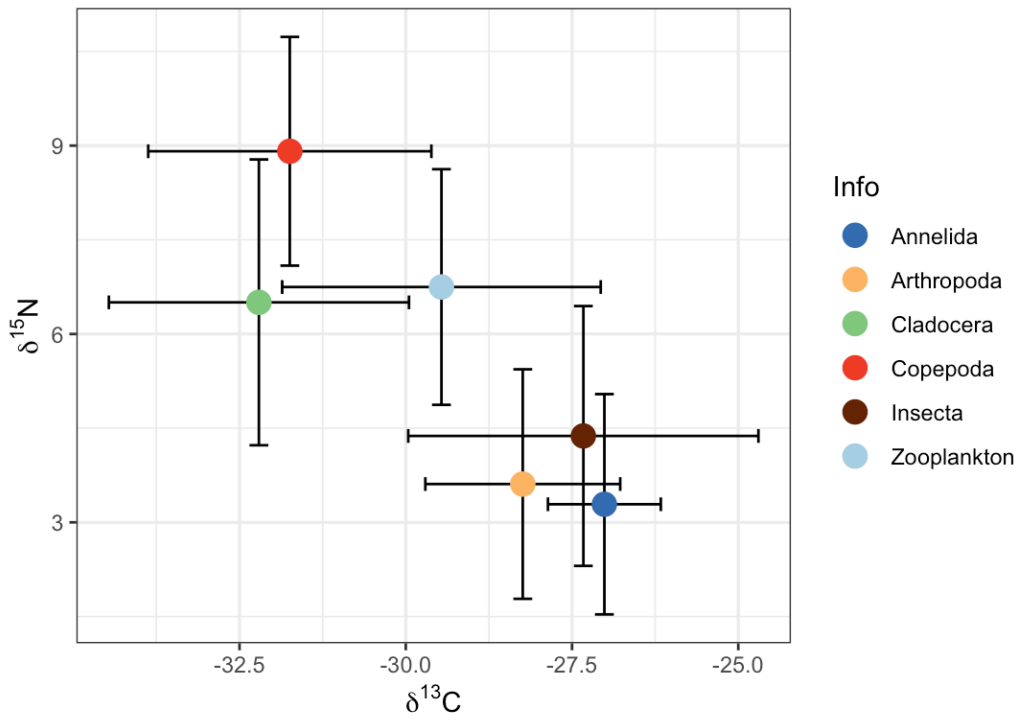

Figure 2.2. Bulk carbon and nitrogen isotope composition of invertebrates collected from the Sacramento-San Joaquin Delta (CA, USA). Nested taxonomic groups are not summarized together. For example, the arthropod group does not include specimens positively identified as insects. Note also that when there was insufficient biomass for taxa-specific analysis, invertebrates from a single date and location were pooled to be analyzed together and coded as zooplankton.

Invertebrates measured had $\delta^{13}C$ between -38.1‰ and -19.3‰, and $\delta^{15}N$ between 1.0‰ and 15.3‰ (Figure 2.2). Cladocerans ($\delta^{13}C$ = -32.2 ± 2.3‰; $\delta^{15}N$ = 6.5 ± 2.3‰ ; n = 42) and copepods ($\delta^{13}C$ = -31.7 ± 2.1‰; $\delta^{15}N$ = 8.9 ± 1.8‰; n= 30) had C:N ratios less than 11 that were uncorrelated to $\delta^{13}C$. Paired samples of cladocera and copepods taken from the same sampling event had similar $\delta^{13}C$; however, $\delta^{15}N$ in cladocera was 3.4‰ to 1.4‰ lower than that found in co-occurring copepods (Paired t-test, n=21; t= -4.9743, p<0.01 95% 3.4‰ to 1.4‰).

Other macroinvertebrates, such as insects ($\delta^{13}C$ = -27.3 ± 2.6‰; $\delta^{15}N$ = 4.4 ± 2.1‰; n = 27), non-insect arthropods ($\delta^{13}C$ = -28.2 ± 1.5‰; $\delta^{15}N$ = 3.6 ± 1.8‰; n = 7), and annelids ($\delta^{13}C$ = -27.0 ± 0.9‰; $\delta^{15}N$ = 3.3 ± 1.8‰; n = 9) generally had lower $\delta^{15}N$ and higher $\delta^{13}C$ than cladocerans and copepods. Mixed zooplankton samples ($\delta^{13}C$ = -29.5 ± 2.4‰; $\delta^{15}N$ = 6.8 ± 1.9‰; n = 99) were generally isotopically intermediate to these two groups, as expected, but most similar to the cladocerans and copepods.

The highest $\delta^{15}N$ and $\delta^{13}C$ values were in fish. Overall, fish $\delta^{13}C$ ranged from -34.7‰ to -19.4‰ and $\delta^{15}N$ ranged from 7.2‰ to 18.1‰ (Figure 2.3). On average, $\delta^{15}N$ in fish (11.2‰) was 4.2‰ to 5.1‰ higher (Welch *t*-test; 95%; $p < 0.01$) than $\delta^{15}N$ in invertebrates (6.5‰). An adult American Shad (*Alosa sapidissima;* FL = 276) had the highest $\delta^{13}C$ and $\delta^{15}N$ in our study, presumably from assimilation of marine resources before inland migration; the next highest $\delta^{15}N$ and $\delta^{13}C$ were found in Striped Bass (*Morone saxatilis*; $\delta^{13}C$ = -24.1 ± 2.9‰; $\delta^{15}N$ = 15.9 ± 1.3‰; FL = 189.2 ± 17.3 ; n = 5). Largemouth Bass (*Micropterus salmoides*; n=1) measurement ($\delta^{13}C$ = -22.5‰; $\delta^{15}N$ = 15.2‰ ; FL = 290 mm) had relatively high $\delta^{13}C$ and $\delta^{15}N$, similar to the Striped Bass measured. On the other hand, Black Crappie (*Pomoxis nigromaculatus*; $\delta^{13}C$ = -32.3 ± 2.0‰; $\delta^{15}N$ = 10.4 ± 0.8‰; FL = 79 ± 8.3 mm ; n = 10) and Golden Shiners (*Notemigonus crysoleucas;* $\delta^{13}C$ = -30.2 ± 0.5‰; $\delta^{15}N$ = 8.6 ± 0.4‰; FL = 88.3 ± 30.2 mm ; n = 3) had some of the lowest $\delta^{13}C$ and $\delta^{15}N$ measured in fish.

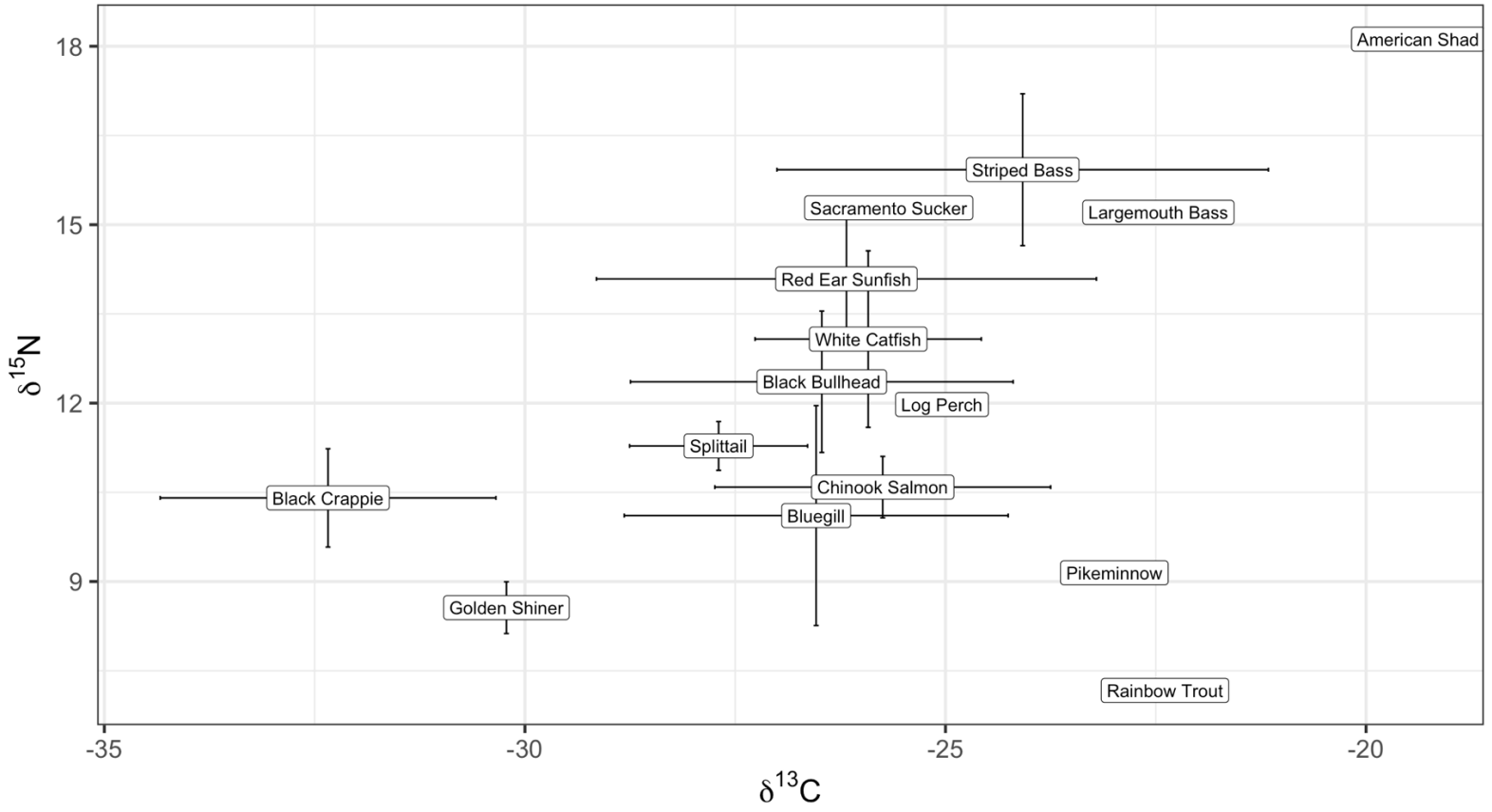

Figure 2.3. Bulk carbon and nitrogen isotope composition of fish collected in the Sacramento-San Joaquin River Delta.

The Chinook salmon (n = 112) analyzed were similarly sized (66.6 ± 8.5 mm) and all had similarly moderate bulk isotope values: $\delta^{13}C$ of -25.7 ± 2.0‰ and $\delta^{15}N$ of 10.6 ± 0.5‰. Sacramento Splittail (*Pogonichthys macrolepidotus;* $\delta^{13}C$ = -27.7 ± 1.1‰; $\delta^{15}N$ = 11.3 ± 0.4‰; n = 10) collected from the disconnected floodplain did not have their length measured, but all seemed to be age-0 juveniles of less than 75 mm standard length. Redear Sunfish (*Lepomis microlophus*; $\delta^{13}C$ = -26.2 ± 3.0; $\delta^{15}N$ = 14.1 ± 1.1‰; FL = 112 ± 19.7 mm ; n = 8) and White Catfish (*Ameirus catus*; $\delta^{13}C$ = -25.9 ± 1.4‰; $\delta^{15}N$ = 13.1 ± 1.5‰; FL = 249.8 ± 55 mm ; n = 10) had slightly higher $\delta^{15}N$, on average, than fish with similar $\delta^{13}C$ as them, such as Bluegill (*Lepomis macrochirus*; $\delta^{13}C$ = -26.5 ± 2.3‰; $\delta^{15}N$ = 10.1 ± 1.9‰; FL = 74.8 ± 6.4 mm ; n = 8) and Black Bullhead (*Ameiurus melas*; $\delta^{13}C$ = -26.5 ± 2.3‰; $\delta^{15}N$ = 12.4 ± 1.2‰; FL = 176.3 ± 18.2 mm ; n = 5). Our measurements of Rainbow Trout (*Oncorhynchus mykiss*; $\delta^{13}C$ = -22.4‰; $\delta^{15}N$ = 7.2‰; FL = 264 mm ; n = 1) and Pikeminnow (*Ptychocheilus oregonensis*; $\delta^{13}C$ = -22.0‰; $\delta^{15}N$ = 9.2‰ ; FL = 51 mm ; n = 1) were unusual, relative to the other fish measured, owing to low $\delta^{15}N$ and high $\delta^{13}C$. On the other hand, our measurements of Log Perch (*Percina sp.*; $\delta^{13}C$ = -25.0‰; $\delta^{15}N$ = 12.0‰ ; FL = 87 mm ; n = 1), and Sacramento Sucker (*Catostomus occidentalis*; $\delta^{13}C$ = -25.7‰; $\delta^{15}N$ = 15.3‰ ; FL = 367 ; n = 1) were similar to other fish analyzed.

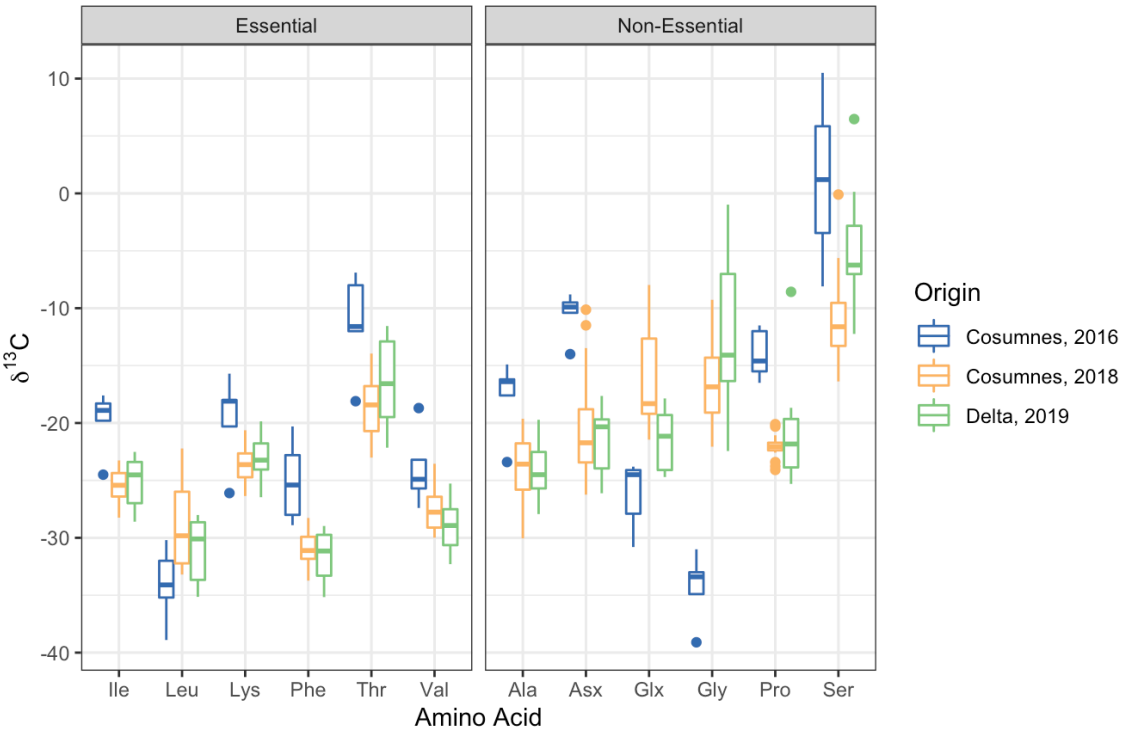

Figure 2.4. Carbon isotope composition of essential and non-essential amino acids in Chinook salmon collected from the Sacramento-San Joaquin River Delta (n=31).

Consumer	Source	n	Gly	Ala	Asx	Glx	Ser
Black Crappie	MWT, 2017	2	-16.8 ± 3.0	-22.7 ± 1.6	-22.5 ± 0.3	-19.9 ± 0.8	-11.0 ± 2.1
Bluegill	MWT, 2017	4	-19.1 ± 3.5	-27.5 ± 2.6	-24.2 ± 2.7	-23.8 ± 1.6	-16.3 ± 4.5
Bullhead sp.	MWT, 2017	3	-19.4 ± 3.0	-25.5 ± 0.7	-25.2 ± 1.5	-22.1 ± 1.4	-15.3 ± 6.1
Chinook Salmon	Cosumnes, 2016	5	-34.3 ± 3.0	-17.7 ± 3.3	-10.5 ± 2.0	-26.2 ± 3.0	1.2 ± 13.2
	Cosumnes, 2018	16	-16.7 ± 3.5	-23.9 ± 2.9	-20.2 ± 5.0	-16.3 ± 4.3	-10.7 ± 4.2
	Delta, 2019	10	-21.5 ± 6.6	-24.2 ± 2.5	-21.5 ± 3.0	-21.5 ± 2.6	-4.6 ± 5.1
Sacramento Splittail	MWT, 2017	6	-22.1 + 1.3	-24.7 ± 2.2	-25.2 ± 1.4	-22.1 ± 1.3	-13.2 ± 1.7
Striped Bass	Cosumnes, 2016	1	-23.7	-12.5	NA	-12.9	-23.2
Zooplankton	Cosumnes, 2016	1	-27.2	-23.7	-30.3	-20.7	-10.2

Table 2.2a. Carbon isotope composition ($\delta^{13}C$) of non-essential amino acids measured in fish.

Consumer	n	Ile	Leu	Lys	Phe	Val	Thr	Pro
Black Crappie	2	-22.2 ± 0.5	-26.6 ± 1.1	-20.6 ± 0.6	-29.3 ± 0.2	-29.1 ± 0.7	-23.7 ± 3.0	-21.6 ± 1.0
Bluegill	4	-28.8 ± 2.1	-35 ± 2.4	-27.8 ± 1.8	-35.9 ± 1.3	-31.4 ± 2.2	-22.9 ± 2.3	-26.6 ± 1.7
Bullhead sp.	3	-24.6 ± 2.2	-28.8 ± 3.4	-22.8 ± 0.7	-31.7 ± 1.2	-30.8 ± 1.4	-26.6 ± 3.3	-24.3 ± 2.3
Chinook Salmon	5	-19.8 ± 2.7	-34.1 ± 3.3	-19.6 ± 4.0	-25.1 ± 3.6	-24.0 ± 3.3	-11.3 ± 4.4	-14.0 ± 2.2
	16	-25.4 ± 1.4	-28.8 ± 3.8	-23.7 ± 1.6	-30.8 ± 1.6	-27.5 ± 1.9	-18.5 ± 2.7	-22.1 ± 1.1
	10	-25.1 ± 2.1	-30.9 ± 2.9	-23.1 ± 2.0	-31.6 ± 2.3	-28.9 ± 2.3	-16.4 ± 3.8	-20.8 ± 4.8
Sacramento Splittail	7	-25.7 ± 2.6	-30.7 ± 4.1	-24.8 ± 3.2	-33.1 ± 2.3	-30.5 ± 0.9	-23.3 ± 1.7	-23.5 ± 1.2
Striped Bass	1	-17.6	-8.0	-23.7	-8.0	-18	-28.8	-19.5
Zooplankton	1	-28.1	-37.3	-10.5	-22.1	-25.8	-31.5	-18.4

Table 2.2b. Carbon stable isotope composition ($\delta^{13}C$) of essential amino acids measured in fish.

Amino Acid C Isotopes

We collected data on 12 amino acids in 49 muscle tissue samples, one mixed zooplankton sample, 9 POM samples and 6 producers (i.e. filamentous algae, macrophytes, and terrestrial vegetation; Appendices 2.4 and 2.5). Our measurements for AA-δ^{13}C in fish muscle spanned from -39.1‰ to 10.5‰ (Figure 2.4; Table 2.2a, and b). In general, non-essential amino acids (i.e. Ala, Gly, Asx, Glx, Pro, Ser) measured had lower δ^{13}C than essential amino acids (i.e. Leu, Ile, Val, Phe, Lys, Thr) (Welch *t*-test; -19.3 vs -26.1; 95% CI Difference 5.7-7.8) and were more variable. Values for δ^{13}C in glycine were the most variable within salmon (~16‰), owing to individuals from 2016 having particularly low Gly-δ^{13}C. In contrast, other essential amino acids from the same fish had relative high δ^{13}C.

LDA and Mixing Model

While many combinations of AA seemed to provide some resolution of the groups we were testing (Algae, Bacteria, Fungi, Plants) we only used the combination of variables which yielded the highest reclassification accuracy of training data points. Our most accurate LDA classification model attained a 91% total reclassification rate using three linear discriminant functions and resulted from inclusion of data on 4 essential amino acids (Leu, Ile, Phe, and Val) and 1 nonessential amino acid (Gly) δ^{13}C values (Appendices 2.6 and 2.7). The first

function captured 52% of the total variance, followed by 37% and 11% in the second and third functions. The model was tested with MANOVA (Pillai trace = 1.7577, $F_{3, 15} = 16.412$, $p < 0.001$) to validate group differences.

When producer data from this study were projected into linear discriminant space, and source class membership was estimated, we found the model correctly identified our local algae sample as algae while categorizing the other producers measured, correctly, as higher plants (Appendix 2.8). Each of the producer samples (n=6) was correctly assigned to its source class with posterior probabilities averaging 0.97 ± 0.4. Performing the same procedure on our data from POM revealed that differing AA sources were dominant contributors of considered amino acids across our POM samples (Appendices 2.9 and 2.10). For example, AA in four out of nine samples were identified as primarily plant derived. On the other hand, fungi were identified as the dominant AA source to our POM three times and algae, only once.

Our mixing model results for POM were mostly consistent with those of the LDA. The mixing model indicated that fungi and bacteria were the major contributors to few samples while algae and higher plants were more pervasive. While the LDA did not indicate that there were any samples that were bacterially dominated, the mixing model did predict that bacteria may have been a major contributor to at least one sample. Overall though, plants had the greatest average estimated contribution to POM samples (Table 2.2). Algae was rarely

identified as the dominant contributor by the mixing model, but was frequently second.

	Mean	SD
Algae	0.15	0.18
Bacteria	0.17	0.29
Fungi	0.16	0.31
Plant	0.52	0.35

Table 2.3. FRUITS estimates for contributions of source classes to particulate organic matter samples.

Class	Posterior	Median
Algae (n=38)	0.91 ± 0.12	0.97
Bacteria (n=4)	0.93 ± 0.8	0.95
Fungi (n=6)	0.86 ± 0.18	0.93
Plant (n=1)	0.52	0.52

Table 2.4. Posterior probabilities for source class membership of fish derived from LDA.

	Average	SD	Lower	Median	Upper
Algae	0.28	0.19	0.02	0.26	0.65
Bacteria	0.22	0.10	0.06	0.21	0.44
Fungi	0.09	0.06	0.01	0.08	0.24
Plant	0.41	0.16	0.15	0.41	0.70

Table 2.5. FRUITS estimates for source contributions to fish.

		Consumers LDA Predicted Class						
		Algae (n=38)	SD	Bacteria (n=4)	SD	Fungi (n=6)	SD	Plant (n=1)
Source Type	Algae	0.32	0.17	0.22	0.16	0.06	0.04	0.35
	Bacteria	0.18	0.18	0.19	0.21	0.18	0.21	0.05
	Fungi	0.06	0.03	0.05	0.02	0.27	0.23	0.06
	Plant	0.44	0.23	0.21	0.26	0.17	0.22	0.54

Table 2.6. FRUITS estimates for source contributions to fish, partitioned by LDA predicted source class.

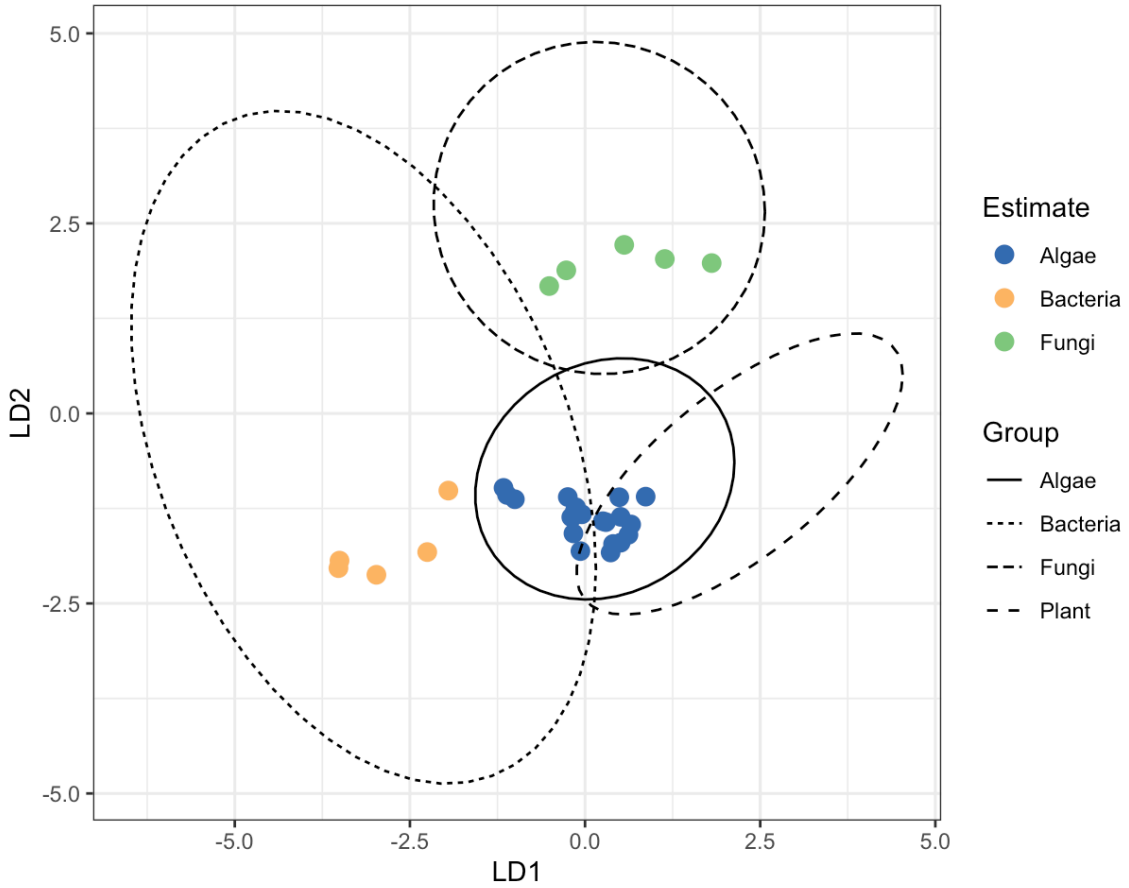

Figure 2.5. Projection of data from Chinook Salmon into linear discriminant space describing variation in the carbon isotope composition of amino acids (i.e. Leucine, Isoleucine, Phenylalanine, Valine, Glycine) in primary producers and microbes.

In contrast to POM, the influence of higher plants was less pronounced when considering consumers. Particularly when considering LDA results alone. LDA identified algae as the primary source of consumer AA in 73% (36 out of 49) consumer samples (Figure 2.5). However, algae were not the only important source identified. Our data from consumers mirrored much of the variability present in our producer groups (Figures 2.6 and 2.7). All potential basal sources were identified as a major contributor to at least one consumer by LDA. While consumers were distributed widely in our linear discriminant space, posterior probabilities for class assignment from LDA were routinely high (Table 2.3). LDA class membership estimation of our non-algae associated consumer samples indicated that six individuals each were classified with bacteria and fungi, respectively. A Striped bass sample was the only consumer assigned to the higher plant source class by LDA. Differences between the defined groups were significant when tested with MANOVA (Pillai trace = 2.046, $F_{3, 15} = 25.602$, $p < 0.001$).

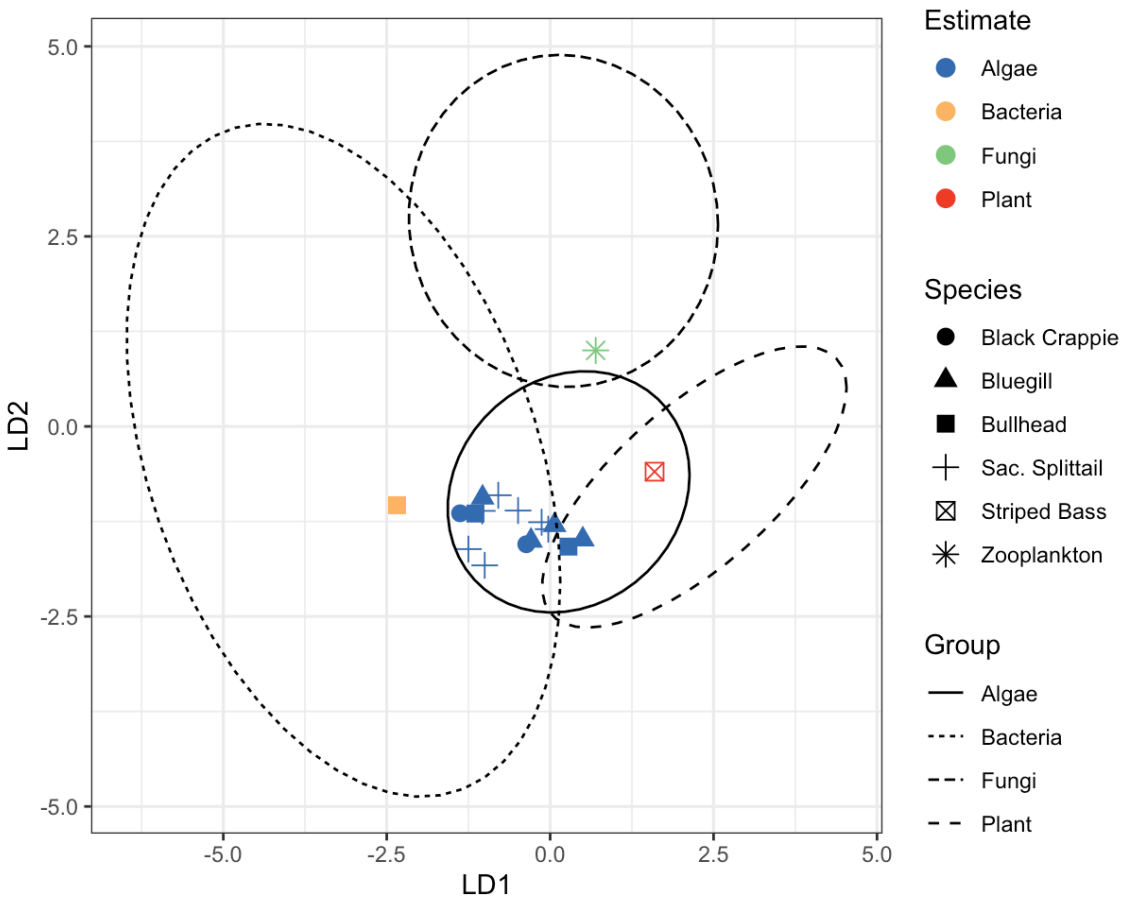

Figure 2.6. Projection of data from fish into linear discriminant space describing variation in the carbon isotope composition of amino acids (i.e. Leucine, Isoleucine, Phenylalanine, Valine, Glycine) in primary producers and microbes.

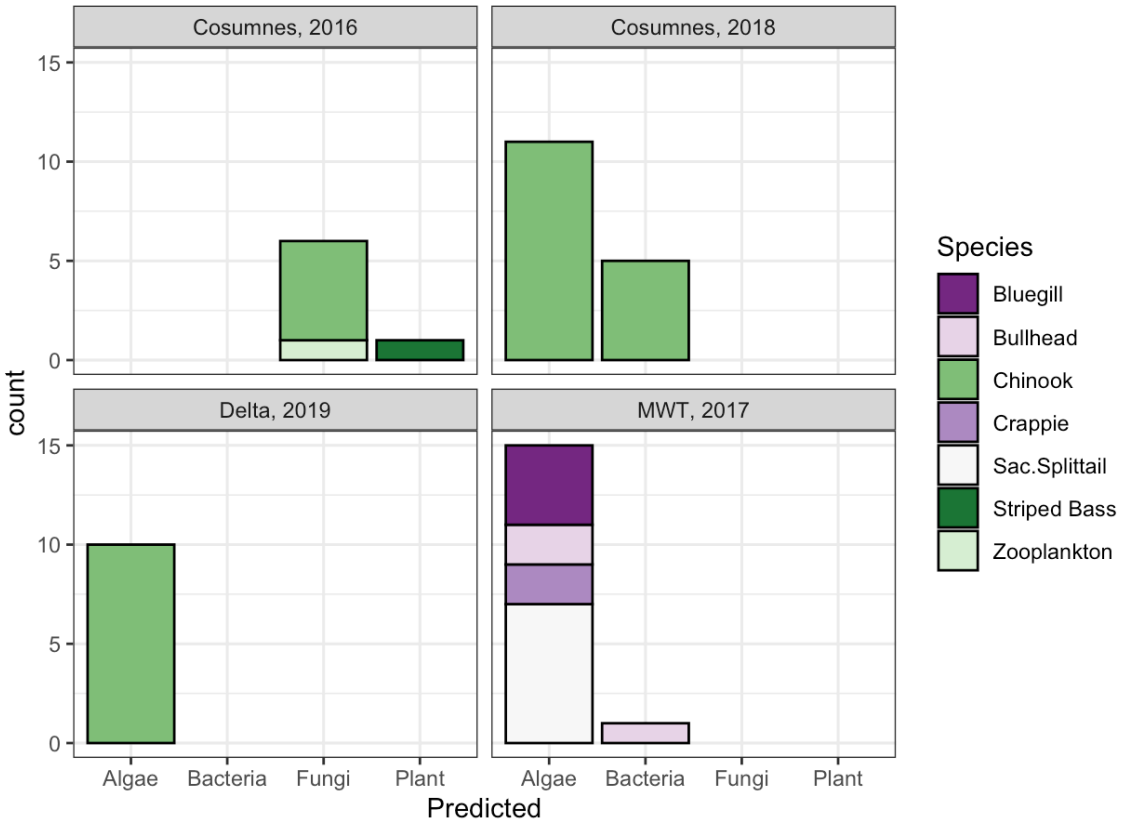

Figure 2.7. Results from consumer class estimation during linear discriminant analysis. Panels separated by sample collection event.

In relative contrast to the stark dominance of algae as indicated by LDA, our mixing model predicted significant inputs from higher plants to consumers (Table 2.4; Figure 2.8). Grouping mixing model results for consumers which were grouped together by LDA narrows the disagreement, indicating that our two methods are telling us similar messages. However, the mixing model does indicate algae are less important than expected based on LDA results alone (Table 2.5). Given the overlap of plants and algae in multivariate space, some confounding of these sources in the mixing model would be unsurprising. Indeed,

the estimated contribution from the corresponding source group of our producer samples only averaged 75% ± 11% (n=6). In contrast, LDA correctly classified producer samples with posterior probabilities averaging 0.97. Similarly, LDA also generated high posterior probabilities (>0.9) for consumer source class assignments. It is also relevant to note that the mean FRUITs estimate for the algal contribution to our algal sample was only 57%, with the second greatest estimated contribution coming from higher plants. Therefore, there seems to be an unresolved bias against algae, in favor of higher plants, in our mixing model results.

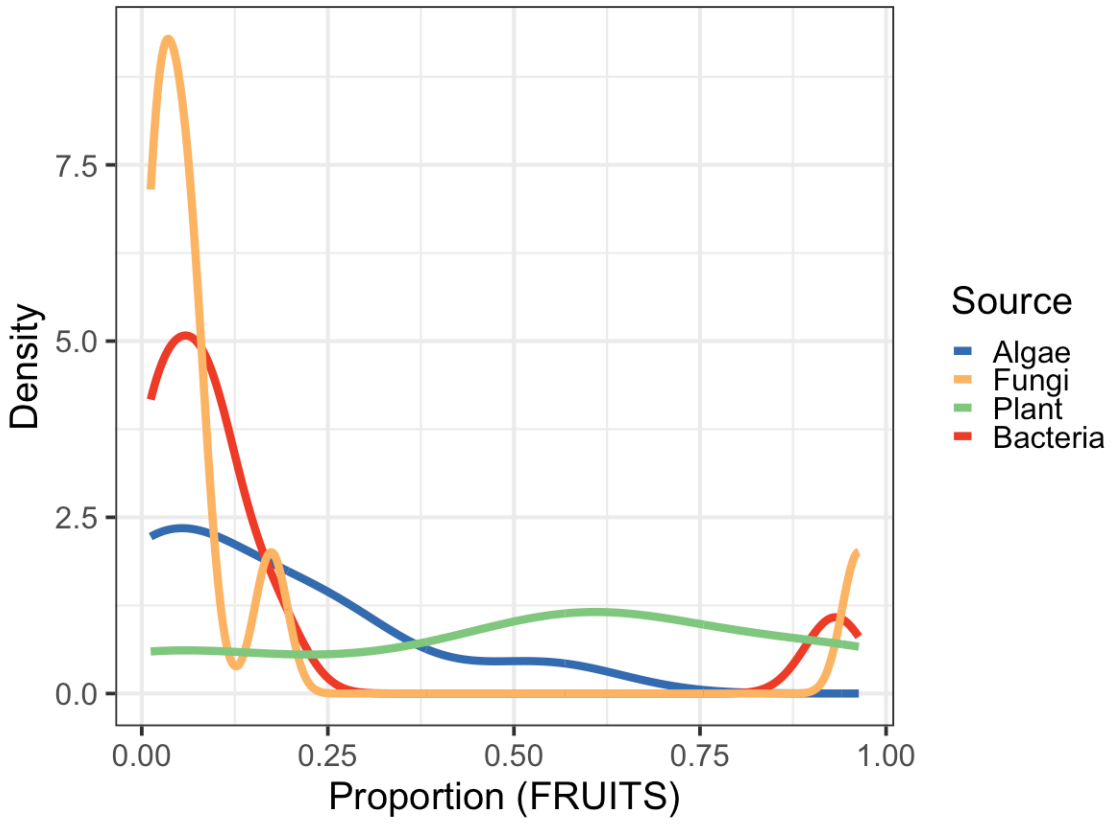

Figure 2.8. Distribution of average estimates for source contributions to fish from FRUITS mixing model.

Discussion

Bulk Isotopes

Our bulk isotope measurements in producers are consistent with previously published values. A 1999 survey of vegetation (n=868) in the San Francisco Estuary, and parts of the SSJD, measured a similar range of values in basal carbon sources (Cloern et al., 2002). Later measurements, including ours, have found that individual source classes (e.g. phytoplankton) have continued to

share similar ranges of $\delta^{13}C$ and $\delta^{15}N$ in the SSJD (Grimaldo et al., 2009; Schroeter et al., 2015).

Isotope overlap of sources is extensive, however, some of the most extreme group features are consistent among datasets. For example, the lowest $\delta^{15}N$ values are found in terrestrial plants; in general, aquatic producers seem to have higher $\delta^{15}N$ values. Presumably, ^{15}N enriched sediment and nutrient runoff (e.g. wastewater) contribute to this trend (Kendall et al., 2015). Also, with the exclusion of C_4 vegetation, the most positive $\delta^{13}C$ values come from algae and the most negative from phytoplankton. Interestingly, our sample of periphyton had a low $\delta^{13}C$ value, more like aquatic plants or phytoplankton than the other attached algae. Presumably, the partially heterotrophic nature of the periphyton imparted the consortium with a $\delta^{13}C$ value closer to that of available DOC sources.

Our measurements illustrate how isotopic similarity between basal carbon sources of interest (e.g. phytoplankton and macrophytes) can make differentiating them, using limited tracers, infeasible. Use of a third isotope in mixing models, i.e. sulfur, has proven useful, however, data of that type are not always available (Bell-Tilcock et al., 2021; E. Howe & Simenstad, 2015; Young et al., 2020). When the value of isotope tracers varies in sources through space and time, as is the case for $\delta^{15}N$, or undifferentiated between sources, $\delta^{13}C$, estimation of trophic structure is not straightforward.

Overall, we found that pelagic zooplankton – namely, cladocerans and copepods- had the lowest invertebrate $\delta^{13}C$ values, and relatively elevated $\delta^{15}N$. Low $\delta^{13}C$ values, relative to other invertebrates, are consistent with prior measurements of similar organisms in the SSJD and reflect selective feeding on phytoplankton (Grimaldo et al., 2009; Young et al., 2020). On the other hand, consumers such as insects and annelids, consistently had higher $\delta^{13}C$ and lower $\delta^{15}N$ than pelagic zooplankton. Potentially due to greater assimilation of benthic, or allochthonous OM. Our mixed/composite zooplankton samples, as expected, had isotope compositions indicative of contributions from cladocerans, or copepods, as well as other macroinvertebrates (e.g. insects).

If typical trophic discrimination factors of 3.4‰ and 1.5‰ are used for nitrogen and carbon, respectively, we find some invertebrates fall beyond the area predicted for consumers relying on the resources we sampled (Post, 2002). For example, some zooplankton have lower $\delta^{13}C$ and higher $\delta^{15}N$ values than would be predicted based on reliance on the producers sampled. Incomplete gut clearance might contribute to low $\delta^{13}C$ values measured in some invertebrate samples. However, relatively low C:N ratios (<10) throughout indicate gut clearance was probably not the root cause of the low $\delta^{13}C$. It is more likely that we did not sample the full extent of dietary item isotope variability in this study. During periods of high productivity, $\delta^{13}C$ of the OM produced can have $\delta^{13}C$ values as low as -37‰ in the same region (Nakamoto et al., 2020). We were

most likely to obtain sufficient zooplankton for isotope analysis from sites with high pelagic productivity, so this was likely a factor. Conversely, δ^{15}N of available nitrogen rises as a result many biogeochemical processes (e.g. uptake) (Kendall et al., 2007). Bulk nitrogen isotopes can be useful tracers of nitrogen cycling processes, and sources. However, in systems with dynamic biogeochemical cycling, trophic information might be overprinted (Kendall et al., 2009; Lehman et al., 2014).

It seems evident from our bulk isotope measurements of larger predatory fish, and is intuitive, that piscivorous fish such as Largemouth bass and Striped bass occupy high trophic positions. This is in contrast to our samples from Sacramento Splittail, Bluegill, and Chinook salmon, who all had a similar bulk isotope composition which seem consistent with insectivory. Our bulk measurements in both Splittail and Chinook were also similar to those made earlier in similar individuals (Feyrer et al., 2007). Other larger fish measured such as White Catfish, Sacramento Suckers, and Bullhead, also had relatively high δ^{15}N. Presumably, Sacramento Sucker δ^{15}N was elevated due to increased uptake of detrital OM. While piscivory in White Catfish and Bullhead probably led to elevated δ^{15}N. On the other hand, the Black Crappie and Golden Shiners sampled had some of the lowest δ^{13}C and δ^{15}N measured in our study, and presumably consumed more pelagic zooplankton, in contrast to insects, than the aforementioned fish (e.g. Splittail and Chinook). In contrast to the low δ^{13}C of the

Black Crappie and Golden Shiners, we suspect the Pikeminnow and Rainbow trout sampled may have more heavily interacted with terrestrial resources, or attached algae, due to relatively elevated $\delta^{13}C$ and low $\delta^{15}N$. These individuals may have also assimilated carbon upstream of our study site in habitat where terrestrial carbon is more important to secondary production before moving downstream during the flooded period.

Basal Sources Supporting Fish

Our results from bulk analysis reveal trends in the data, but are inadequate to cleanly tease apart fish resource utilization. Variability in the bulk isotope composition of producers and invertebrates, along with inadequate source differentiation, renders application of conventional C/N mixing models infeasible. In the subset of samples AA-$\delta^{13}C$ was available for, however, CSIA-AA indicated that algal carbon was important to most consumers sampled. We show that groups with dissimilar bulk compositions and predicted feeding (e.g. Splittail, Chinook, and Crappie) might be interacting with similar basal resources (i.e. algae). The disparity in bulk values indicates there may be a decoupling in utilization of algal resources (e.g. benthic vs pelagic) though. In addition to providing support for the importance of algae, we also demonstrate that other sources, such as fungi, bacteria, and higher plants, might be significant as well.

Sacramento Splittail are a native species that is reliant on floodplain habitat to complete their life-cycle (Moyle et al., 2007). Annually, Splittail move upstream from the San Francisco Estuary to spawn on freshwater floodplains. The Splittail analyzed in our study seem to be post-larval fish which did not emigrate from the floodplain before disconnection and were stranded. Splittail floodplain emigration consistently takes place between 30-40mm SL, indicating the signal may be ontogenetic (Feyrer et al., 2006). The early success of these individuals in their migration to downstream habitats seems to be linked to the hydroperiod of the floodplain and their success in resource acquisition. Usable habitat for Splittail in the Cosumnes watershed is principally a function of hydrology and year class strength is correlated to the days of flooding (T. Sommer et al., 1997; Whipple, 2018). Resource acquisition is more likely a function of production and competition and our data indicate that age-0 Splittail are competing with co-located fish for algal resources. Competition from more opportunistic floodplain foraging species we identified as consuming similar resources, such as Bluegill, can only reduce the availability of resources for populations (i.e. Splittail) for which those resources might be more critical (Fletcher et al., 2019; Moyle et al., 2007).

Fish such as Bluegill, Bullhead, and Crappie were usually associated with algal-AA. Although, one of our bullhead samples stood apart by having AA we associated with a bacterial source. The sole fish closely associated with higher

plant AA by our LDA was an adult striped bass. We measured high bulk muscle δ^{15}N in Striped Bass as well, which is consistent with piscivory in these fish (Nobriga & Feyrer, 2007). Notably, the Striped Bass sampled was large, and thus mobile, enough to have assimilated this organic matter in a downstream estuarine habitat, where higher plants are more important to secondary production, and moved upstream into our study site to spawn (Brown et al., 2016; Nobriga & Feyrer, 2007). Migration after assimilation in a different habitat seems likely, given that the other fish captured in our study area were predominantly associated with algal resources.

All Chinook analyzed in this study were juveniles and our results confirm the significance of algal OM to juvenile Chinook in the SSJD (Figures 5 and 6). On the other hand, we also demonstrate that individuals might receive significant AA subsidies from other sources (e.g. fungi). Pelagic zooplankton populations integrate, and concentrate, local resources into fish. The fungal-AA associated mixed zooplankton sample was comprised of zooplankton samples taken from the same site as the fungal-AA associated Chinook. To what extent fungal and bacterial components of the gut microbiome might contribute to the amino acid balance of these consumers is unknown.

Utilization of increasingly scarce, off-channel habitats has been identified as an important factor in juvenile salmon growth and success (Jeffres et al., 2008; Katz et al., 2017). In particular, high densities of invertebrates, relative to

the river channel, seem to make them great foraging grounds (Grosholz & Gallo, 2006; T. R. Sommer et al., 2001). The high nutritional quality of the phytoplankton (i.e., presence of essential fatty acids), that flourish on floodplains and support pelagic zooplankton, is what makes them such important basal carbon sources for fish, even in the presence of other resources (Müller-Solger et al., 2002; Taipale et al., 2014).

In addition to increased aquatic production, inundation of floodplains can also increase the amount of allochthonous, or detrital, OM available to aquatic communities (Junk et al., 1989; Junk & Wantzen, 2004). Allochthonous resources are generally less nutritionally dense than phytoplankton. However, bacterial or fungal conditioning could substantially improve the nutritional quality of the OM and excess can always be oxidized to help meet metabolic demand (Sobczak et al., 2002). An understudied, and potentially significant, vector for detrital OM to reach aquatic consumers in the SSJD is periphyton.

Periphyton refers to the community of autotrophic and heterotrophic microbiota adhering to surfaces in aquatic environments. In particular, this microbial consortium could serve as in important conduit for detrital food webs. Heterotrophs, such as fungi and bacteria, living in association with algae might be primed by algal carbon inputs coming from the autotrophic component of the biofilm. With respect to invertebrate, and fish, consumer communities, this priming has a dual benefit. First, the easily metabolized algal carbon can be

respired or provide substrate to increase extracellular metabolic potential (i.e. potentiating breakdown of recalcitrant organic matter). Secondly, uptake of algal biomolecules (e.g. highly unsaturated fatty acids) can increase the nutritional value of the fungi, or bacteria. The efficiency at which this OM pathway operates in the SSJD is unknown, but is significant in other systems, and warrants further interest (Jardine et al., 2012, 2013).

Composition of POM

Particulate organic matter (POM) is a major pool of OM available to pelagic consumers in most aquatic environments and is comprised of a spatiotemporally varying mix of phytoplanktonic, bacterial, fungal, and vegetative OM (Nakamoto et al., 2020). Thus, alterations to the composition of POM through space and time impact consumer communities by adjusting the quality and abundance of potential dietary items. Selective suspension feeders might be more affected by the presence, or absence, of phytoplankton than more indiscriminate feeders who could potentially uptake significant OM from other sources.

Algae are considered the dominant basal OM source for higher trophic levels in our system and chlorophyll-*a* is rarely below detection, so some prevalence of algal AA in POM was expected (Ahearn et al., 2006; Nakamoto et al., 2020). However, the SSJD is turbid and light-limited, which curtails pelagic

production. Regardless, data from this study are consistent with the idea that algae are an important source of nutritive biomolecules (e.g. EAA) to fish, and the aquatic invertebrates they feed on (Galloway et al., 2014; Grimaldo et al., 2009; Taipale et al., 2014). However, our somewhat limited survey also suggests that material from higher plants dominates the POM matrix frequently. In general, higher plant inputs seem more prominent in our POM samples than in consumer samples which is still consistent with OM from algae being preferentially used by consumer communities.

Macrophyte structural tissues and allochthonous inputs are generally of low nutritional quality (e.g. low concentration of AA). However, high macrophyte biomass in the SSJD, regardless of quality, potentially constitutes a significant subsidy of OM and nutrients to consumers (Greenfield et al., 2007). Utilization of lower quality basal resources by consumers may be potentiated by microbial conditioning (i.e. immobilization and concentration of resources in microbial biomass). While bacteria are conventionally considered to be the most active players in this process, aquatic fungi also play an active role in decomposition, dominating bacteria in some cases (Kagami et al., 2017; Mille-Lindblom et al., 2006). Our results indicate that fungi might contribute significant OM to both POM and consumers, under some circumstances. On the other hand, we did not have a POM sample that was assigned to a bacterial source by LDA. However, in contrast to the LDA result, our mixing model indicated that one POM sample

may have been mostly bacterial in origin. An overabundance of senescing plant matter, mostly invasive or exotic species, in the SSJD could provide ample substrate for fungi, along with other decomposers, and represent the base of an alternative detrital-based trophic channel (Gulis & Suberkropp, 2003; Mount et al., 2012).

LDA and Mixing Model

Our results support previous work demonstrating the utility of δ^{13}C-AA in ecological studies, and provide some evidence for the generalizable nature of, so-called, AA-fingerprints. Although our test set was limited to plants and algae, when analyzed with LDA, our reference dataset correctly classified our samples of local AA sources with the appropriate reference group (i.e. algae, bacteria, fungi, plant). The necessity of variable selection in improving the accuracy of our classification model (LDA) indicates that not all AA provide equally diagnostic information for differentiation of groups. Different sets of AA may prove more useful under different circumstances. The prominence of data from EAA in our most effective model is unsurprising though, given previous studies have shown EAA to be critical in differentiating taxonomically diverse AA sources (Liew et al., 2019). In the future, studies attempting to resolve taxonomically similar sources may be better served by comparing AA more tightly tied to central metabolic processes (e.g. simple AA's tied directly to glycolysis or the TCA cycle) (Wang et

al., 2019). This work provides an example of how complex δ^{13}C-AA analysis can be. Selection of amino acids for analysis and the modelling technique used to interrogate the data can have a significant impact on the result. Further work on systematics of isotopic variation in amino acids during biosynthesis, trophic transfer, metabolism, and diagenesis will continue to increase δ^{13}C-AA's utility.

Incorporating the full isotopic range of our source groups as the source uncertainty in mixing model, as opposed to using estimates from samples of local producers or a smaller estimation of uncertainty, resulted in significant uncertainty surrounding FRUITS source contribution estimates. LDA source classification and mixing model results were not entirely consistent with one another for this reason also.

The intent of LDA is transformation of the data to attain the greatest possible resolution between source groups. Our mixing model, on the other hand, simply estimated credible formulations of the sources that could result in the observed data. Mixing models can easily underestimate the contribution of major sources and overestimate the impact of minor sources. Indeed, we found that our model underestimated the contribution from our producer samples own source classes. The model also seemed to overestimate the contribution from higher plants relative to algae.

The compositional variability of sources used in the mixing model may be beyond that typically available to consumers within our constrained environment.

Allowing for significant within-group variation in sources could have exacerbated the aforementioned overestimation and underestimation of minor and major sources, respectively. However, variation could be even greater and the effect of metabolism and diagenesis on the mixing model result is unconstrained. In the absence of sensitivity testing of trophic discrimination factors and without explicit information on the true variability of AA-fingerprints in the environment, use of conservative uncertainties in conjunction with discretion during interpretation is appropriate. There is a pressing need to develop a more systematic understanding of variation in δ^{13}C-AA.

Conclusion

Our measurements of the bulk carbon and nitrogen isotope ratio in producers and consumers do not cleanly dissect differences in resource utilization and only sketch out a rough trophic structure. Bulk carbon and nitrogen isotope analyses do not always offer adequate resolution between dietary items in the SSJD. Currently, bulk sulfur isotope analysis and gut content analysis are promising compliments to carbon and nitrogen isotope data. However, these methods all lack the resolution to fully disentangle the role of more cryptic carbon sources in the SSJD (e.g. heterotrophic food webs and periphyton) (Jassby & Cloern, 2000; Sobczak et al., 2005; Young et al., 2020).

Our results from CSIA-AA are consistent with the idea that algal production is critical to overall ecosystem functioning in the SSJD. The majority of fish sampled, including a significant number of juvenile Chinook salmon, had amino acids in their tissues mostly associated with our algae source class. However, we cannot definitively say whether these resources were pelagic (i.e. phytoplankton), benthic (i.e. periphyton) or otherwise (e.g. benthic diatoms) for the individuals sampled. Algae were also not the only important source of AA to consumers. Our data indicate that fungi, bacteria, and higher plants all may have contributed significantly to higher trophic level consumers. Those individuals assimilating significant amounts of non-algal OM may have interacted with a heterotrophic food web; fueled by microbial breakdown of vegetative OM. The role that food items such as bacteria and fungi play in floodplains of the SSJD is currently unknown, but may be significant. As the climate warms and the extent of floodplain habitat declines, concurrent with increasing prevalence of invasive vegetation, the importance of heterotrophic resources (e.g. OM routed through microbes) may grow in the SSJD.

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Works Cited

Ahearn, D. S., Viers, J. H., Mount, J. F., & Dahlgren, R. A. (2006). Priming the productivity pump: flood pulse driven trends in suspended algal biomass distribution across a restored floodplain. *Freshwater Biology*, *51*(8), 1417–1433. https://doi.org/10.1111/j.1365-2427.2006.01580.x

Bell-Tilcock, M., Jeffres, C. A., Rypel, A. L., Sommer, T. R., Katz, J. V. E., Whitman, G., & Johnson, R. C. (2021). Advancing diet reconstruction in fish eye lenses. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210x.13543

Bowes, R. E., & Thorp, J. H. (2015). Consequences of employing amino acid vs. bulk-tissue, stable isotope analysis: a laboratory trophic position experiment. *Ecosphere*, *6*(1), 14. https://doi.org/10.1890/es14-00423.1

Chikaraishi, Y., Ogawa, N. O., Doi, H., & Ohkouchi, N. (2011). 15N/14N ratios of amino acids as a tool for studying terrestrial food webs: a case study of terrestrial insects (bees, wasps, and hornets). *Ecological Research*, *26*(4), 835–844. https://doi.org/10.1007/s11284-011-0844-1

Cloern, J. E., Canuel, E. A., & Harris, D. (2002). Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. *Limnology and Oceanography*, *47*(3), 713–729. https://doi.org/10.4319/lo.2002.47.3.0713

Cloern, J. E., Robinson, A., Grenier, L., Grossinger, R. M., Boyer, K., Burau, J. R., Canuel, E. A., DeGeorge, J., Drexler, J. Z., Enright, C., Howe, E., Kneib, R., Mueller-Solger, A., Naiman, R. J., Pinckney, J., Safran, S., Schoellhamer, D. H., & Simenstad, C. A. (2016). Primary Production in the Delta: Then and Now. *San Francisco Estuary and Watershed Science*, *14*(3). https://doi.org/10.15447/sfews.2016v14iss3art1

Fernandes, R., Millard, A. R., Brabec, M., Nadeau, M.-J., & Grootes, P. (2014). Food reconstruction using isotopic transferred signals (FRUITS): a Bayesian model for diet reconstruction. *PloS One*, *9*(2), e87436. https://doi.org/10.1371/journal.pone.0087436

Feyrer, F., Sommer, T., & Harrell, W. (2006). Managing floodplain inundation for native fish: production dynamics of age-0 splittail (Pogonichthys macrolepidotus) in California's Yolo Bypass. *Hydrobiologia*, *573*(1), 213–226. https://doi.org/10.1007/s10750-006-0273-2

Feyrer, F., Sommer, T., & Hobbs, J. (2007). Living in a Dynamic Environment: Variability in Life History Traits of Age-0 Splittail in Tributaries of San Francisco Bay. *Transactions of the American Fisheries Society*, *136*(5), 1393–1405. https://doi.org/10.1577/t06-253.1

Fletcher, C. M., Collins, S. F., Nannini, M. A., & Wahl, D. H. (2019). Competition during early ontogeny: Effects of native and invasive planktivores on the growth, survival, and habitat use of bluegill. *Freshwater Biology*, *64*(4), 697–707. https://doi.org/10.1111/fwb.13255

Fox, M. D., Smith, E. A. E., Smith, J. E., & Newsome, S. D. (2019). Trophic plasticity in a common reef-building coral: Insights from δ13C analysis of essential amino acids. *Functional Ecology*, *33*(11), 2203–2214. https://doi.org/10.1111/1365-2435.13441

Galloway, A. W. E., Taipale, S. J., Hiltunen, M., Peltomaa, E., Strandberg, U., Brett, M. T., & Kankaala, P. (2014). Diet-specific biomarkers show that high-quality phytoplankton fuels herbivorous zooplankton in large boreal lakes. *Freshwater Biology*, *59*(9), 1902–1915. https://doi.org/10.1111/fwb.12394

Greenfield, B. K., Siemering, G. S., Andrews, J. C., Rajan, M., Andrews, S. P., & Spencer, D. F. (2007). Mechanical shredding of water hyacinth (Eichhornia crassipes): Effects on water quality in the Sacramento-San Joaquin River Delta, California. *Estuaries and Coasts*, *30*(4), 627–640. https://doi.org/10.1007/bf02841960

Grimaldo, L. F., Stewart, A. R., & Kimmerer, W. (2009). Dietary Segregation of Pelagic and Littoral Fish Assemblages in a Highly Modified Tidal Freshwater Estuary. *Marine and Coastal Fisheries*, *1*(1), 200–217. https://doi.org/10.1577/c08-013.1

Grosholz, E., & Gallo, E. (2006). The influence of flood cycle and fish predation on invertebrate production on a restored California floodplain. *Hydrobiologia*, *568*(1), 91–109. https://doi.org/10.1007/s10750-006-0029-z

Gulis, V., & Suberkropp, K. (2003). Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology*, *48*, 123–134. https://onlinelibrary.wiley.com/doi/epdf/10.1046/j.1365-2427.2003.00985.x

Howe, E. R., & Simenstad, C. A. (2011). Isotopic Determination of Food Web Origins in Restoring and Ancient Estuarine Wetlands of the San Francisco Bay

and Delta. *Estuaries and Coasts*, *34*(3), 597–617. https://doi.org/10.1007/s12237-011-9376-8

Howe, E., & Simenstad, C. (2015). Using stable isotopes to discern mechanisms of connectivity in estuarine detritus-based food webs. *Marine Ecology Progress Series*, *518*, 13–29. https://doi.org/10.3354/meps11066

Jardine, T. D., Hunt, R. J., Faggotter, S. J., Valdez, D., Burford, M. A., & Bunn, S. E. (2012). Carbon from Periphyton Supports Fish Biomass in Waterholes of a Wet-Dry Tropical RIver. *River Research and Applications*, *29*, 560–573. https://doi.org/10.1002/rra.2554

Jardine, T. D., Hunt, R. J., Faggotter, S. J., Valdez, D., Burford, M. A., & Bunn, S. E. (2013). CARBON FROM PERIPHYTON SUPPORTS FISH BIOMASS IN WATERHOLES OF A WET–DRY TROPICAL RIVER. *River Research and Applications*, *29*(5), 560–573. https://doi.org/10.1002/rra.2554

Jassby, A. D. (2008). Phytoplankton in the Upper San Francisco Estuary: Recent Biomass Trends, Their Causes, and Their Trophic Significance. *San Francisco Estuary and Watershed Science*, *6*(1 SN-).

Jassby, A. D., Cloern, J. E., & Cole, B. E. (2002). Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem. *Limnology and Oceanography*, *47*(3), 698–712. https://doi.org/10.4319/lo.2002.47.3.0698

Jeffres, C. A., Holmes, E. J., Sommer, T. R., & Katz, J. V. E. (2020). Detrital food web contributes to aquatic ecosystem productivity and rapid salmon growth in a managed floodplain. *PLOS ONE*, *15*(9), e0216019. https://doi.org/10.1371/journal.pone.0216019

Jeffres, C. A., Opperman, J. J., & Moyle, P. B. (2008). Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environmental Biology of Fishes*, *83*(4), 449–458. https://doi.org/10.1007/s10641-008-9367-1

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Proceedings of the International Large River Symposium Canadian Journal of Fisheries and Aquatic Sciences*, *106*, 110–127.

Junk, W. J., & Wantzen, K. M. (2004). *The Flood Pulse Concept: New Aspects, Approaches and Applications—An Update*. 1–25. https://www.researchgate.net/publication/274511459_The_Flood_Pulse_Concept_New_Aspects_Approaches_and_Applications-An_Update

Kagami, M., Motoki, Y., Masclaux, H., & Bec, A. (2017). Carbon and nutrients of indigestible pollen are transferred to zooplankton by chytrid fungi. *Freshwater Biology*, *62*(5), 954–964. https://doi.org/10.1111/fwb.12916

Katz, J. V. E., Jeffres, C., Conrad, J. L., Sommer, T. R., Martinez, J., Brumbaugh, S., Corline, N., & Moyle, P. B. (2017). Floodplain farm fields provide novel rearing habitat for Chinook salmon. *PloS One*, *12*(6). https://doi.org/10.1371/journal.pone.0177409

Kendall, C., Elliott, E. M., & Wankel, S. D. (2007). *Tracing Anthropogenic Inputs of Nitrogen to Ecosystems* (R. H. Michener & K. Lajtha, Eds.; Second, pp. 375–449). Blackwell Publishing Ltd. http://www2.pitt.edu/~eelliott/uploads/1/1/5/3/11534391/kendallelliottwankel_2007.pdf

Kendall, C., Young, M. B., & Silva, S. R. (2009). Applications of Stable Isotopes for Regional to National-Scale Water Quality and Environmental Monitoring Programs. In J. B. West, G. J. Bowen, T. E. Dawson, & K. P. Tu (Eds.), *Isoscapes* (pp. 89–111). Springer Netherlands. https://doi.org/10.1007/978-90-481-3354-3_5

Kendall, C., Young, M. B., Silva, S. R., Kraus, T., Peek, S., & Guerin, M. (2015). *Tracing nutrient and organic matter sources and biogeochemical processes in the Sacramento River and Northern Delta: proof of concept using stable isotope data*.

Kiernan, J. D., & Moyle, P. B. (2012). Flows, droughts, and aliens: factors affecting the fish assemblage in a Sierra Nevada, California, stream. *Ecological Applications*, *22*(4), 1146–1161. https://doi.org/10.1890/11-1047.1

Larsen, T., Bach, L. T., Salvatteci, R., Wang, Y. V., Andersen, N., Ventura, M., & McCarthy, M. D. (2015). Assessing the potential of amino acid 13C patterns as a carbon source tracer in marine sediments: effects of algal growth conditions and sedimentary diagenesis. *Biogeosciences*, *12*, 4979–4992. https://doi.org/10.5194/bg-12-4979-2015

Larsen, T., Ventura, M., Maraldo, K., Triadó-Margarit, X., Casamayor, E. O., Wang, Y. V., Andersen, N., & O'Brien, D. M. (2016). The dominant detritus-feeding invertebrate in Arctic peat soils derives its essential amino acids from gut symbionts. *Journal of Animal Ecology*, *85*(5), 1275–1285. https://doi.org/10.1111/1365-2656.12563

Larsen, T., Wooller, M. J., Fogel, M. L., & O'Brien, D. M. (2012). Can amino acid carbon isotope ratios distinguish primary producers in a mangrove ecosystem? *Rapid Communications in Mass Spectrometry*, *26*, 1541–1548. https://doi.org/10.1002/rcm.6259

Lehman, P. W., Kendall, C., Guerin, M. A., Young, M. B., Silva, S. R., Boyer, G. L., & Teh, S. J. (2014). Characterization of the Microcystis Bloom and Its Nitrogen Supply in San Francisco Estuary Using Stable Isotopes. *Estuaries and Coasts*, *38*(1), 165–178. https://doi.org/10.1007/s12237-014-9811-8

Lehman, P. W., Sommer, T. R., & Rivard, L. (2008). The influence of floodplain habitat on the quantity and quality of riverine phytoplankton carbon produced during the flood season in San Francisco Estuary. *Aquatic Ecology*, *42*, 363–378. https://doi.org/10.1007/s10452-007-9102-6

Liew, J. H., Chua, K. W. J., Arsenault, E. R., Thorp, J. H., Suvarnaraksha, A., Amirrudin, A., & Yeo, D. C. J. (2019). Quantifying terrestrial carbon in freshwater food webs using amino acid isotope analysis—case study with an endemic cave fish. *Methods in Ecology and Evolution*, 2041-210X.13230-33. https://doi.org/10.1111/2041-210x.13230

McMahon, K. W., Thorrold, S. R., Houghton, L. A., & Berumen, M. L. (2016). Tracing carbon flow through coral reef food webs using a compound-specific stable isotope approach. *Oecologia*, 1–14. https://doi.org/10.1007/s00442-015-3475-3

Mille-Lindblom, C., Fischer, H., & Tranvik, L. J. (2006). Litter-associated bacteria and fungi - a comparison of biomass and communities across lakes and plant species. *Freshwater Biology*, *51*(4), 730–741. https://doi.org/10.1111/j.1365-2427.2006.01532.x

Mount, J. F., Bennett, W. A., Durand, J. R., & Fleenor, W. E. (2012). Aquatic Ecosystem Stressors in the Sacramento–San Joaquin Delta. *Public Policy Institute of California*.

Moyle, P. B. (1995). Conservation of Native Freshwater Fishes in the Mediterranean-Type Climate of California, USA: A Review. *Biological Conservation*, *72*, 271–279.

Moyle, P. B., Brown, L. R., Durand, J. R., & Hobbs, J. A. (2016). Delta Smelt: Life History and Decline of a Once-Abundant Species in the San Francisco Estuary. *San Francisco Estuary and Watershed Science*, *14*(2). https://doi.org/10.15447/sfews.2016v14iss2art6

Moyle, P. B., Crain, P. K., & Whitener, K. (2007). Patterns in the Use of a Restored California Floodplain by Native and Alien Fishes. *San Francisco Estuary and Watershed Science*, *5*(3). https://doi.org/10.15447/sfews.2007v5iss3art1

Moyle, P. B., & Mount, J. F. (2007). Homogenous rivers, homogenous faunas. *PNAS*, *104*(14), 5711–5712. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1851555/pdf/zpq5711.pdf

Müller-Solger, A. B., Jassby, A. D., & Müller-Navarra, D. C. (2002). Nutritional quality of food resources for zooplankton (Daphnia) in a tidal freshwater system (Sacramento-San Joaquin River Delta). *Limnology and Oceanography*, *47*(5), 1468–1476. https://doi.org/10.4319/lo.2002.47.5.1468

Nakamoto, B. J., Fogel, M. L., Jeffres, C. A., & Viers, J. H. (2020). Dynamic river processes drive variability in particulate organic matter over fine spatiotemporal scales. *Freshwater Biology*, *65*(9), 1569–1584. https://doi.org/10.1111/fwb.13522

Newsome, S. D., Clementz, M. T., & Koch, P. L. (2010). Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science*, *52*, 837–864. https://doi.org/10.1111/j.1748-7692.2009.00354.x

Newsome, S. D., Nakamoto, B. J., Curras, M. R., & Fogel, M. L. (2020). Compound-specific δ2H analysis highlights the relationship between direct assimilation and de novo synthesis of amino acids from food and water in a terrestrial mammalian omnivore. *Oecologia*, *193*(4), 827–842. https://doi.org/10.1007/s00442-020-04730-9

Newsome, S. D., Rio, C. M. del, Bearhop, S., & Phillips, D. L. (2007). A niche for isotopic ecology. *Frontiers in Ecology …*. https://doi.org/10.1890/060150.01

Newsome, S. D., Wolf, N., Peters, J., & Fogel, M. L. (2014). Amino Acid 13C Analysis Shows Flexibility in the Routing of Dietary Protein and Lipids to the Tissue of an Omnivore. *Integrative and Comparative Biology*, *54*(5), 890–902. https://doi.org/10.1093/icb/icu106

Nobriga, M. L., & Feyrer, F. V. (2007). Shallow-Water Piscivore-Prey Dynamics in California's Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science*, *5*(2), 1–14. https://doi.org/10.15447/sfews.2007v5iss2art4

O'Brien, D. M., Fogel, M. L., & Boggs, C. L. (2002). Renewable and nonrenewable resources: Amino acid turnover and allocation to reproduction in Lepidoptera. *Proceedings of the National Academy of Sciences*, *99*(7), 1–6. https://www.pnas.org/content/pnas/99/7/4413.full.pdf

Post, D. M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology*, *83*(3), 703–718.

Schroeter, R. E., O'Rear, T. A., Young, M. J., & Moyle, P. B. (2015). The Aquatic Trophic Ecology of Suisun Marsh, San Francisco Estuary, California, During Autumn in a Wet Year. *San Francisco Estuary and Watershed Science*, *13*(3). https://doi.org/10.15447/sfews.2015v13iss3art6

Smith, E. A. E., Harrod, C., & Newsome, S. D. (2018). The importance of kelp to an intertidal ecosystem varies by trophic level: insights from amino acid δ 13C analysis. *Ecosphere*, *9*(11), e02516-14. https://doi.org/10.1002/ecs2.2516

Sobczak, W. V., Cloern, J. E., Jassby, A. D., Cole, B. E., Schraga, T. S., & Arnsberg, A. (2005). Detritus fuels ecosystem metabolism but not metazoan food webs in San Francisco estuary's freshwater delta. *Estuaries*, *28*(1), 124–137. https://doi.org/10.1007/bf02732759

Sobczak, W. V., Cloern, J. E., Jassby, A. D., & Müller-Solger, A. B. (2002). Bioavailability of organic matter in a highly disturbed estuary: the role of detrital and algal resources. *PNAS*, *99*(12), 8101–8105. https://doi.org/10.1073/pnas.122614399

Sommer, T., Baxter, R., & Herbold, B. (1997). Resilience of Splittail in the Sacramento–San Joaquin Estuary. *Transactions of the American Fisheries Society*, *126*(6), 961–976. https://doi.org/10.1577/1548-8659(1997)126<0961:rosits>2.3.co;2

Sommer, T. R., Armor, C., Baxter, R. D., Breuer, R., Brown, L. R., Chotkowski, M., Culberson, S. D., Feyrer, F., Gingras, M., Herbold, B., Kimmerer, W. J., Mueller-Solger, A., Nobriga, M. L., & Souza, K. (2007). The Collapse of Pelagic Fishes in the Upper San Francisco Estuary. *Fisheries*, *32*(6), 270–277. https://doi.org/10.1577/1548-8446(2007)32[270:tcopfi]2.0.co;2

Sommer, T. R., Harrell, W. C., & Nobriga, M. L. (2005). Habitat Use and Stranding Risk of Juvenile Chinook Salmon on a Seasonal Floodplain. *North American Journal of Fisheries Management*, *25*(4), 1493–1504. https://doi.org/10.1577/m04-208.1

Sommer, T. R., Nobriga, M. L., Harrell, W. C., Batham, W., & Kimmerer, W. J. (2001). Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(2), 325–333. https://doi.org/10.1139/cjfas-58-2-325

Taipale, S. J., Brett, M. T., Hahn, M. W., Martin-Creuzburg, D., Yeung, S., Hiltunen, M., Strandberg, U., & Kankaala, P. (2014). Differing Daphnia magna assimilation efficiencies for terrestrial, bacterial, and algal carbon and fatty acids. *Ecology*, *95*(2), 563–576.

Thorp, J. H., & Bowes, R. E. (2016). Carbon Sources in Riverine Food Webs: New Evidence from Amino Acid Isotope Techniques. *Ecosystems*, *20*, 1029–1041. https://doi.org/10.1007/s10021-016-0091-y

Thorp, J. H., & Covich, A. P. (2010). *Ecology and Classification of North American Freshwater Invertebrates (Third Edition)* (J. H. Thorp & A. P. Covich, Eds.). Elsevier. https://doi.org/10.1016/b978-0-12-374855-3.00001-7

Wang, Y. V., Wan, A. H. L., Krogdahl, Å., Johnson, M., & Larsen, T. (2019). 13C values of glycolytic amino acids as indicators of carbohydrate utilization in carnivorous fish. *PeerJ*, *7*(5), e7701-20. https://doi.org/10.7717/peerj.7701

Wang, Y. V., Wan, A. H. L., Lock, E.-J., Andersen, N., Winter-Schuh, C., & Larsen, T. (2018). Know your fish: A novel compound-specific isotope approach for tracing wild and farmed salmon. *Food Chemistry*, *256*, 380–389. https://doi.org/10.1016/j.foodchem.2018.02.095

Whipple, A. A. (2018). *Managing Flow Regimes and Landscapes Together: Hydrospatial Analysis for Evaluating Spatiotemporal Floodplain Inundation Patterns with Restoration and Climate Change Implications*. UC Davis.

Young, M., Howe, E., O'Rear, T., Berridge, K., & Moyle, P. B. (2020). Food Web Fuel Differs Across Habitats and Seasons of a Tidal Freshwater Estuary. *Estuaries and Coasts*, 1–16. https://doi.org/10.1007/s12237-020-00762-9

Chapter 3

Isotope Biogeochemistry of Fatty Acids in Chinook Salmon (*Oncorhynchus tshawytscha*)

Bobby J. Nakamoto

Introduction

Background

A consumer's capacity to acquire the high quality dietary items it needs to fulfill its nutritional requirements is partially predicated on its ability to interact with the right habitat at the right times (Österblom et al., 2008). All habitat patches provide different conditions for growth, and can affect future success differently. These differences can be subtle or substantial. For example, easy access to food may be offset by increased risk of predation. In other cases, certain habitat patches may not provide adequate, or the right kind, of dietary items. Failure of the diet to meet nutritional needs has negative impacts —notably, death. Alternatively, access to adequate nutrition can improve body condition and promote success (i.e. growth and/or reproduction). Determining how habitat impacts nutrition, and thus success, is an important step in understanding and managing species of conservation concern, such as Chinook Salmon (*Oncorhynchus tshawytscha*).

The Chinook salmon is a fish of cultural, ecological, and economic significance. Chinook are native to the Pacific coast of North America and are anadromous, meaning they spend alternate portions of their life in freshwater and saltwater. Specifically, Chinook are born in freshwater, but often mature in the ocean. Due to conservation actions and hatchery supplementation of wild populations, Chinook are not at risk of extinction. However, reproductive site-

specificity and differences in the timing of freshwater immigration have partitioned the species into distinct subpopulations. Their portfolio life histories provide resiliency in an unpredictable environment, and decreases intraspecific density-dependent pressures (e.g. competition for space and food) (Bourret et al., 2016; Waples et al., 2004). Unfortunately, several subpopulations are listed as threatened or endangered under the US Endangered Species Act. Specifically, Chinook populations using the Sacramento-San Joaquin Delta (SSJD; CA, USA) have declined significantly (Welch et al., 2021; Willmes et al., 2018; Yoshiyama et al., 1998).

Due to anthropogenic alteration of hydrological and geomorphological conditions, Chinook are no longer favored in the SSJD (Bennett & Moyle, 1996; J. Katz et al., 2013; Mount et al., 2012). In the SSJD, the delivery of variable amounts of rain and snowfall is confined to the Winter and early Spring. Newly hatched juvenile Chinook emigrating from the SSJD cued on these cool seasonal flow pulses to successfully complete their migration to the ocean (Buchanan & Skalski, 2020; Marston et al., 2012; Michel et al., 2015; Perry et al., 2018). Furthermore, activation of floodplains during those high discharge periods may have provided high quality rearing habitat for the Chinook (Jeffres et al., 2008, 2020; J. V. E. Katz et al., 2017). The historic spatiotemporal patterns of disturbance and habitat availability that Chinook adapted to are largely absent in the modern SSJD.

The modern SSJD is heavily altered by anthropogenic pressures (Kraus-Polk & Fulton, 2020). The SSJD currently has a significant proportion of its water diverted for municipal and agricultural usages, and levees and dams are maintained for flood control and water storage (Hanak et al., 2017; Ray et al., 2020). The result is a SSJD environment with a transformed temperature, sediment, salinity, and flow regime (Monsen et al., 2007). The seasonal flow pulses that Chinook emigrants historically cued on are captured in reservoirs and distributed by resource managers during drier months. Rivers are largely disconnected from their floodplains by levees, and a significant proportion of habitats previously used by Chinook are now inaccessible (McClure et al., 2008). What was historically a lush mosaic of intertidal wetlands and grasslands, subject to seasonal flooding of anastomosing rivers, has been transformed into a maze of channelized and urbanized waterways bearing little resemblance to the Chinook's adaptive environment.

Life history plasticity allows for variations in the timing of migration; however, most Chinook in the SSJD migrate to the ocean within one year of birth. During early marine residency, there is a spike in Chinook mortality focused on individuals unable to grow enough to escape predation (Beamish & Mahnken, 2001; Woodson et al., 2013). Another spike in marine mortality occurs later, when individuals with insufficient energy reserves for low-productivity periods (i.e. Winter) starve (Hertz et al., 2016; Hurst, 2007). It seems that accelerated growth,

development, and stockpiling of energy while still in freshwater could be critically important to the future success of the Chinook in the ocean (Beamish & Mahnken, 2001). It is known that longer bodied out-migrants are more likely to return to reproduce, and rearing in floodplain habitat has been correlated with increased growth rates in juvenile Chinook (Claiborne et al., 2014; Jeffres et al., 2008; Satterthwaite et al., 2014). Therefore, rearing in floodplain habitat seems likely to increase marine returns in SSJD Chinook.

The dynamics of Chinook rearing in the SSJD are not fully understood though. Neither, the relative quality of SSJD rearing habitats nor the reasons for differences in quality among habitats are fully resolved. Moreover, access to habitats and resources to provide new habitats are limited by available space, funding, and socioeconomic concerns. Identification of habitats supporting Chinook, and descriptions of their role, is a step towards efficient management of land and water resources.

Presently, floodplain and other off-channel habitats are thought to be the best habitats for rearing Chinook (J. V. E. Katz et al., 2017; Takata et al., 2017). Basically, higher invertebrate secondary production, than in river channels, is thought to supply fish with abundant food (Grosholz & Gallo, 2006). Autochthonous photoautotrophs, i.e. algae and phytoplankton, are thought to be the most important source of carbon for consumers in large river systems (e.g. SSJD). Direct consumption of these primary producers provides essential

biomolecules and is associated with high consumer assimilation efficiencies. However, it is not known whether similar basal carbon sources support secondary production throughout the SSJD (Jeffres et al., 2020). Detrital organic matter often lacks nutritive biomolecules, may contain toxic compounds, and is not an efficient food source for invertebrates and fish (Fouilland & Mostajir, 2010; Martin-Creuzburg et al., 2011; Mcmeans et al., 2015; S. J. Taipale et al., 2014). Nonetheless, relatively poor quality dietary items may provide an energy subsidy in certain habitats and ultimately promote Chinook success, as long as basic nutritional needs can be met (Wetzel, 1995). Developing an understanding of how Chinook nutrition varies across habitats is an important part of managing the species and the spaces they require.

Fatty Acids

A class of compounds that can be used to characterize diet and nutrition are fatty acids (FA). There are over 70 biologically relevant FA, however, only a few comprise a major fraction of cellular lipids in fish (Ackman, 1967; Tocher, 2003). FA are ubiquitous as energy storage and membrane structural molecules, and specific FA are important in supporting neural, eye, and immune-functioning, healthy pigmentation, and behavioral development in fish; acquiring adequate amounts of the necessary FA is important for optimal fitness (Alcorn et al., 2003; M. V. Bell et al., 1999; Ishizaki, 2001; Masuda et al., 1998; Nicolaides & Woodall,

1962; Watters et al., 2012). There is a diversity of FA forms in nature, and complex biochemical regulatory processes control the metabolism of these molecules. However, a relatively small number of major transformations dominate the FA pool.

Different FA forms are identified by the length of their carbon chain, as well as the number and position of double bonds using the nomenclature: [Chain Length]:[Number of Double Bonds]n-[Double Bond Position]. For example, the FA C18:1n-9 has 18 carbons in its chain and one double bond. The n-9 indicates that the first carbon in the double bond is the ninth carbon, counted from the methyl end. Other common unsaturated fatty acid types are the n-3 and n-6, frequently referred to as omega-3 and omega-6, respectively. In some cases, there are differences in the orientation of the double bond (i.e. cis vs trans stereochemistry) and branching in the carbon chain (e.g. bacterial iso-FA), however, these types of FA generally are not common in animals (Ackman, 1967; Kaneda, 1991).

The FA found in an organism's tissues arise from two sources: assimilation directly from the diet and synthesis using available precursors (Budge et al., 2006). FA biosynthesis is part of lipogenesis, or the formation of lipids. When excess carbohydrates and protein are available in the diet, lipogenesis is upregulated in fish and energy, in the form of FA, can be stored (Brauge et al., 1995). FA can be transported between depositional sites and

other tissues that may need them, either as substrate for energy production, or for anabolism (Tocher, 2003). In fish, the majority of lipogenesis is confined to the liver, while deposition or oxidation of lipids occurs in other tissues (Henderson & Sargent, 1985). The carbon substrate used by fish to form most lipids during lipogenesis is acetyl coenzyme-A (Acetyl-CoA) and the process is catalyzed by a family of fatty acid synthetase (FAS) enzymes (Wakil et al., 1983). Fatty acids grows two carbons at a time, such that synthesis requires eight acetyl-CoA, 42 ATP, and 112 NAD(P)H to produce a C16 FA (Tocher, 2003).

In herbivorous or omnivorous species, the carbon source for acetyl-CoA formation is often pyruvate formed during glycolysis. Predators adapted to high protein diets, such as salmon, may suffer when provided with high carbohydrate diets due to glucose intolerance (Polakof et al., 2012). Previous work has demonstrated salmonids may synthesize a significant amount of their FA from amino acid substrate (i.e. alanine) instead, also relying on significant routing from their lipid rich diets (Bou et al., 2016; Tocher, 2003).

Regardless of substrate, the most common products of FAS are the saturated FA C16 and C18 and these are synthesized widely by most organisms including fish (Sargent, 1989). The aforementioned FA initially synthesized by FAS are saturated with hydrogens (i.e. possess no double bonds) and relatively short, however, different organisms biosynthetically alter (e.g. desaturate or elongate) FA to different degrees. Moving forward, it is useful to distinguish

between saturated (i.e. those with no double bonds), unsaturated (i.e. those that possess double bonds), monounsaturated (MUFA; one double bond), and polyunsaturated (PUFA; multiple double bonds).

The degree of metabolic activity associated with a particular FA is a function of organismal need, metabolic resources, and that organisms' ability to acquire the compound in their usual diet. It seems predators, such as Chinook, may attempt to minimize metabolic alteration in favor of acquiring preformed FA in their diet. For example, in marine settings where bioactive n-3 PUFA (e.g. C22:6n-3) are abundant in dietary items, fish seem to be unable or unwilling to undertake de novo synthesize of n-3 PUFA (Colombo et al., 2017; Henderson, 1996; Jin et al., 2018). This is an intuitive shortcoming considering the metabolic waste (i.e. energy and substrate consumed) involved in utilizing resources to biosynthesize unnecessary excess of any given compound. Conversely, freshwater fish, in habitats where preformed n-3 PUFA are scarce have a greater capacity for metabolism of n-3 PUFA precursors.

In general, three processes dominate metabolism of preformed FA: elongation, desaturation, and oxidation/shortening. Elongation generally occurs on the cytosolic face of the endoplasmic reticulum, and the biosynthetic mechanism is not entirely dissimilar from the activity of FAS. However, the enzymes and regulatory mechanisms are independent. Briefly, elongation involves the enzyme mediated transfer of an acetyl moiety from a carrier (i.e.

acetyl-CoA) to a growing FA through consumption of ATP and NADPH. NADPH required to complete FA synthesis comes from both the pentose phosphate pathway, and glycolysis (Dias et al., 1999). The result of each sequential elongation cycle is a FA with 2 more carbons in the hydrocarbon chain.

The second major biochemical reaction determining the FA composition of organisms is β-oxidation, which results in shortening of the FA chain. ☙oxidation most frequently takes place in the mitochondria and involves the sequential liberation of acetyl-CoA from a FA chain (Schulz, 1991). β-oxidation results in loss of the carboxyl and α-carbon. The acetyl-CoA produced can then be used in the TCA cycle, or elsewhere. In addition to producing acetyl-CoA, β-oxidation also produces NADPH and $FADH_2$ which can be consumed by the electron transport chain to produce ATP. In a healthy fish, β-oxidation is likely to comprise a significant amount of their energy production (Frøyland et al., 2000; Sargent, 1989). When this reaction takes place in the mitochondria it is usually allowed to proceed to completion, entirely catabolizing the FA. However, the peroxisome is an organelle with similar enzymatic machinery to the mitochondria where incomplete β-oxidation can take place (Frøyland et al., 2000; Henderson & Sargent, 1985). If the FA exits the cycle of having acetyl-CoA extracted from it before being entirely decomposed, the product is a shortened FA.

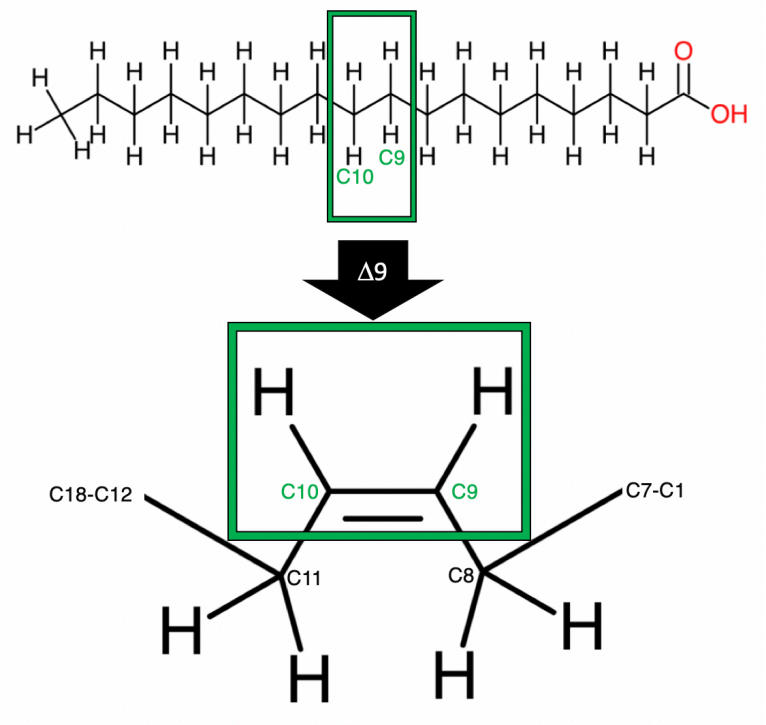

Figure 3.1. The activity of delta-nine desaturase on palmitic acid (C18:0) inserts a double bond between C10 and C11 and results in the loss of 2 hydrogens.

A third reaction that is important in altering cellular FA is desaturation, or the insertion of a carbon-carbon double bond in the FA chain (Figure 3.1). Desaturation of FA is a multi-enzyme process occurring primarily in the endoplasmic reticulum, ultimately catalyzed by a family of site specific desaturase enzymes (Cook & McMaster, 2002). Desaturation is an aerobic process that, like elongation, consumes NAD(P)H. The enzymes responsible for these desaturations are categorized based on the location they insert the double bond. In contrast to the FA naming nomenclature described above, which indicates the double bonds position by counting from the methyl tail, desaturase

enzymes are labeled based on their recognition distance from the carboxyl end of the FA. For example, the enzyme responsible for desaturating C16 to C16:1n-7 is Δ9-desaturase (Brenner, 1974; Hastings et al., 2001; Tocher, 2003); Δ9-desaturase inserts a double bond, starting on the ninth carbon, counted from the FA carboxyl carbon (Figure 3.2). Figure 3.3 provides an overview of the FA synthetic network in fish. The necessity of both possessing the genes for specific enzymatic machinery, and expending energy to express those genes, in order to synthesize and alter FA mean that not all organisms synthesize and alter FA to the same extent.

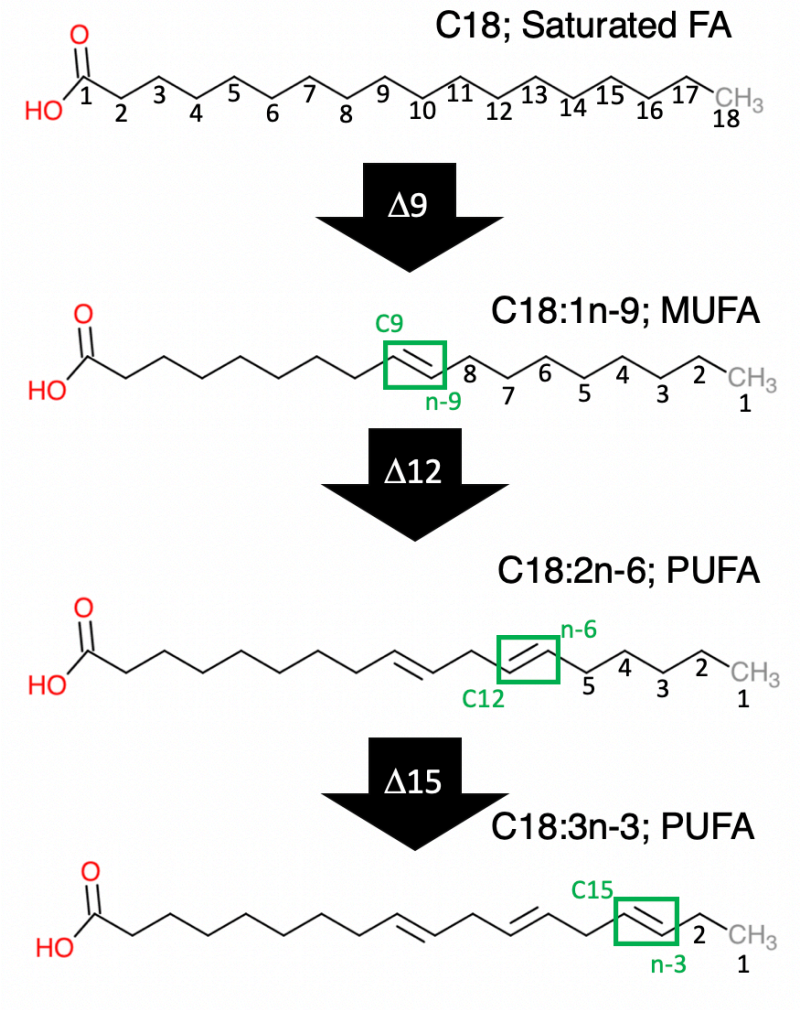

Figure 3.2. Schematic showing sequential desaturation of a C18 fatty acid. Trans-bonding is shown here, however, most common desaturase enzymes produce cis-stereochemistry.

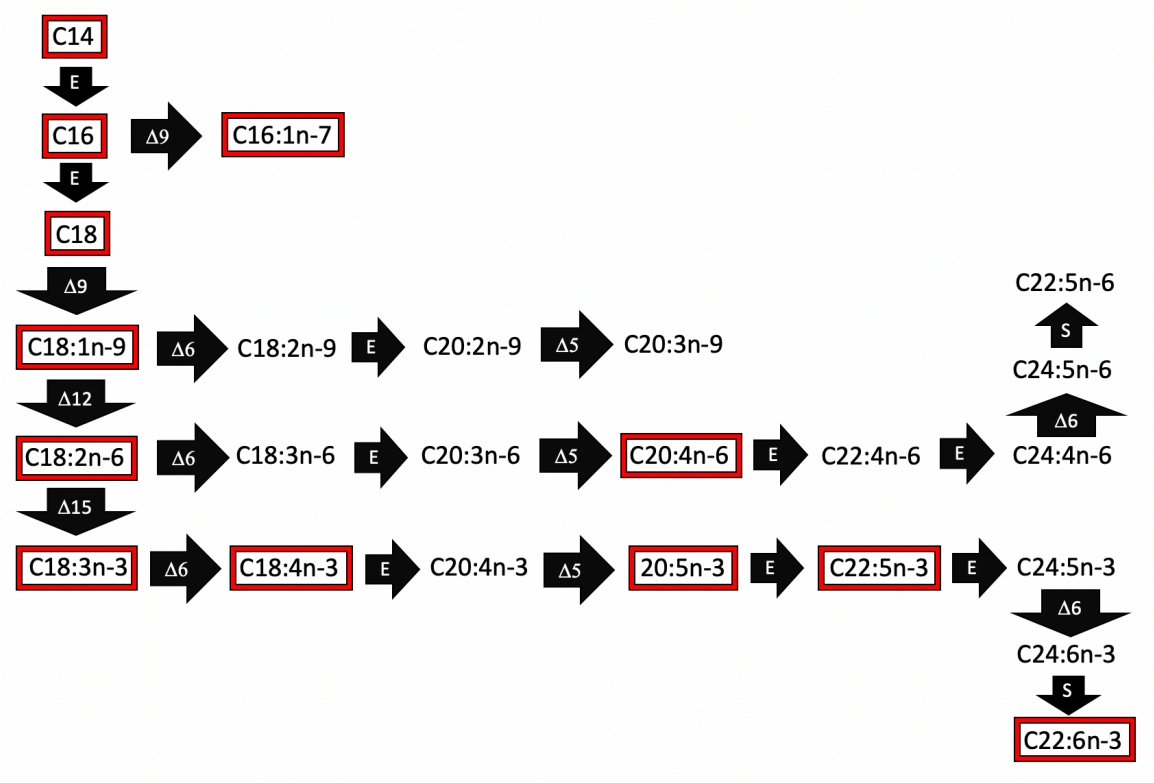

Figure 3.3. Diagrammatic overview of the fatty acid synthesis network in fish. Δ5, Δ6, Δ9, Δ12, and Δ15 desaturase enzymes are identified as black arrows. Retro-conversion (chain-shortening) is identified with S, and elongation with E. Adapted from Tocher et al. 2003.

For most consumers, certain PUFA must be supplied in the diet for healthy development and cell functioning (Gladyshev & Sushchik, 2019; Glencross, 2009). FA that must be supplied in the diet are called essential fatty acids (EFA). EFA exist because not all organisms can synthesize all FA in adequate amounts by themselves. Because some EFA play important biological roles, an inadequate supply can negatively impact growth, development, and performance (Takeuchi, 1997). Specifically, vertebrates lack the desaturase enzymes responsible for forming C18:2n-6 and C18:3n-3 (Δ12, and Δ15 desaturases).

The varying capacity of organisms, and their propensity, to catabolize FA or supplement their diet with de novo biosynthesis is underlain by a complex polygenic framework. De novo biosynthesis can help meet physiological needs but inters a cost to the organism relative to acquiring FA directly from the diet, due to energy consumption during anabolism. Nonetheless, some EFA might be considered only conditionally essential if the organism is able to synthesize adequate amounts if provided with specific precursors in the diet. For Chinook, C18:2n-6 and C18:3n-3 are undoubtedly EFA. If C18:2n-6 and C18:3n-3 are supplied in the diet, Rainbow Trout (Oncorhynchus mykiss) are able to synthesize downstream PUFA and it is likely Chinook can, as well. Thus, FA such as C20:4n-6, C20:5n-3, C22:5n-3, and C22:6n-3 might be conditionally essential in Chinook if C18:2n-6 and C18:3n-3 are provided in the diet.

The FA composition of predator tissues reflects their diet, although metabolism can play a role in decoupling predator-prey FA compositions (Budge et al., 2011; Burns et al., 2011). Nonetheless, the FA composition of Chinook should be affected by significant differences in community supporting them. For example, n-6 and relatively short n-3 PUFA (e.g. C18:2n-6, C18:3n-3 and C20:4n-6) are more abundant in freshwater and terrestrial systems while longer n-3 PUFA (e.g. C20:5n-3, C22:5n-3, C22:6n-3) are abundant in marine systems (Colombo et al., 2017). Terrestrial plants also produce more long chain FA (>22 carbons) and C18:2n-6 than do microbes or algae (Shanab et al., 2018; S. Taipale et al., 2013). For this reason, the ratio of n-3/n-6 FA have been used to estimate whether resources are primarily terrestrial (<1) or aquatic (>1). Data indicate healthy fish growth, reproduction, and immune function are promoted when consuming diets with n-3/n-6 ratios from 2-3 (Ahlgren et al., 2009; Makhutova et al., 2011).

Due to differences in the FA synthesized by producers, differences in the FA profile of consumers may be related to differences in their diet (Budge et al., 2006, 2007). However, in situations where the diet is incongruous with biological need, or where the diet and tissues are not in equilibrium, the assumption of diet-tissue FA parity is unlikely to hold true (Robin et al., 2003). Interpretation of differences in the FA composition of Chinook may shed light on the primary producers supporting them, but must be contextualized by metabolism. An

increasingly utilized tool to further scrutinize the sources and metabolism of FA, is stable isotope analysis (SIA).

Stable Isotopes

The stable isotope ratio of organic matter reflects the source or synthetic processes underlying the atoms comprising it (Deniro & Epstein, 1978, 1981; Macko et al., 1983, 1987). For this reason, SIA is a powerful tool for studying ecological systems (Peterson & Fry, 1987). Bulk SIA, or the measurement of whole tissues, can be used to determine the sources of organic matter assimilated into consumer tissues, nutrients assimilated into producers, or estimate trophic level (Dover et al., 1992; Layman et al., 2011; Post, 2002; Victoria et al., 1992). However, bulk SIA is limited in its ability to identify the source of specific compounds. Compound specific isotope analysis, on the other hand, determines the stable isotope composition of specific molecules in organic matrices. Compound specific isotope analysis can help determine the source of, or the nature of transformations affecting, specific biomolecules.

FA are comprised, almost entirely, of hydrogen and carbon. Therefore, these are obvious elements to target during compound specific analysis (Twining et al., 2020). The hydrogen in FA is bound to carbon and is non-exchangeable on ecological timescales (Sessions et al., 2004). However, the two elements may provide complementary information. Carbon isotopes in FA have been used to

produce mixing models estimating inputs of different organic matter sources to consumers (Budge et al., 2008, 2012; Graham et al., 2014), whereas hydrogen isotopes, on the other hand, have promise as a trophic tracer or a location proxy (Bowen et al., 2005; Coulter et al., 2017; Pilecky et al., 2021; Suzuki et al., 2013). Most isotope analysis of FA, to this point, have been observational. Experimental work has focused on marine systems, soil organisms, and invertebrates. For this reason, the effect that biophysical status (e.g. ontogenetic changes) and diet quality can have on FA metabolism and isotope fractionation in juvenile Chinook salmon are not well described.

Despite lacking a systematic understanding of intracellular isotopic variation, lessons from bulk analysis can inform interpretation of compound specific isotope data. In the case of δ^2H, bulk measurements of organic matter in freshwater systems have already demonstrated it to be a powerful tracer of allochthonous inputs (Doucett et al., 2007; Solomon et al., 2009). Presumably, evapotranspiration from photosynthesizing leaves results in significantly increased δ^2H in allochthonous resources relative to collocated autochthonous production. Conversely, the δ^2H of organic matter produced during anaerobic acetogenesis is extremely negative relative to what would be expected for photoautotrophs (Valentine et al., 2004). In the case of carbon, coupled methanogenesis-methanotrophy in freshwater habitats can inject organic matter with low δ^{13}C into food webs (Deines, Bodelier, et al., 2007; Deines, Grey, et al.,

2007; Deines & Grey, 2006). For these reasons, a significant offset of individual FA δ^2H in the positive direction could indicate inputs of allochthonous materials, however, extremely negative δ^2H and/or δ^{13}C could be the result of inputs from anaerobic microbes.

When direct assimilation from the diet (i.e. dietary routing) occurs the carbon and hydrogen isotope composition of biomolecules (i.e. FA) in consumers is expected to reflect the isotopic composition of those molecules in their diet (Fujibayashi et al., 2016; Newsome et al., 2014; Stott et al., 1997). Therefore, differences in the carbon and hydrogen isotope fractionation associated with FA synthesis across different producer taxa are reflected in the consumer tissues assimilating those FA (Galloway et al., 2014; S. Taipale et al., 2013). Previous measurements indicate this is true in some cases, although unexplained variability between consumer FA and their diet has been observed (Chiapella et al., 2021; Ruess et al., 2005). Ongoing reductions to δ^{13}C values of C18:2n-6 and C18:3n-3 have also been observed with increasing trophic level (Gladyshev et al., 2012). In other cases, differences in the carbon isotope fractionation between EFA in consumers and their diet have ranged between positive and negative values (Fujibayashi et al., 2016; Gladyshev et al., 2016; Lau et al., 2009; Twining et al., 2020). Unexplained variability in the isotope composition of FA is generally attributed to differences in metabolism. Namely, differences in the amount of FA biosynthesis and alteration.

Currently, too little is known about the interacting impacts of diet quality and metabolic demands on the metabolism and associated isotopic fractionation of FA to confidently attribute the isotope differences observed to a single cause. Determining the FA composition of potential food sources can help tease these factors apart. It seems that FA in high abundance, within the diet, relative to organismal need constitute the best trophic tracers for mixing models. Furthermore, FA with limited sources (EFA) are also considered the best trophic markers due to their biosynthetic novelty. However, there is currently no framework allowing for direct metabolic interpretation of FA stable isotope compositions in consumers. Ontogenetic changes, environmental changes, or changes in food availability could affect rates of lipogenesis and potentially the isotope composition of the lipids produced in fish (Daly et al., 2009; Lai & Yamada, 1992; Litz et al., 2017; Mizuno et al., 2012). In general, processes removing FA (e.g. oxidation) are expected to remove FA depleted in 13C and 2H most readily. This, presumably, leaves behind a residual pool of FA with higher δ^{2}H and δ^{13}C. However, enzymatic fractionations associated with biosynthetic alteration (e.g. elongation and desaturation) could be non-trivial and of varying directionality. To maximize the utility of isotope analysis in FA, the dynamics between depositional pools, de novo synthesis, and dietary intake need to be resolved.

Objective

The present study is concerned with determining the differences that arise in the FA composition of Chinook salmon rearing in different freshwater habitats. Here, we present data on the FA contents and isotopic compositions of experimentally enclosed Chinook salmon from six habitats in the SSJD. To simulate freshwater rearing, juvenile Chinook from a hatchery were enclosed in natural habitats like those they might encounter during seaward migration. Following the experimental enclosure, we determined and compared the FA contents of Chinook tissues to assess the quality of rearing habitats with respect to FA nutrition. Namely, whether utilization of certain habitats might contribute more towards Chinook success. We also assessed the FA composition of the experimental Chinook to estimate whether the primary pathways of secondary production vary between these habitats. To this end, we also measured the carbon and hydrogen isotope composition of individual FA. We hypothesized that individuals rearing in off-channel habitats were likely to accumulate greater FA concentrations in their tissues. Furthermore, we anticipated these individuals might receive FA from alternative basal sources (e.g. microbial recycling detrital organic matter) which could result in drastic difference in FA relative abundances, and extreme isotope values. Overall, these data increase our understanding of Chinook nutrition in the SSJD.

Methods

Enclosure Experiment

Juvenile Chinook salmon collected from the Feather River hatchery were transported to the study site in a fish transportation trailer and the abdominal cavity of each fish was implanted with an 8 mm. passive integrated transponder (PIT) tag. At the study sites (Table 3.1), fish were held in plastic tanks for two days to ensure tag retention. Following this retention period, fish were weighed, measured, and placed in the experimental enclosures for 45 days. The dates of enclosure were February 16, 2019 to April 2, 2019, with a deviation of one day between sites for deployment and retrieval due to logistics.

The experimental enclosures consisted of a PVC pipe (25.4 mm.) frame measuring 1.2 m. x 1.2 m. x 0.6 m., enclosed in a 6.3 mm. pore size plastic mesh. Floats on the frame ensure that, when deployed, the top mesh floats even with the waters' surface. Following the 45-day enclosure period, fish were collected. At this time, they were measured, weighed, and euthanized via a quick blow to the head. Chinook were then stored frozen until bulk isotope and FA analysis. This work was carried out in strict accordance with the recommendations set forth by the UC Davis Institutional Animal Care and Use Committee (Protocol #18883).

During enclosure deployment, zooplankton samples were collected weekly using a 30 cm. diameter, 153 μM-mesh net. The net was towed through the

water column on a 5 m. rope for 5-10 minutes, depending on zooplankton density. Following collection, zooplankton were kept live in ambient water for transport to the lab. In the lab, zooplankton were filtered into DI water and left overnight. With the help of a dissecting microscope, zooplankton were separated from detritus and stored in 1.5 mL micro-centrifuge tubes before preparation for isotopic analysis.

Enclosure Locations

Six sites in the SSJD were selected to house fish enclosures (Table 3.1). The habitats chosen for the experiment were selected based on their potential use by Chinook, managerial significance, and differences in environmental characteristics. The timing of our enclosure placement was designed to mimic patterns of use by out-migrating juvenile salmon.

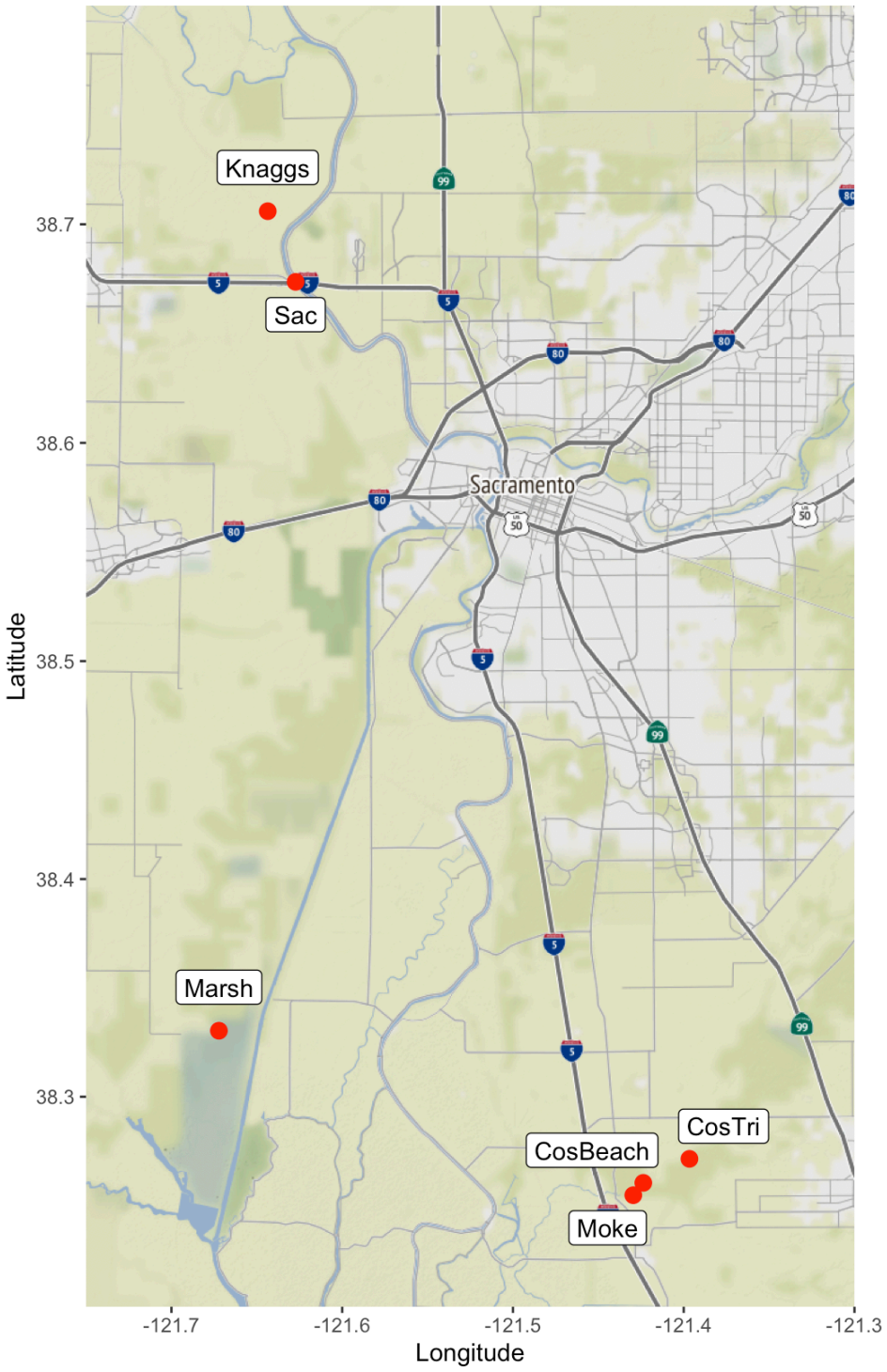

Figure 3.4. Map of Chinook salmon enclosure locations in the Sacramento-San Joaquin River Delta.

Two of our sites are representative of many of the major river channels throughout the SSJD, the Mokelumne River site (Moke) in particular (Whipple et al. 2016). The Mokelumne has multiple dams along its watercourse and is entirely disconnected from its floodplain. The Sacramento River site (Sac) is similar to Moke; these sites are both situated in habitats with low water residence times that function principally as water conveyance channels. Like the Mokelumne, the Sacramento is a highly impounded and managed river. Unlike the Mokelumne site, Sac does have some upstream floodplain habitats that may support downstream production through export of floodplain organic matter.

Two of our sites were in the Cosumnes River watershed, the only major river in the SSJD that is not dammed (Whipple et al. 2016). One of these sites, the Cosumnes Triangle (CosTri), was on conserved floodplain. During wet years, this area might be productive rearing habitat for fish. However, during dry years it may never become inundated. The second site within the Consumnes river watershed (CosBeach) was downstream of CosTri, near the Cosumnes River's confluence with the Mokelumne River. The CosBeach site was situated in a side-channel of the Cosumnes river. During periods of low flow in the Cosumnes River, CosBeach is tidally influenced and experiences relatively little directional flow. However, when the Cosumnes River's discharge is high, as it was during our study, there is directional downstream flow due to overland flow flooding into

the distal end of the channel. During the period of our experiment, both sites on the Cosumnes river were subject to flow-through conditions.

The final two sites were in the Sacramento river, upstream of the Sac channel site. One of these sites, Knaggs Ranch (Knaggs), was on flooded agricultural land. The prospect of utilizing agricultural infrastructure to provide floodplain-like habitat has attracted significant interest recently, primarily due to its promise as rearing habitat for salmonids. The other off-channel Sacramento River site, Baby Marsh (Marsh), is at the north end of the Sacramento river's primary floodplain —the Yolo Bypass. Similar to the aforementioned floodplain habitat in the Cosumnes (CosTri), during wet years the Yolo bypass may provide high quality habitat and an alternate migratory route for rearing Chinook. However, in dry years it may provide little, or no, benefit to fish.

Bulk Isotope Measurements

Bulk stable isotope measurements of zooplankton and Chinook muscle tissue were completed at the UC Davis Stable Isotope Facility. Samples of muscle tissue and zooplankton were dried for 48 hours at 55° C. Approximately 1mg. was weighed into 10mm. x 8mm. tin capsules that were then crimped and stored in a 96 well-plate. Samples were analyzed for their carbon isotope compositions using an Elementar Vario EL Cube Elemental Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20-20

isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Samples were analyzed via continuous-flow, using helium as a carrier, and unknowns were interspersed with laboratory reference materials calibrated against the international reference materials: IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64, and USGS-65. We report all isotope compositions in delta notation relative to the international standard Vienna PeeDee Belemnite. Long term reproducibility of standard values is 0.2‰ for $\delta^{13}C$.

Fatty Acid Measurements

To quantify and measure the $\delta^{2}H$ and $\delta^{13}C$ of our FA we used an adaptation of the method set forth by O'Fallon et al. (2007). Briefly, frozen samples of muscle tissue extracted from along the lateral line (0.5g wet weight) were hydrolyzed in 1N KOH in methanol at 55°C for 1.5 hours. KOH was neutralized by, and esterification of free fatty acids catalyzed by, addition of 24N H_2SO_4. Samples were incubated again at 55°C for 1.5 hours to allow the reaction to run to completion. After esterification, fatty acid methyl esters (FAME) were extracted with 3mL of hexane accompanied by vortex mixing for 5 minutes. After vortex mixing, the hexane was pipetted off and reserved in GC vials at -20°C until analysis. Derivative molecules were analyzed in triplicate for $\delta^{2}H$ and $\delta^{13}C$ with a Delta V Plus isotope ratio mass spectrometer after separation on a 60 m HP-88 column in a Trace 1310 gas chromatograph (Thermo-Fisher Scientific; Waltham,

MA, USA) at the EDGE Isotope Lab, UC Riverside. Quantitation was done via parallel derivatization and measurement of a C13:0 fatty acid standard. Reproducibility of isotope measurements of standard material was 0.8‰ for $\delta^{13}C$ and 8.5‰ for $\delta^{2}H$ The carbon and hydrogen isotope composition of the C13 FA standard was measured, underivatized, using conventional bulk combustion and pyrolysis methods in order to correct for the methyl carbon and hydrogen added during derivatization. This correction assumes that the isotope fractionation associated with methylation is constant among FA.

Statistical Analysis

We tested for differences in $\delta^{13}C$, $\delta^{2}H$, and FA content using one-way ANOVA. ANOVA was followed by Tukey's Honest Significant Difference (HSD) test when significant differences were detected. Significance was assessed at $p<0.05$. Before testing for differences in $\delta^{13}C$ between habitat type we normalized our FA-$\delta^{13}C$ using the mean bulk measurement of zooplankton from the same site according to the equation: $\delta^{13}C_{FA} - \delta^{13}C_{zoop} = \delta^{13}C_{norm}$. We did not perform a normalization on our $\delta^{2}H$ data. To compare our bulk zooplankton and fish isotope data we used the typical trophic discrimination factors of 0.4‰ and 3.4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. All statistical analyses were completed in R.

Results

Bulk Isotope Analysis

Our bulk measurements indicate there were only slight differences in the carbon and nitrogen isotope of composition of the invertebrates collected from our study sites. In general, all the sites had invertebrates with a similar carbon and nitrogen isotope composition ($\delta^{13}C$ = -30.1 ± 3.0‰; $\delta^{15}N$ = 7.3 ± 2.4‰; n =147). An exception was the Moke site, which stood out as having invertebrates with relatively lower $\delta^{15}N$ and higher $\delta^{13}C$ than other sites. We determined that our Chinook samples from all sites, except Moke and Sac, had isotope compositions mostly consistent with feeding on the zooplankton collected at that site (Figure 3.4). Although, fish from every site, except Knaggs, had more positive $\delta^{13}C$ values than would be predicted based on the collocated zooplankton. Fish from Moke and Sac were also enriched in ^{15}N relative to their expected isotopic compositions, based on measurements in local zooplankton.

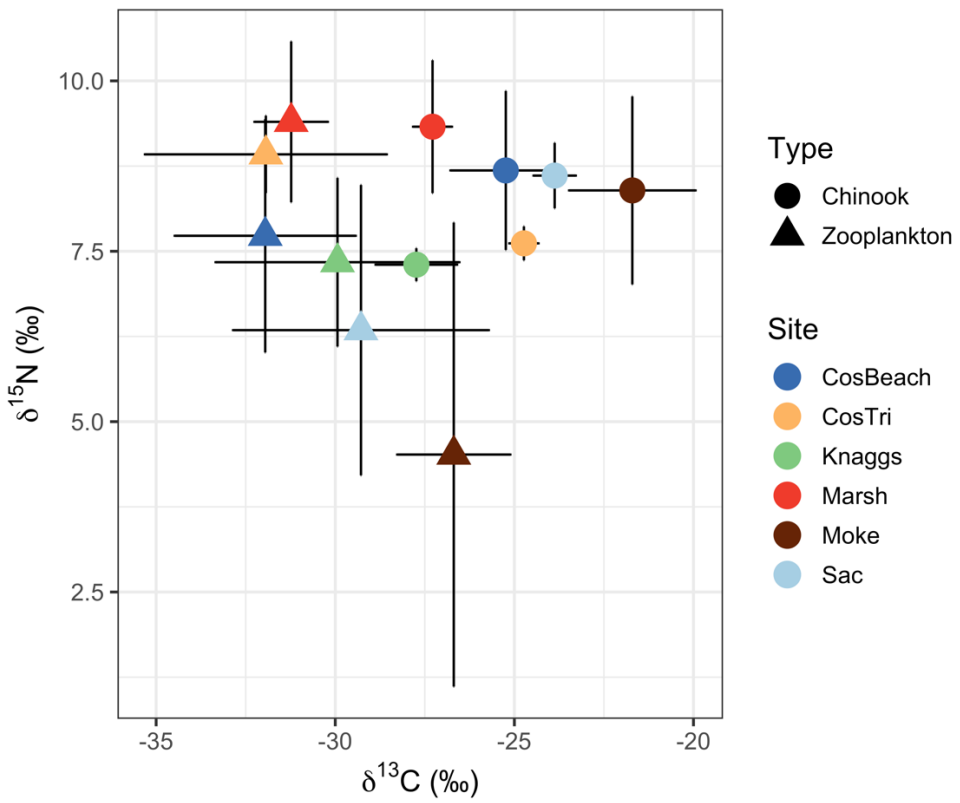

Figure 3.5. Summary of the bulk carbon and nitrogen isotope composition of Chinook salmon and collocated zooplankton.

Fatty Acid Abundances

We quantified, and measured the δ^2H and $\delta^{13}C$ values of 12 FA, ranging from saturated to highly unsaturated: C14:0, C16:0, C18:0, C16:1n-7, C18:1n-9, C18:2n-6, C18:3n-3, C18:4n-3, C20:4n-6, C20:5n-3, C22:5n-3, C22:6n-3. Overall, there were differences in the amounts (ANOVA: $F_{(11, 204)} = 61.46$; $p < 0.05$; n = 216; Figure 3.5) of individual FA when fish from every habitat were considered together. Saturated FA and MUFA such as C16, C18, C16:1n-7, and C18:1n-9 were the most abundant, while n-3 PUFA such as C18:4n-3 and

C18:3n-3 were generally scarce. Other n-3 and n-6 PUFA, such as C22:6n-3, C20:5n-3, C20:4n-6, and C18:2n-6, occurred in intermediate amounts.

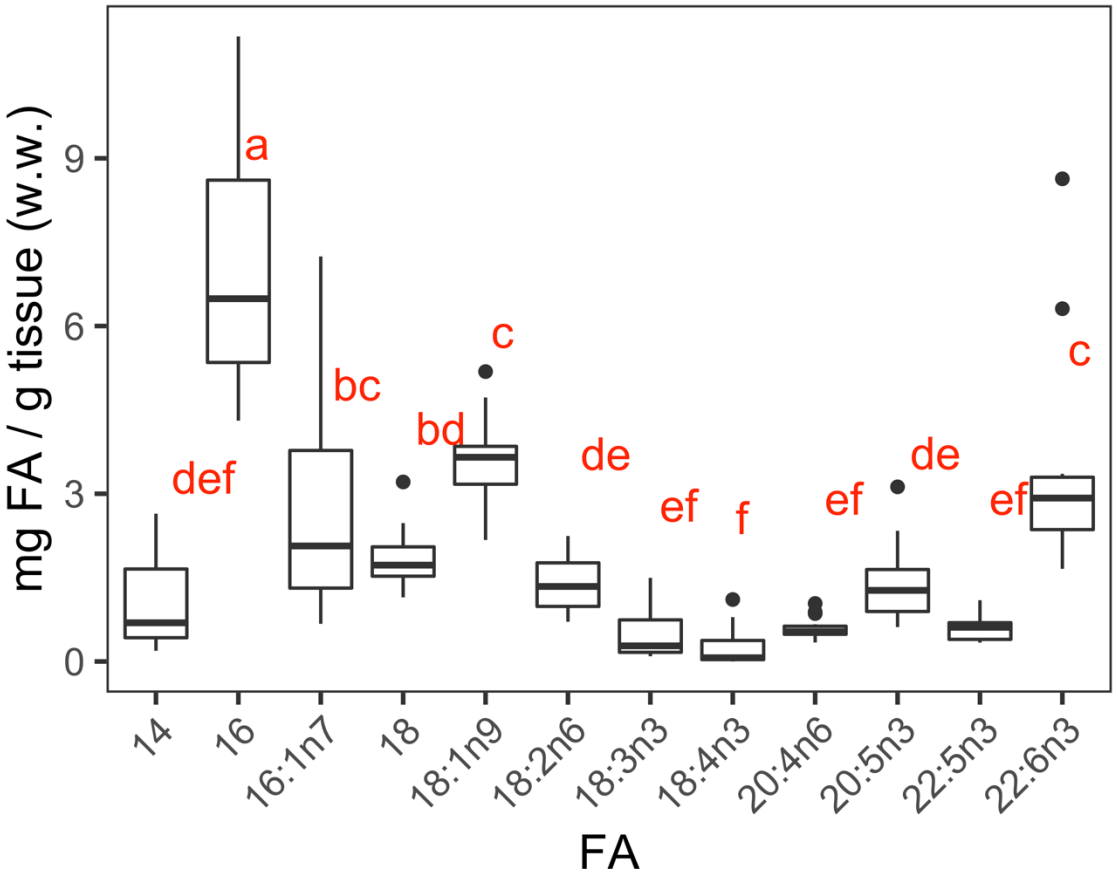

Figure 3.6. Summary of muscular fatty acid concentrations in Chinook salmon with labels indicating significant differences ($p < 0.05$; Tukey HSD).

Overall, the FA profiles of fish were similar between sites and the high n-3/n-6 ratios (>3) indicate an aquatic source. One major surprise was the increased proportion of C22:6n-3 in fish from Sac (Figure 3.6). Fish from Knaggs and Marsh, on the other hand, had higher proportions of C16:1n-7 (Figure 3.7). We found that the n-3/n-6 ratio at all sites was above 1 in all samples. Although the overall composition was similar, we determined that the total amount of FA varied with site (ANOVA: $F_{(5, 12)} = 4.368$; $p < 0.05$; $n = 18$; Figure 3.8). Individuals from the Marsh had some of the highest total concentrations of FA, seemingly followed by individuals from Knaggs. In comparison, Chinook from Sac, Moke, CosBeach, and CosTri all had slightly lower total FA concentrations.

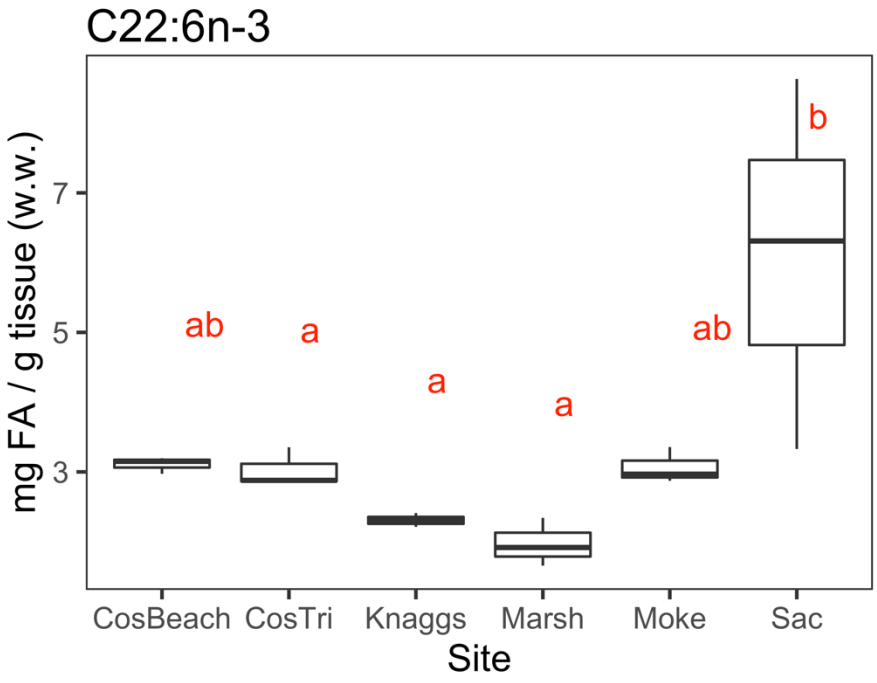

Figure 3.7. Comparison of Chinook salmon muscular concentrations of C22:6n-3 between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

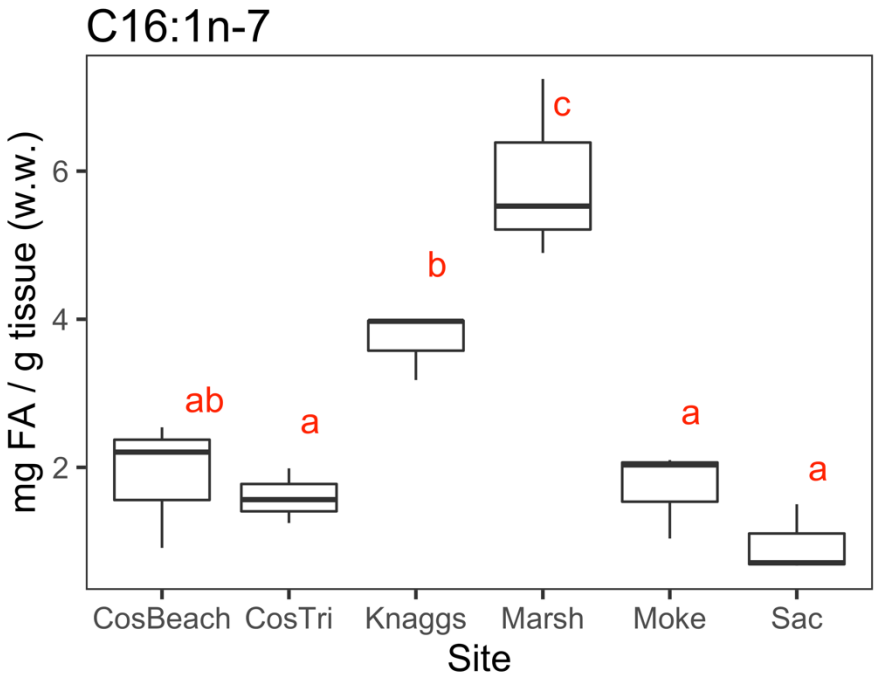

Figure 3.8. Comparison of Chinook salmon muscular concentrations of C16:1n-7 between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

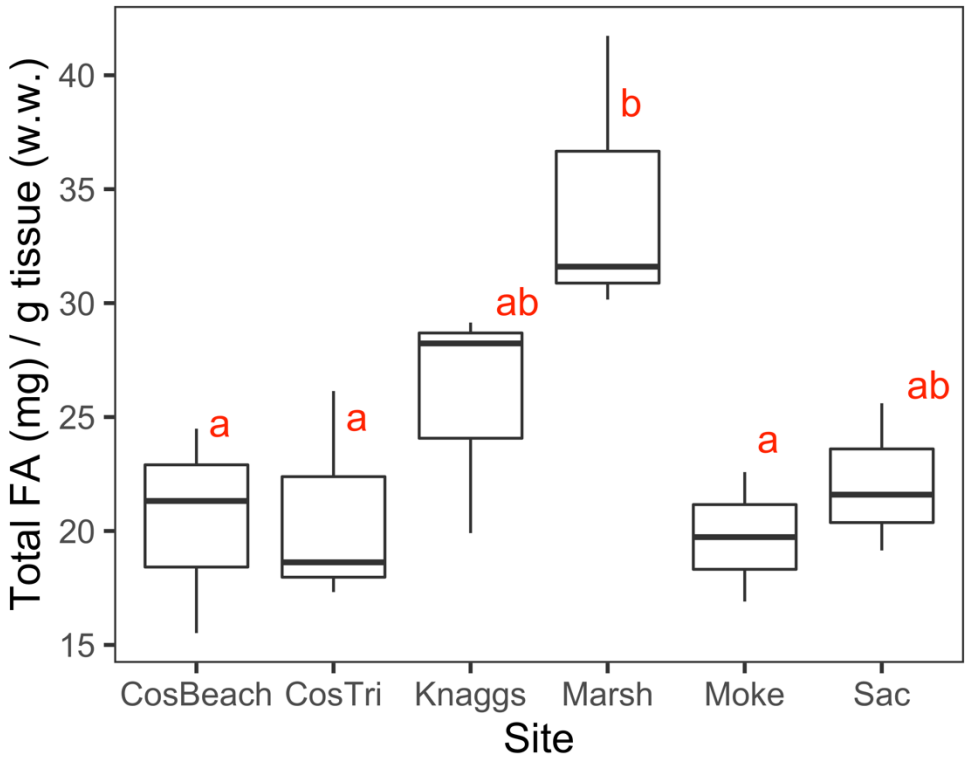

Figure 3.9. Comparison total muscular fatty acid concentrations between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

We used ANOVA to detect differences in the amount of FA coming from each FA class (i.e. Saturated, MUFA, and n-3/n-6 PUFA) between habitat types, however, these significant ANOVA results were not always supported by a significant post hoc test result. We determined that Marsh fish had the highest concentrations of saturated FA, slightly more than individuals from Knaggs and CosTri, and significantly more than individuals from CosBeach, Moke, or Sac (ANOVA: $F_{(5, 12)} = 5.079$; $p < 0.05$; $n = 18$; Figure 3.9). A similar trend to the saturated FA was evident in MUFA, among sites (ANOVA: $F_{(5, 12)} = 6.53$; $p <$

0.05; n = 18; Figure 3.10). While ANOVA indicated there were significant differences in n-3 (ANOVA: $F_{(5, 12)} = 3.577$; $p < 0.05$; n = 18; Figure 3.11) and n-6 (ANOVA: $F_{(5, 12)} = 2.099$; $p < 0.05$; n = 18; Figure 3.12) PUFA concentrations among sites, none of these differences were significant when tested with Tukey's HSD.

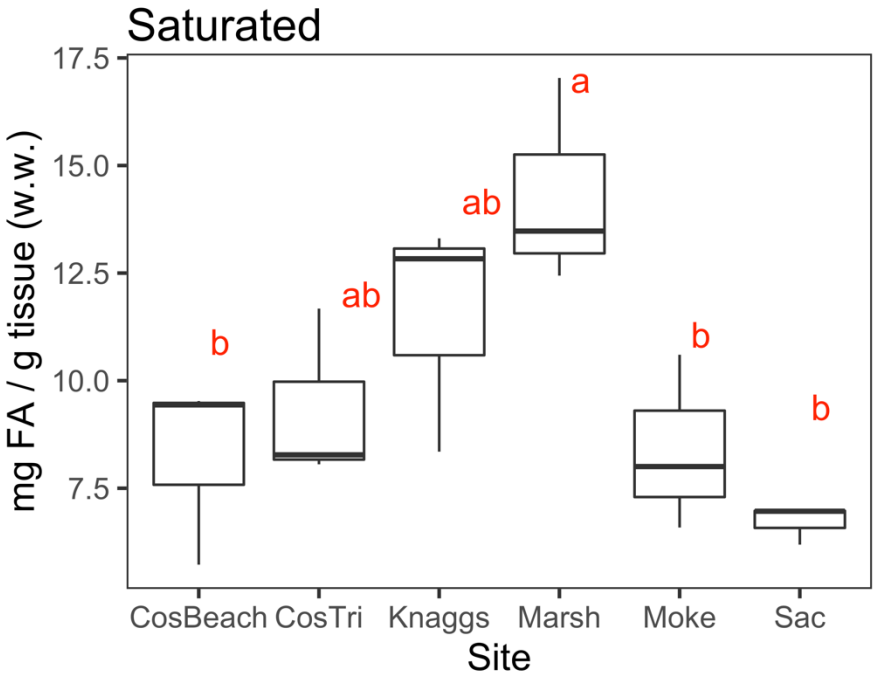

Figure 3.10. Comparison saturated fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

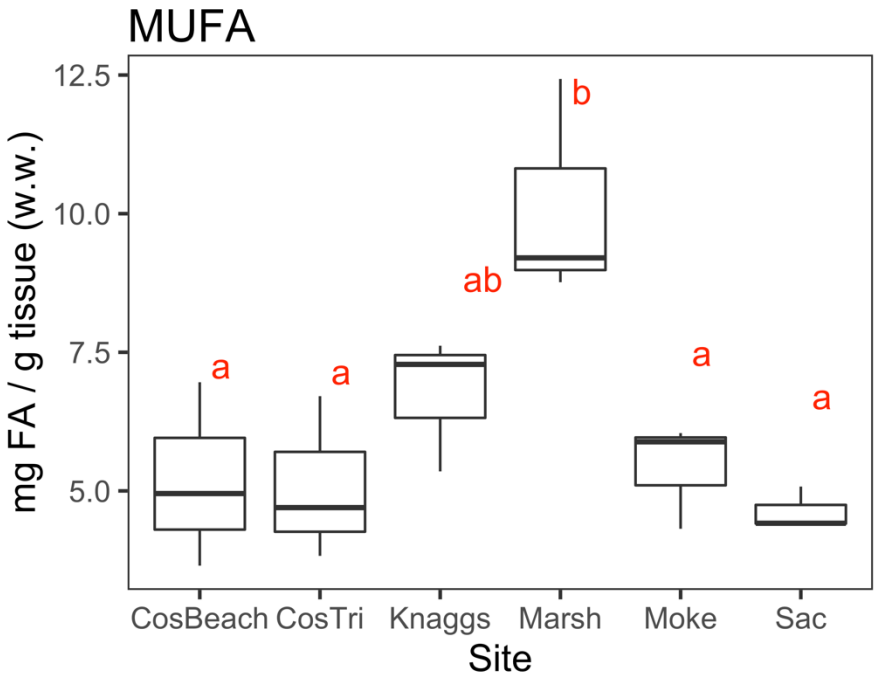

Figure 3.11. Comparison monounsaturated fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

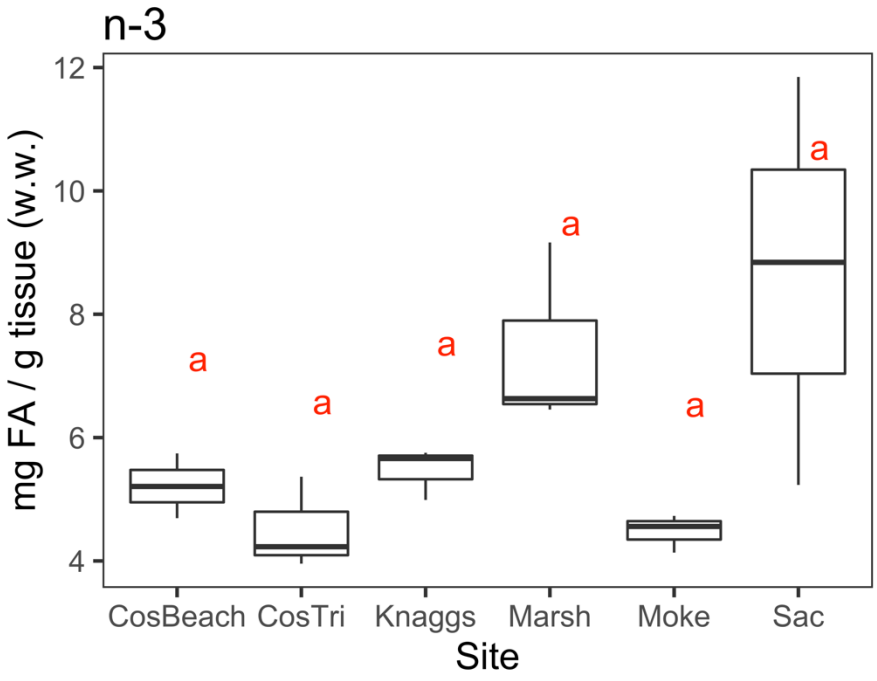

Figure 3.12. Comparison n-3 (omega-3) fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

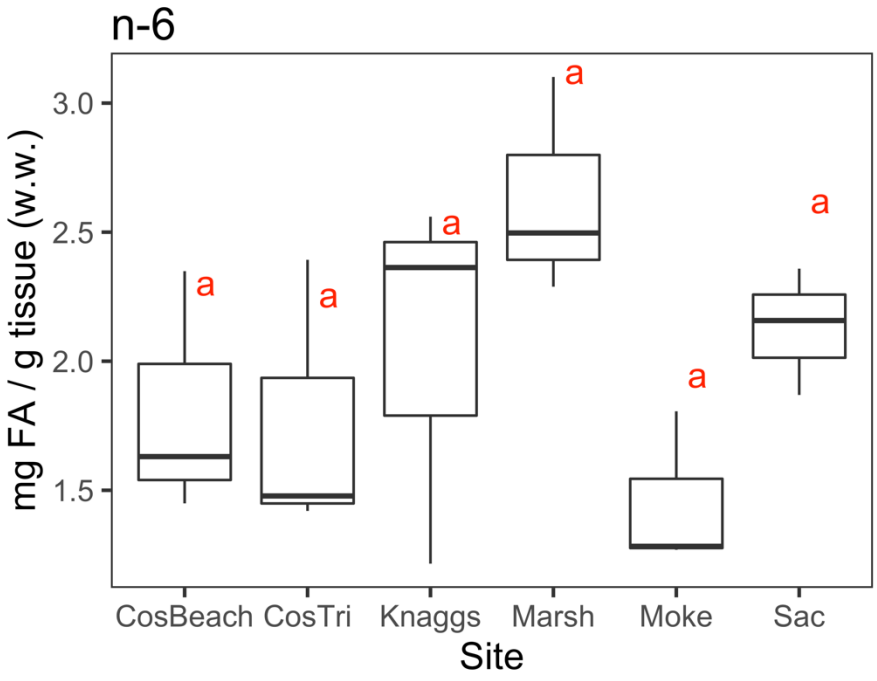

Figure 3.13. Comparison n-6 (omega-6) fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

Differences in FA class totals between habitats were underpinned by differences in the amount of individual FA. ANOVA found significant differences between sites in the concentration of every FA (C14: $F_{(5, 12)} = 11.68$; C16: $F_{(5, 12)} = 3.954$; C16:1n7: $F_{(5, 12)} = 19.5$; C18: $F_{(5, 12)} = 4.979$; C18:3n-3: $F_{(5, 12)} = 20.1$; C18:4n-3: $F_{(5, 12)} = 27.77$; C20:4n-6: $F_{(5, 12)} = 3.243$; C20:5n-3: $F_{(5, 12)} = 11.51$; C22:5n-3: $F_{(5, 12)} = 3.886$; C22:6n-3: $F_{(5, 12)} = 5.232$; $p < 0.05$ and n=18; Figure 3.13 – Figure 3.22) except for C18:2n-6 and C18:1n-9. Chinook from the Marsh and Knaggs sites stood out as having some of the highest FA concentrations, containing significantly more C16:1n-7, C18:3n-4, and C18:4n-3 than most other

sites. For some other FA, such as C16, C18, C20:5n-3, and C22:5n-3, the Marsh and Knaggs sites were not significantly greater, but still near the top of the distribution. Despite relatively high amounts of other FA, the Marsh and Knaggs fish had some of the lowest concentrations of C22:6n-3 measured.

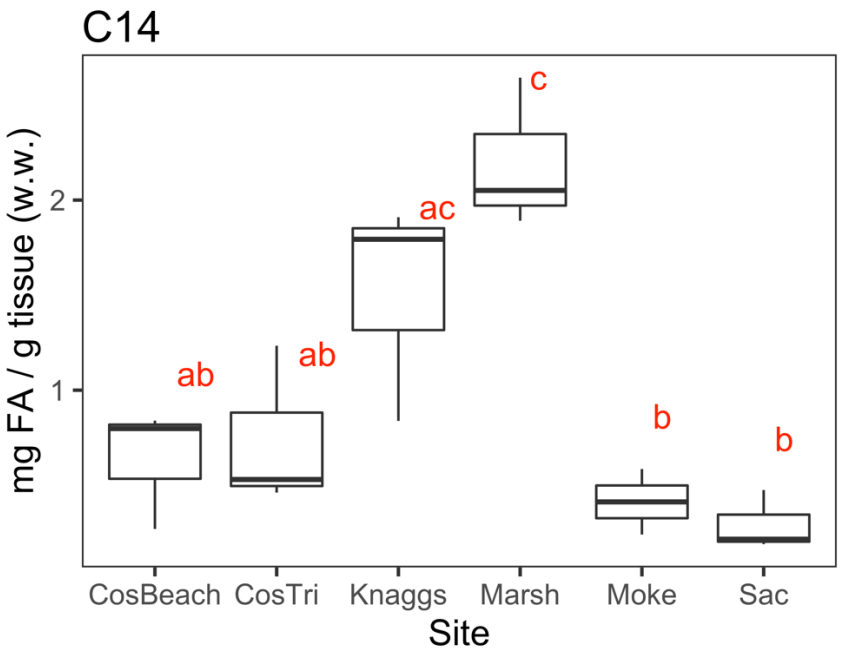

Figure 3.14. Comparison C14 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

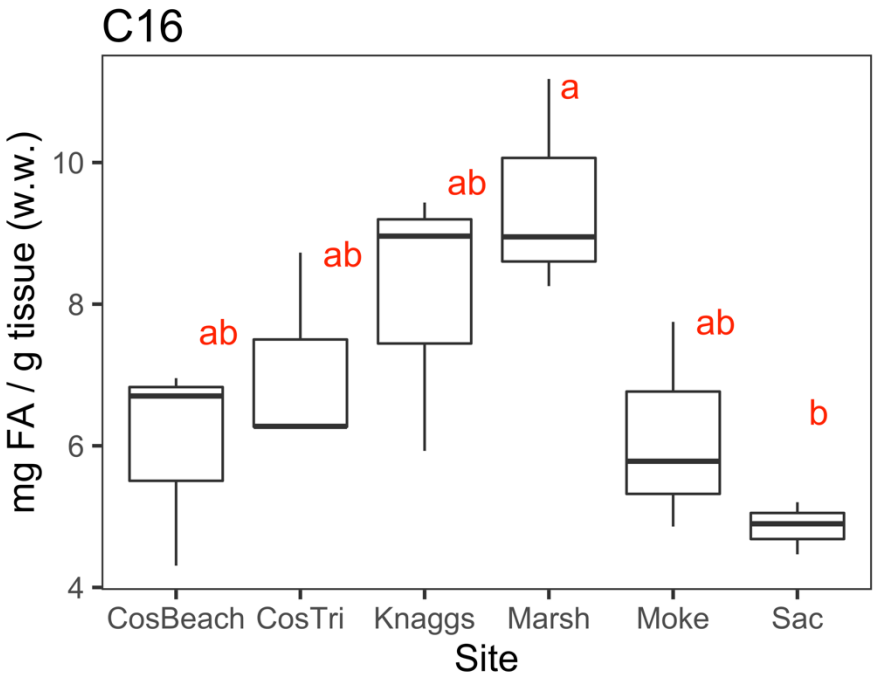

Figure 3.15. Comparison C16 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

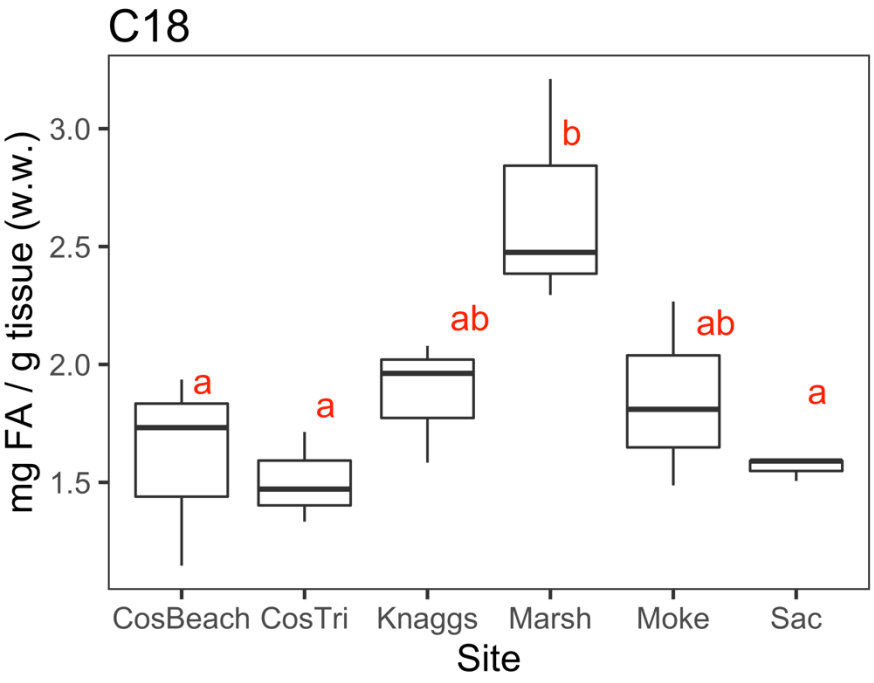

Figure 3.16. Comparison C18 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

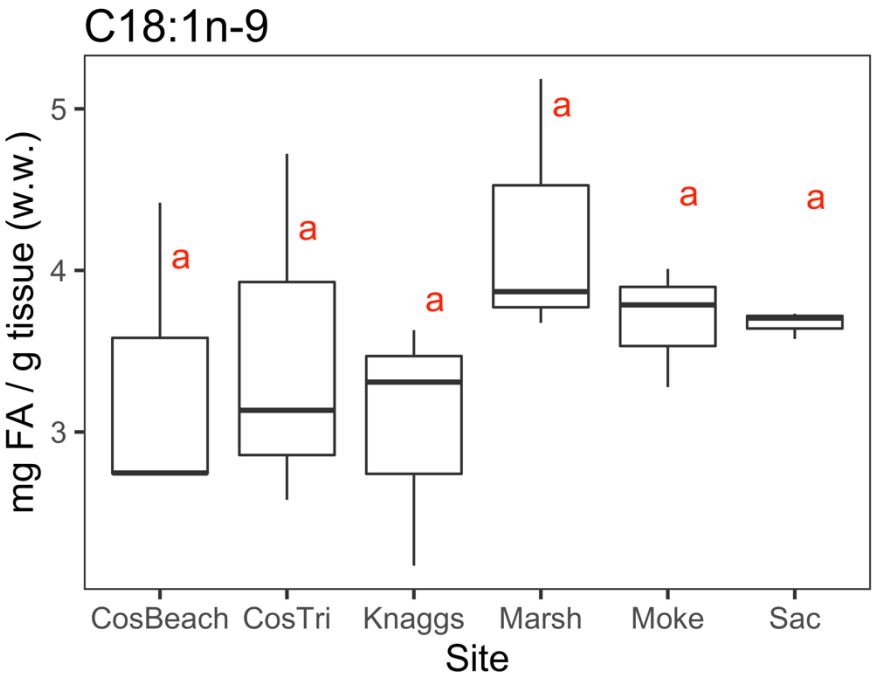

Figure 3.17. Comparison C18:1n-9 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

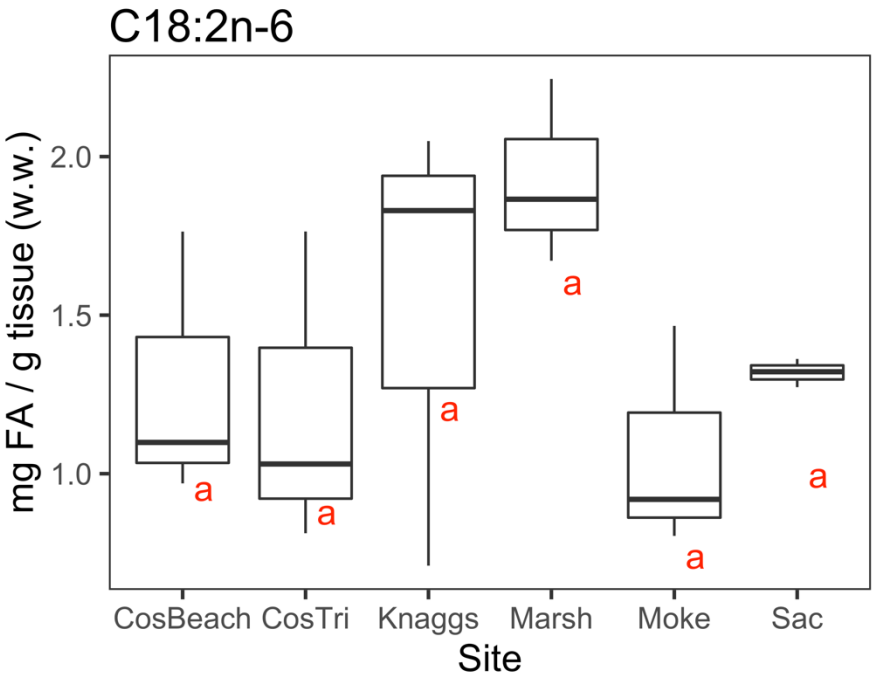

Figure 3.18. Comparison C18:2n-6 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

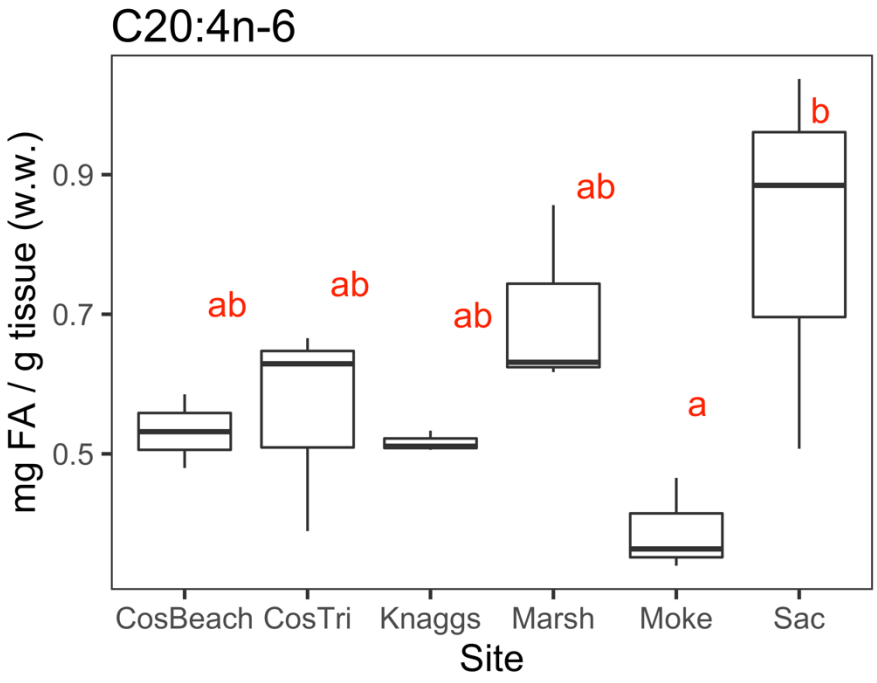

Figure 3.19. Comparison C20:4n-6 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

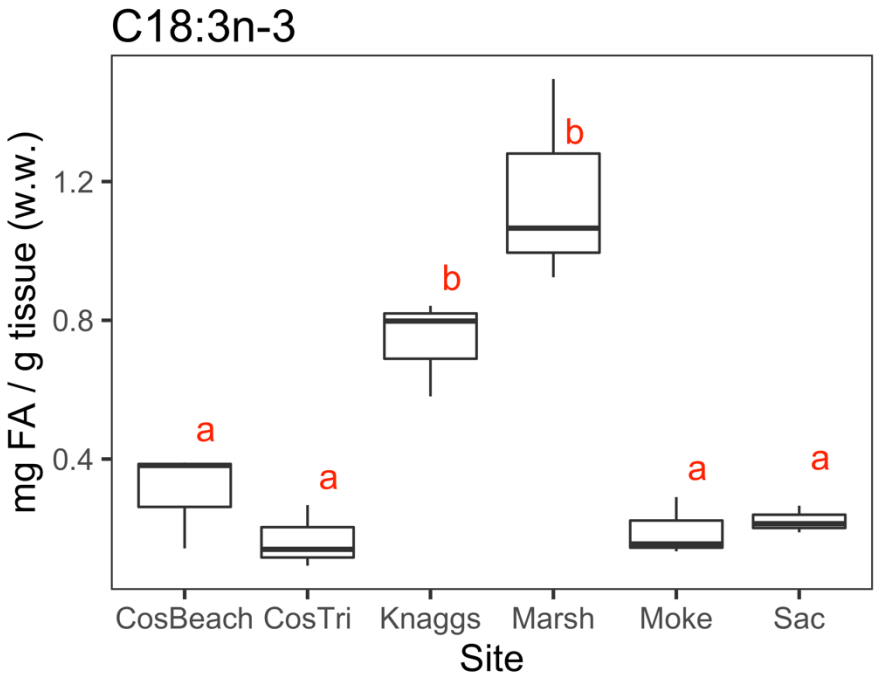

Figure 3.20. Comparison C18:3n-3 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

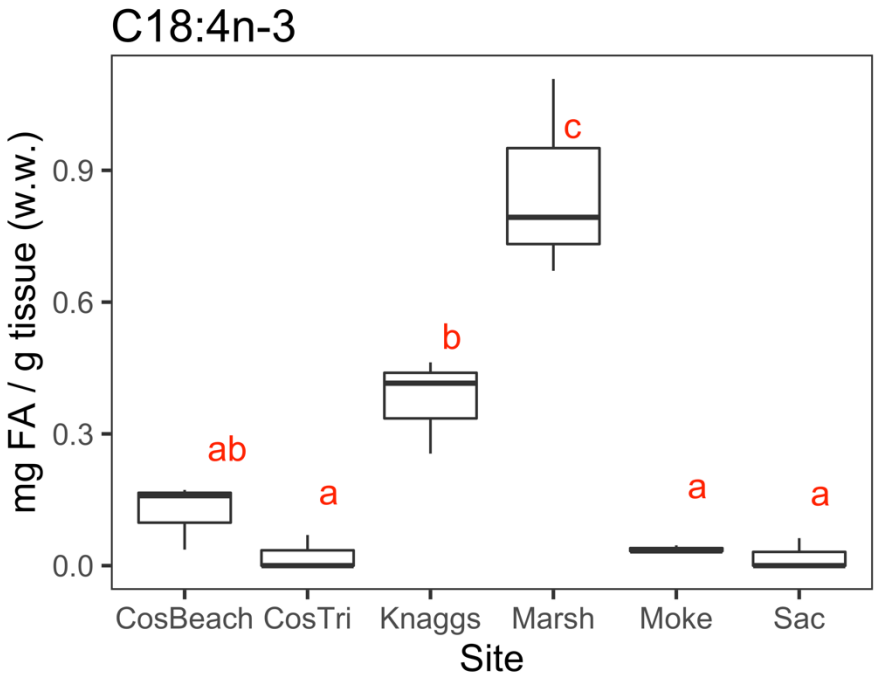

Figure 3.21. Comparison C18:4n-3 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

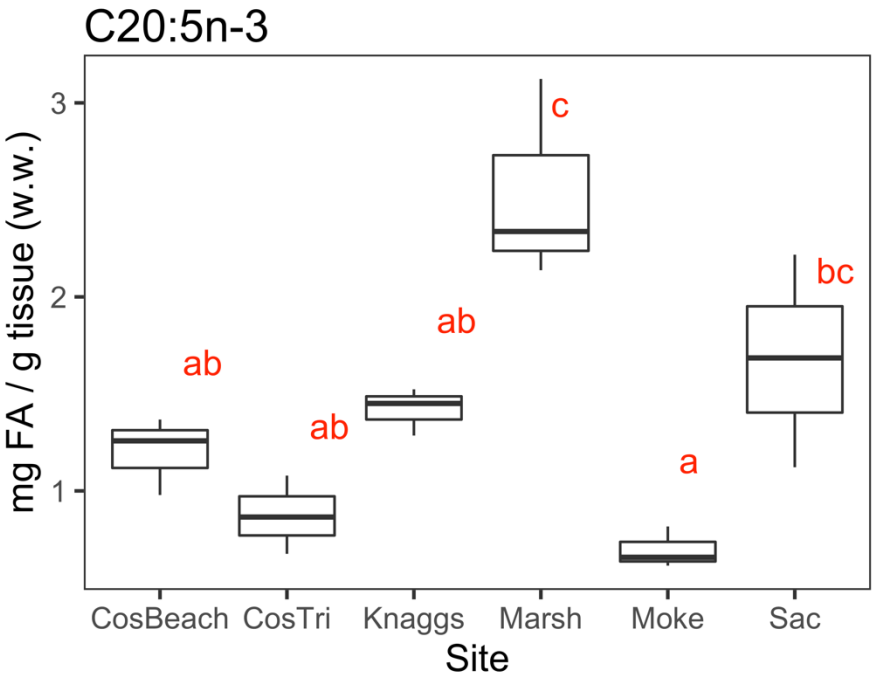

Figure 3.22. Comparison C20:5n-3 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

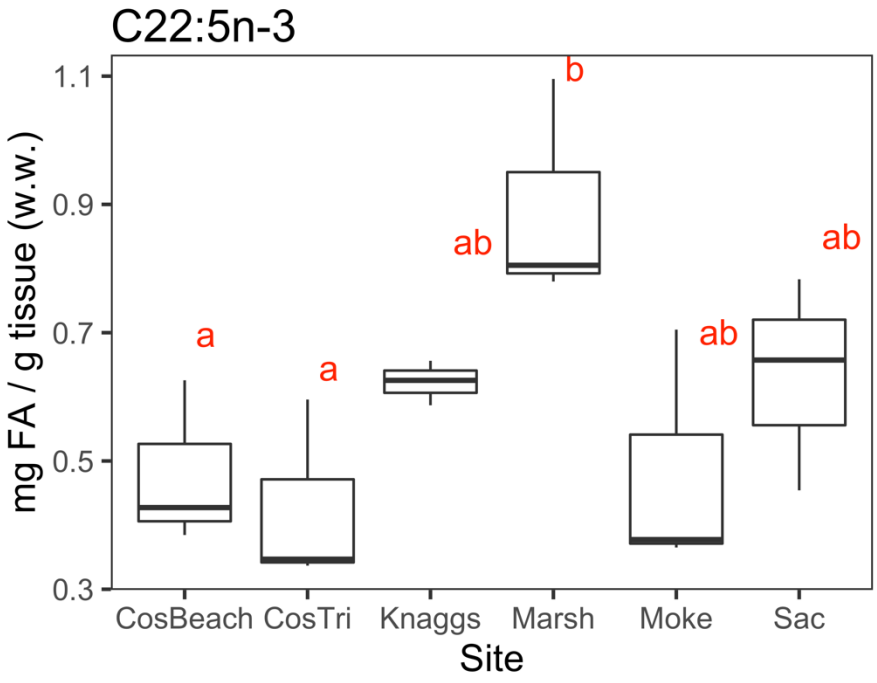

Figure 3.23. Comparison C22:5n-3 fatty acid concentrations in muscle tissue between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

Individuals from river channel sites (i.e. Moke and Sac) had lower concentrations of FA like C14, C18:4n-3, C18:3n-3 and to a lesser degree C16, and C16:1n-7. But, fish from Moke and Sac had relatively high concentrations of C20:5n-3, C22:5n-3, and C22:6n-3. Overall, individuals from Moke and Sac had individual FA concentrations that were similar to one another between sites for most FA (i.e. C14, C16, C18, C16:1n-7, C18:1n-9, C18:2n-6, C18:4n-3, C18:3n-3, C22:5n-3, and C22:6n-3). But, in cases where their FA concentrations were significantly dissimilar (i.e. C20:4n-6, and C20:5n-3), fish from Sac had the higher concentration. The mean concentration of FA in fish tissues from CosBeach and

CosTri was similar for every FA. In general, fish from CosBeach and CosTri did not have the highest concentrations of individual FA, nor did they have the lowest.

Stable Isotopes in Fatty Acids

In addition to differences in concentrations, we also determined there were differences in δ^2H (ANOVA: $F_{(11, 204)} = 124.6$; $p < 0.05$; $n = 216$; Figure 3.23), and δ^{13}C (ANOVA: $F_{(11, 204)} = 65.65$; $p < 0.05$; $n = 216$; Figure 3.24) across all FA, independent of site.

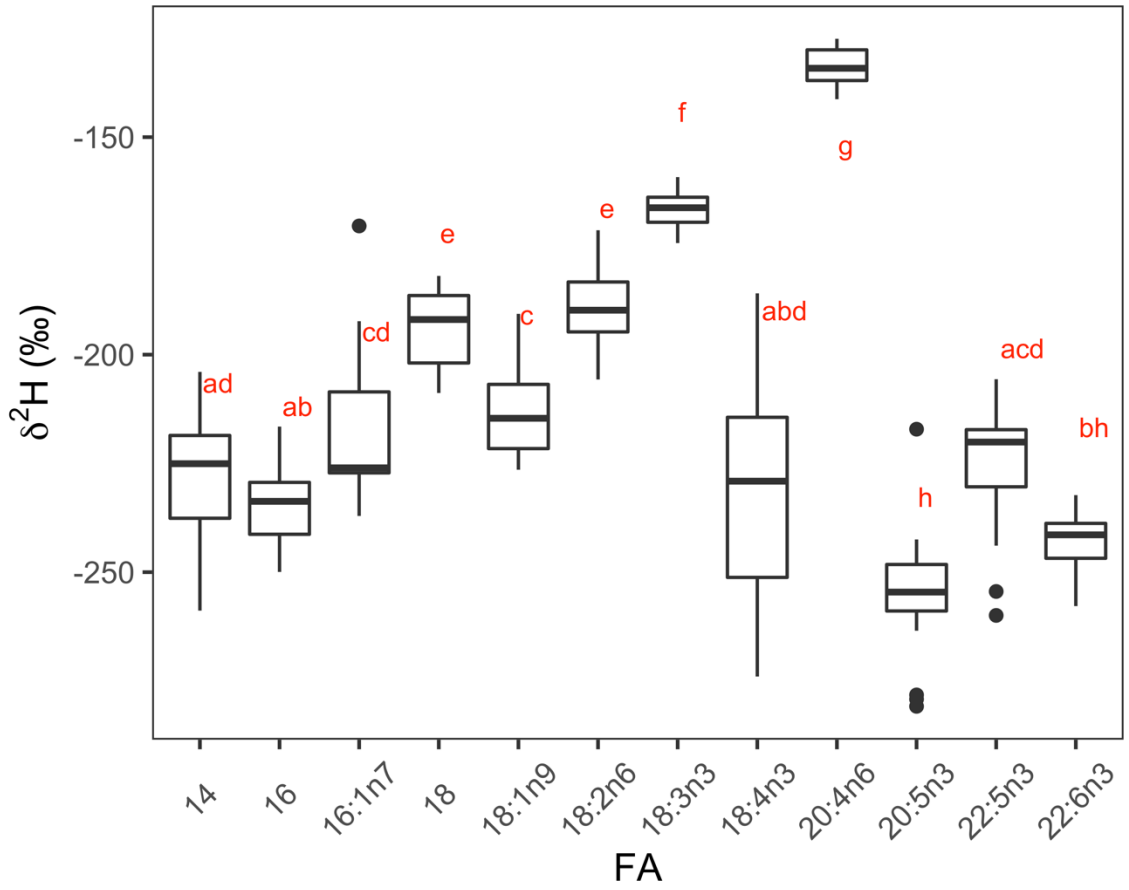

Figure 3.24. Comparison the hydrogen isotope composition of fatty acids. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

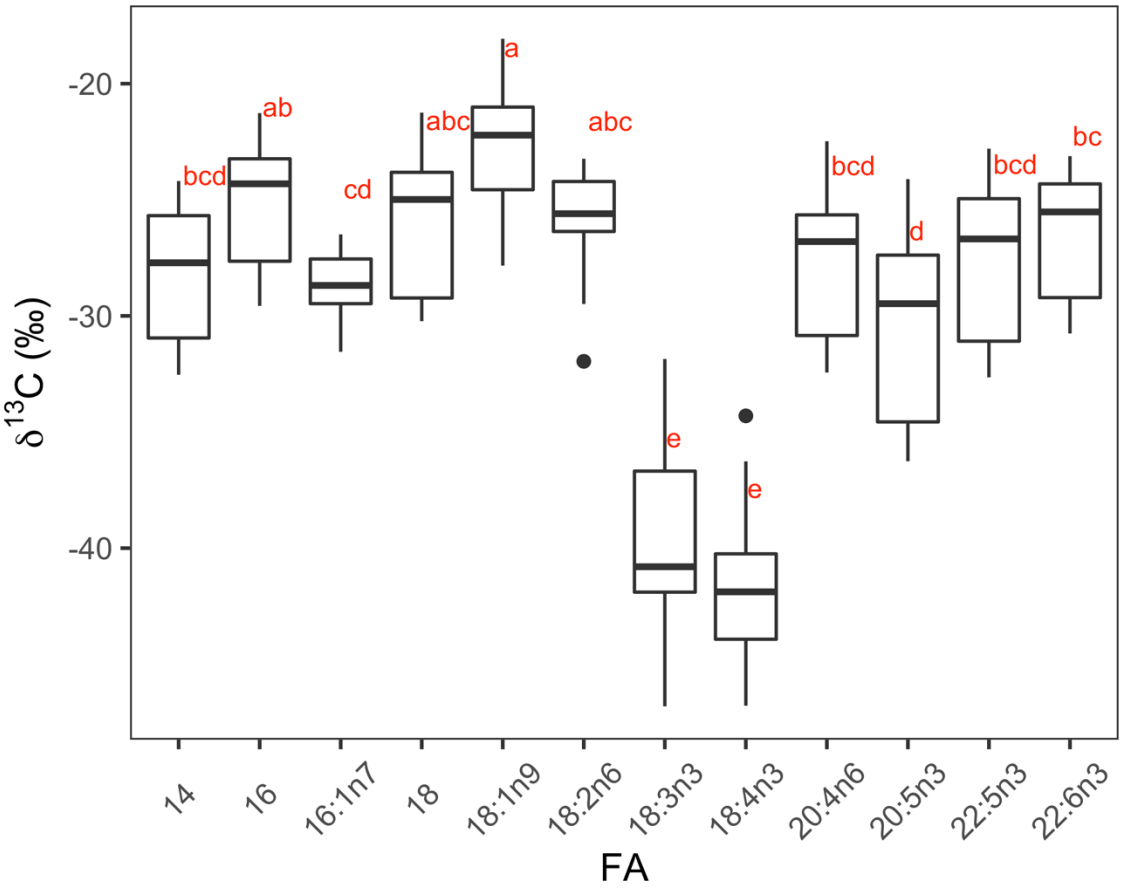

Figure 3.25. Comparison the carbon isotope composition of fatty acids. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

Overall, both $\delta^{13}C$ and $\delta^{2}H$ spanned a relatively large range. $\delta^{13}C$ ranged from -18.1‰ to -46.8‰, while $\delta^{2}H$ ranged between -162.8‰ and -304.4‰. In general, variability in the $\delta^{13}C$ and $\delta^{2}H$ of specific FA between habitats was smaller than that of variability among FA within an individual. C18:1n-9 had the highest average $\delta^{13}C$ (-22.6 ± 2.5‰ ; n = 18), while C18:3n-3 (-39.4 ± 3.9‰ ; n = 18) and C18:4n-3 (-41.6 ± 3.2‰ ; n = 18) had the lowest. In the case of $\delta^{2}H$, the FA C20:4n-6 (-168.6 ± 4.1‰ ; n = 18) had the highest values while C20:5n-3 (-281.1 ± 13.5‰ ; n = 18) had the lowest. In some cases, FA with fewer double bonds had higher $\delta^{2}H$ and lower $\delta^{13}C$ than their less saturated products (e.g. C16 and C16:1n-7, as well as C18:1n-9 and C18:2n-6). In other cases, the reverse was true, $\delta^{13}C$ was higher and $\delta^{2}H$ lower in FA with more double bonds (e.g. C18 and C18:1n-9). In general, the FA with the highest $\delta^{13}C$ values were shorter and more saturated, while FA with lower $\delta^{13}C$ values were those with longer carbon chains (> 18) and were PUFA.

When FA $\delta^{13}C$ values were normalized using data from collocated zooplankton we found that a significant number had values near, or above, 0 (i.e. FA in fish had higher $\delta^{13}C$ values than their presumed bulk food source). We determined that similar significant differences in $\delta^{13}C$ between habitat types as in the non-normalized data remained after normalization (ANOVA: $F_{(5, 210)} = 9.979$; $p < 0.05$; n = 216). We further determined there were significant differences between sites in the normalized $\delta^{13}C$ of every FA measured (C14: $F_{(5, 12)} = 20.61$;

C16: $F_{(5, 12)}$ = 25.81; C16:1n7: $F_{(5, 12)}$ = 57.17; C18: $F_{(5, 12)}$ = 42.7; C18:1n-9: $F_{(5, 12)}$ = 11.19; C18:2n-6: $F_{(5, 12)}$ = 6.063; C18:3n-3: $F_{(5, 12)}$ = 18.33; C18:4n-3: $F_{(5, 12)}$ = 17.64; C20:4n-6: $F_{(5, 12)}$ = 81.1; C20:5n-3: $F_{(5, 12)}$ = 31.4; C22:5n-3: $F_{(5, 12)}$ = 27.47; C22:6n-3: $F_{(5, 12)}$ = 28.83; ANOVA: $p < 0.05$ and n=18; Figure 3.25 – Figure 3.36).

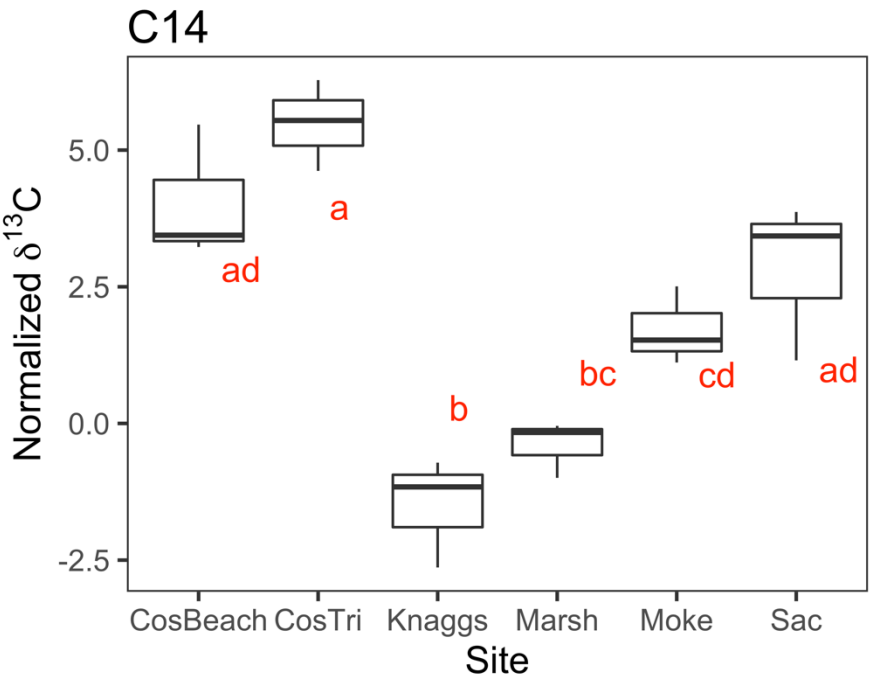

Figure 3.26. Comparison of the normalized carbon isotope composition of C14:0 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

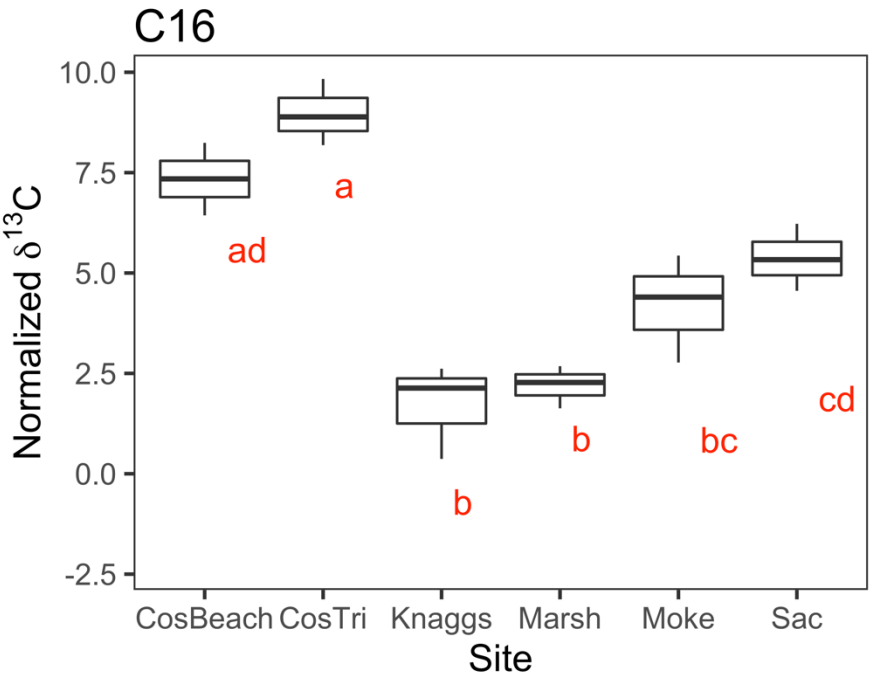

Figure 3.27. Comparison of the normalized carbon isotope composition of C16:0 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

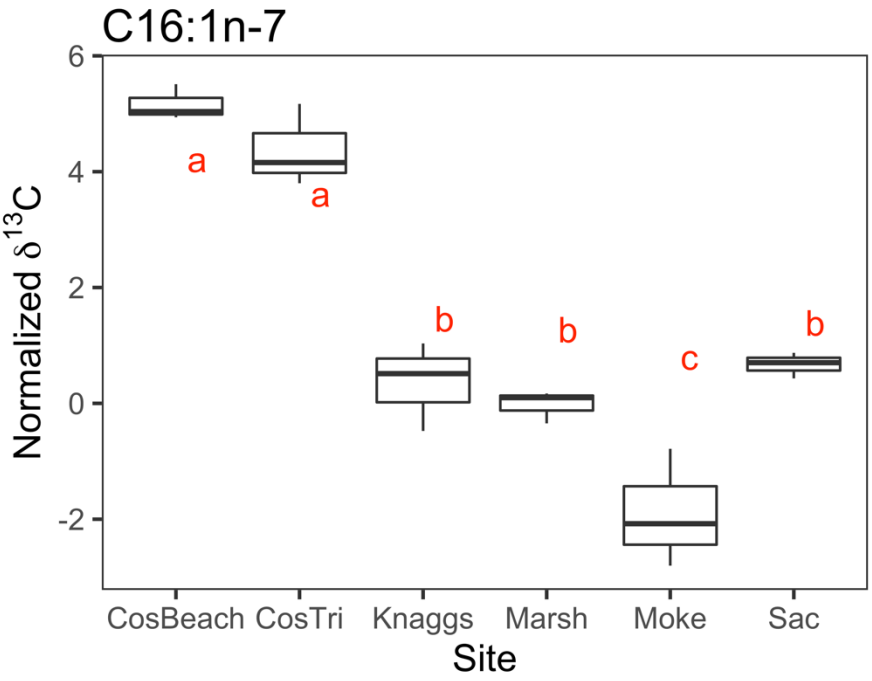

Figure 3.28. Comparison of the normalized carbon isotope composition of C16:1n-7 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

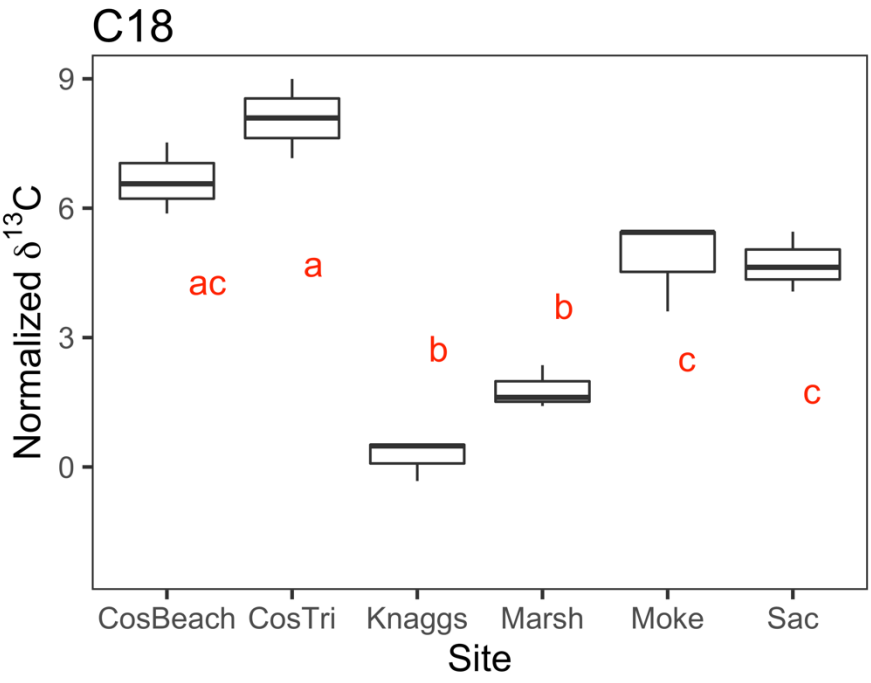

Figure 3.29. Comparison of the normalized carbon isotope composition of C18:0 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

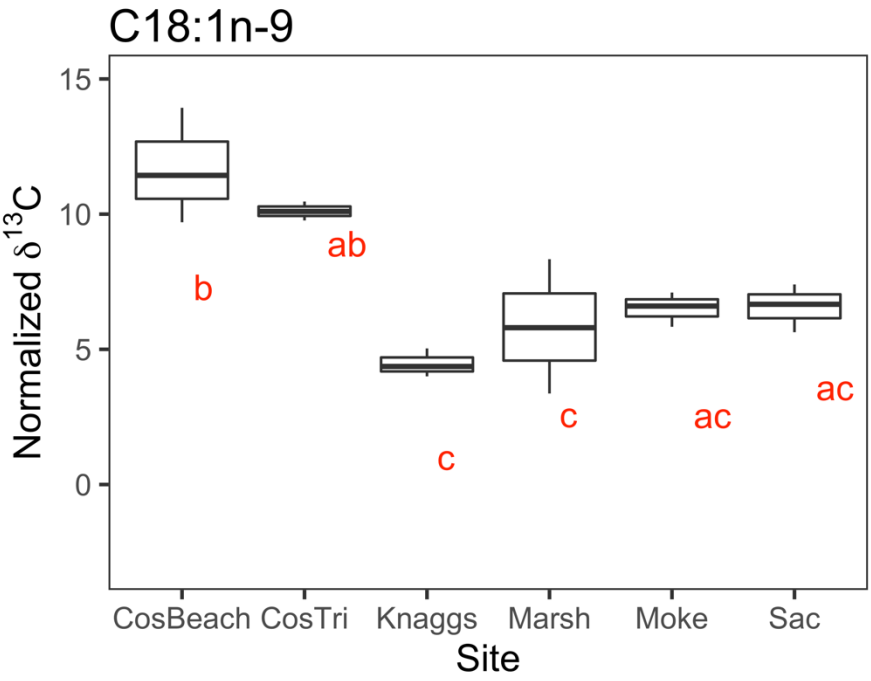

Figure 3.30. Comparison of the normalized carbon isotope composition of C18:1n-9 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

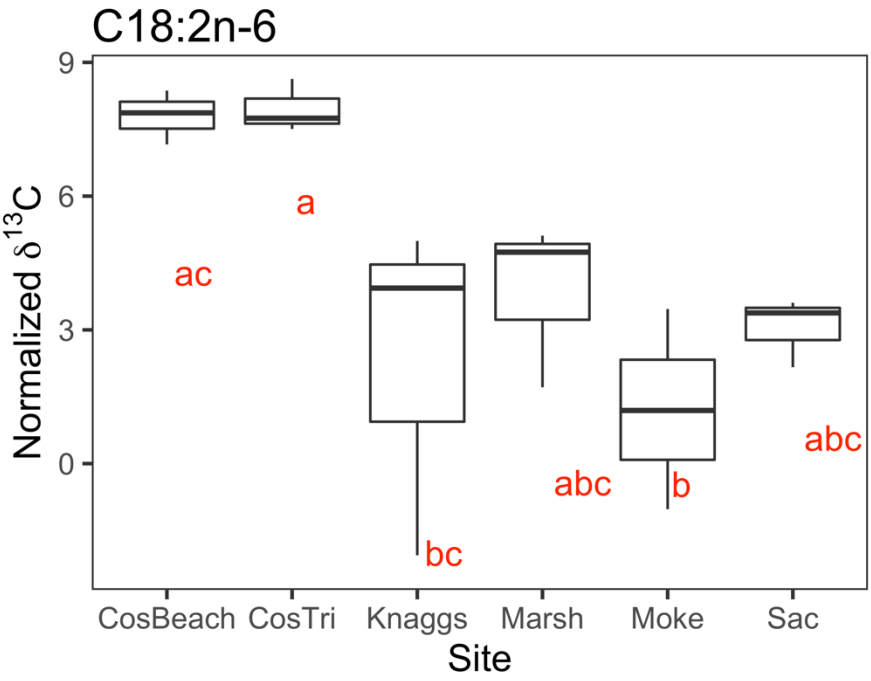

Figure 3.31. Comparison of the normalized carbon isotope composition of C18:2n-6 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

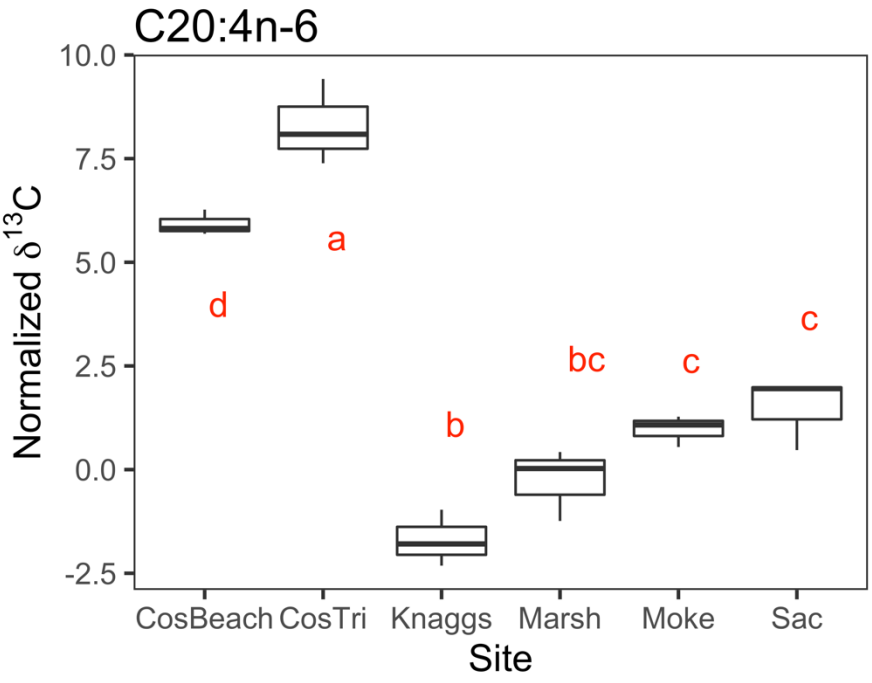

Figure 3.32. Comparison of the normalized carbon isotope composition of C20:4n-6 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

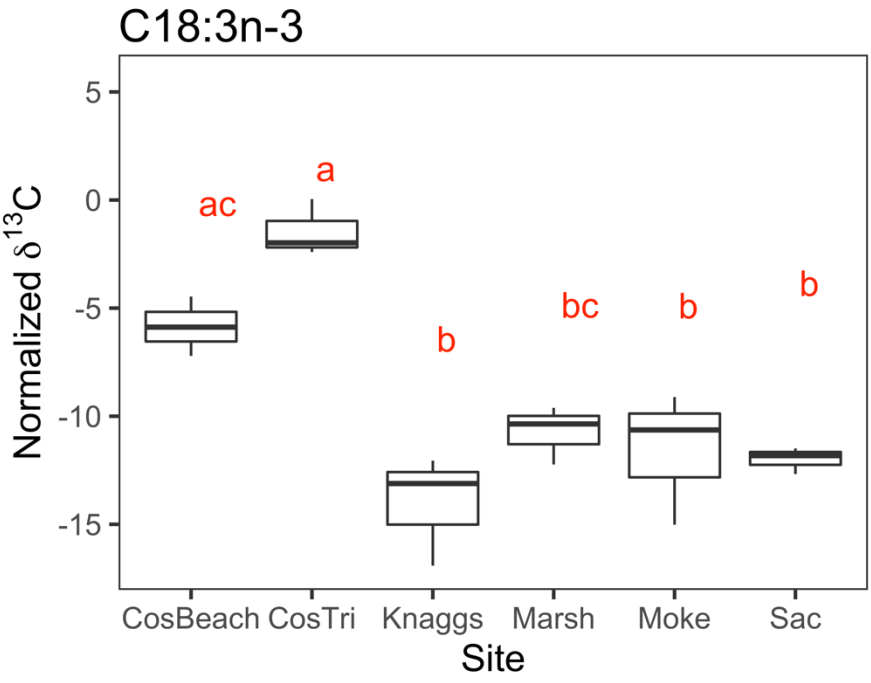

Figure 3.33. Comparison of the normalized carbon isotope composition of C18:3n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

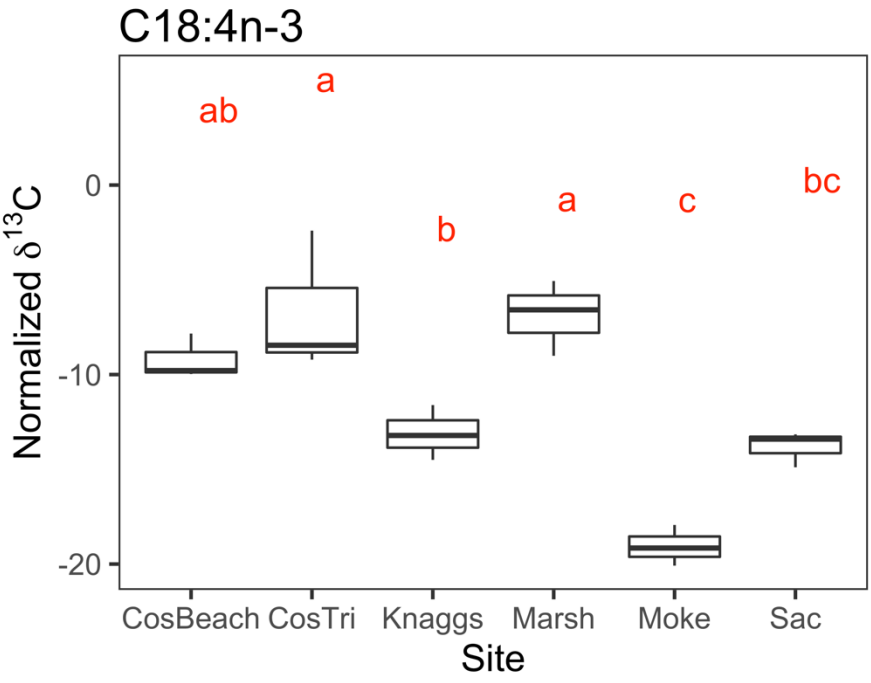

Figure 3.34. Comparison of the normalized carbon isotope composition of C18:4n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

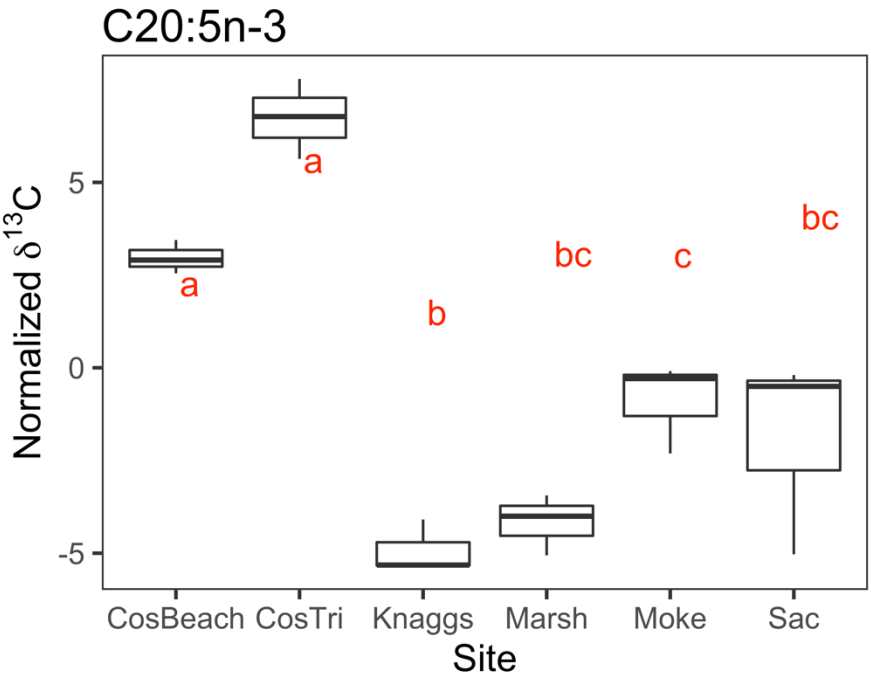

Figure 3.35. Comparison of the normalized carbon isotope composition of C20:5n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

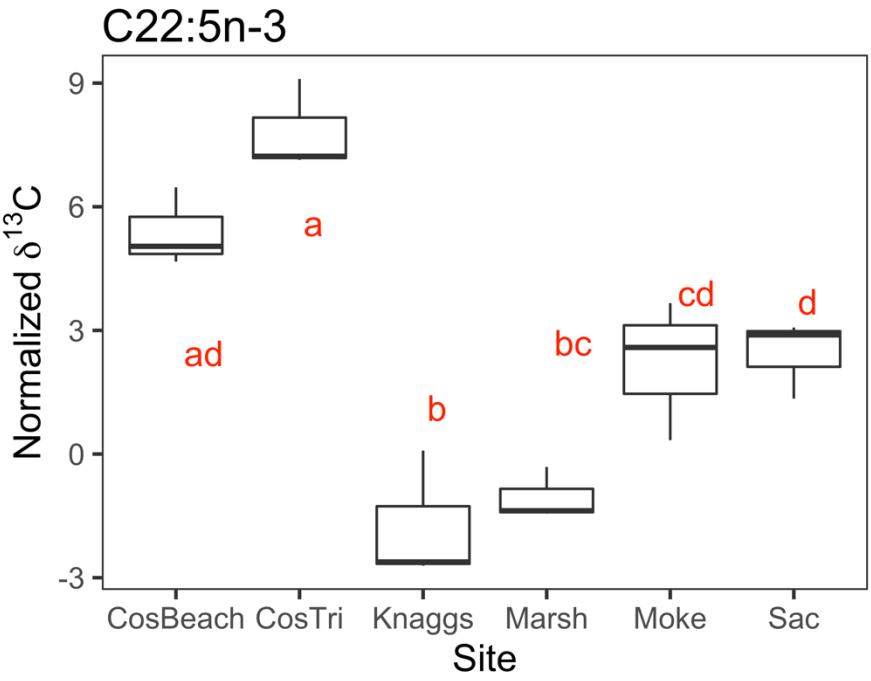

Figure 3.36. Comparison of the normalized carbon isotope composition of C22:5n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

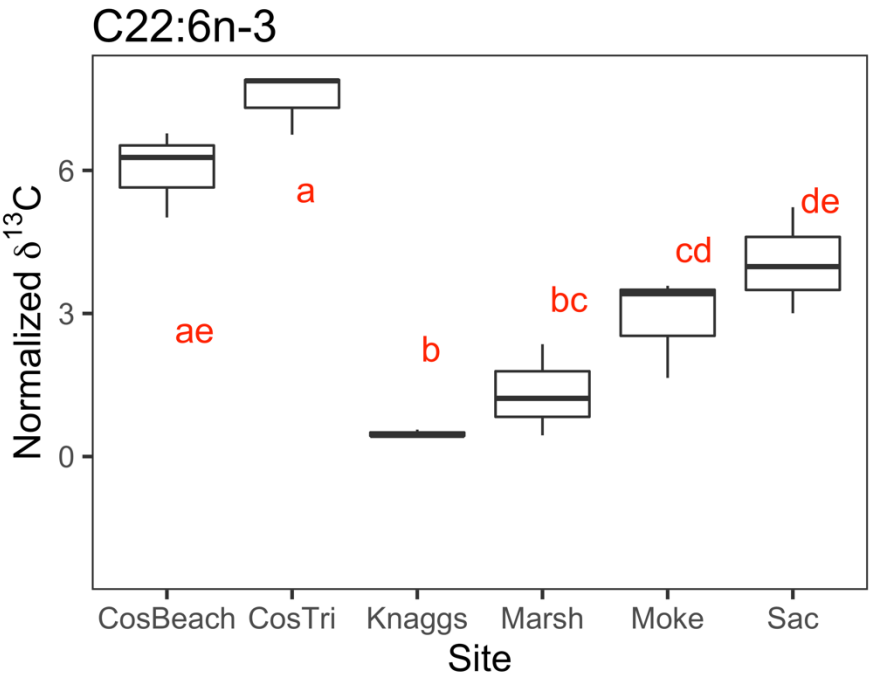

Figure 3.37. Comparison of the normalized carbon isotope composition of C22:6n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

One feature of our normalized $\delta^{13}C$ data were high $\delta^{13}C$ values in fish from CosBeach and CosTri, relative to other sites. In direct comparison, CosTri seemed to have slightly higher normalized $\delta^{13}C$ than CosBeach when comparing individual FA (e.g. C20:4n-6). In most cases, though, CosBeach and CosTri FA-$\delta^{13}C$ were not significantly different from each other. Similarly, Moke and Sac FA-$\delta^{13}C$ differed only for C16:1n-7. However, the FA-$\delta^{13}C$ values of Moke and Sac fish were generally intermediate to the other sites. In contrast, we found that individuals from Knaggs and Marsh tended to have particularly low normalized FA-$\delta^{13}C$ (e.g. C18), although this was not always significant.

We determined there were also differences in the δ^2H of most individual FA between sites (C14: $F_{(5, 12)} = 4.728$; C16: $F_{(5, 12)} = 13.53$; C16:1n7: $F_{(5, 12)} = 9.578$; C18: $F_{(5, 12)} = 16.52$; C18:1n-9: $F_{(5, 12)} = 19.31$; C18:2n-6: $F_{(5, 12)} = 7.677$; C18:4n-3: $F_{(5, 12)} = 5.564$; C20:5n-3: $F_{(5, 12)} = 11.91$; C22:5n-3: $F_{(5, 12)} = 16.59$; C22:6n-3: $F_{(5, 12)} = 11.6$; ANOVA: $p < 0.05$ and n=18; Figure 3.37 – 3.48). We did not find significant differences in δ^2H between sites for C18:3n-3 or C20:4n-6 and there were no clear site-specific trends in the differences in δ^2H of FA. Considering the FA for which we did find significant differences in δ^2H across sites, it was usually only one or two sites driving those significant differences. One common feature of our δ^2H data, apparent in a handful of FA (i.e. C14, C18, C22:5n-3, and C22:6n-3), is that individuals from the Marsh site had FA-δ^2H that was significantly lower than at every other site. δ^2H of C16 and C18:1n-9, on the other hand, was generally higher in fish from Knaggs than at any other site. Similarly, δ^2H of C16:1n-7 was higher in fish from Moke and Knaggs than at other sites.

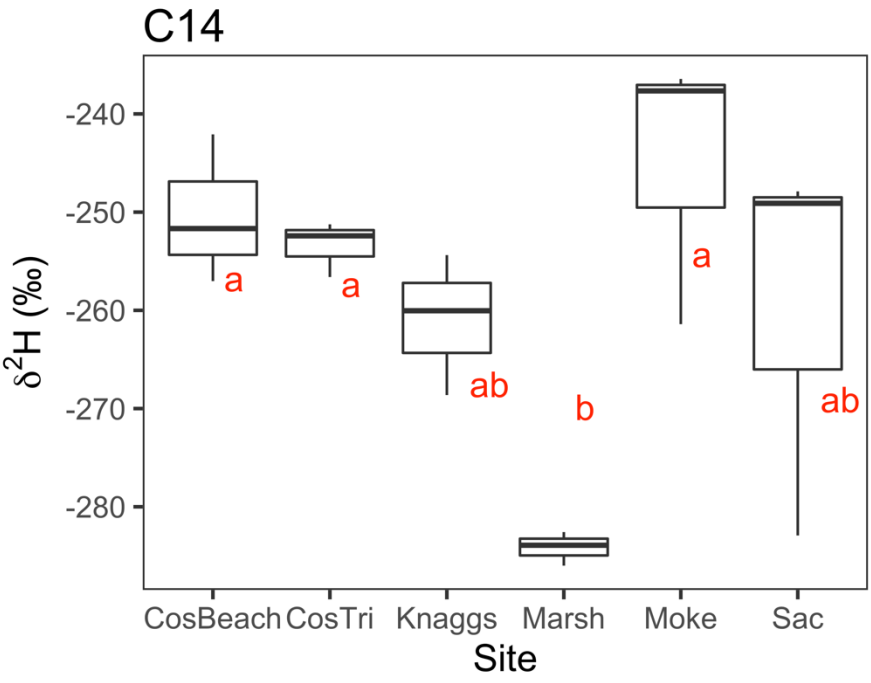

Figure 3.38. Comparison of the hydrogen isotope composition of C14:0 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

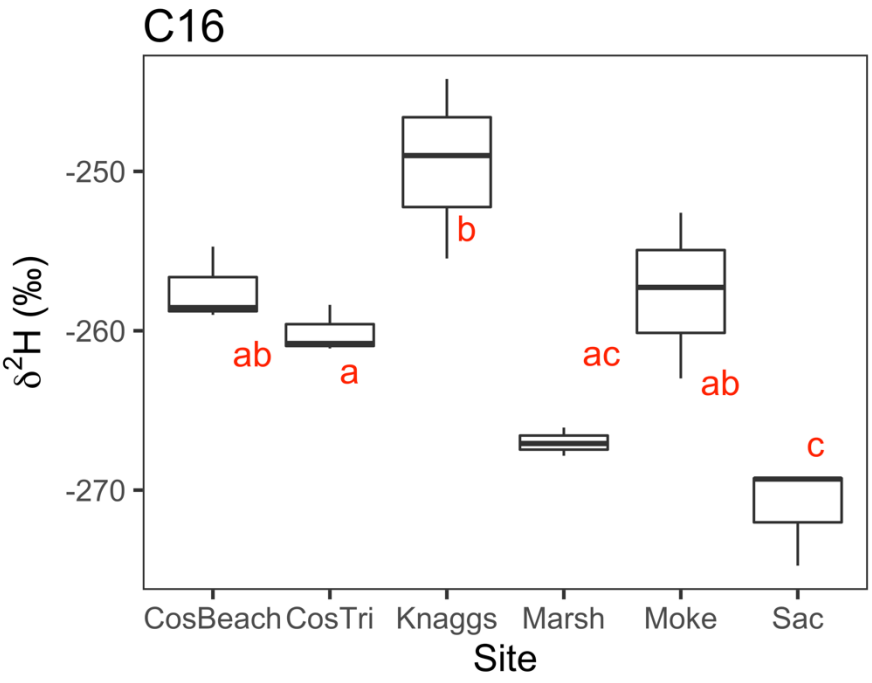

Figure 3.39. Comparison of the hydrogen isotope composition of C16:0 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

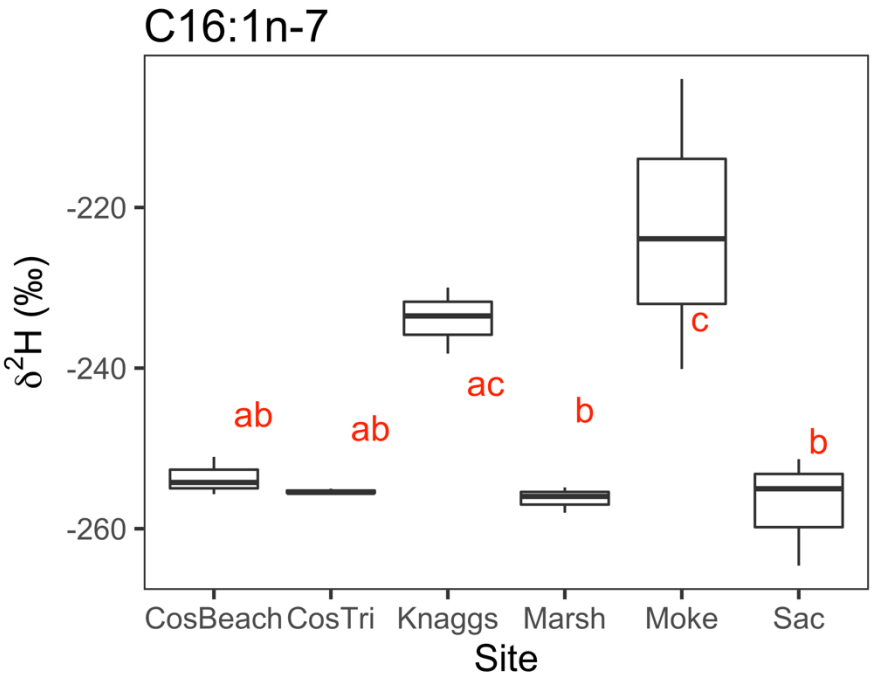

Figure 3.40. Comparison of the hydrogen isotope composition of C16:1n-7 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

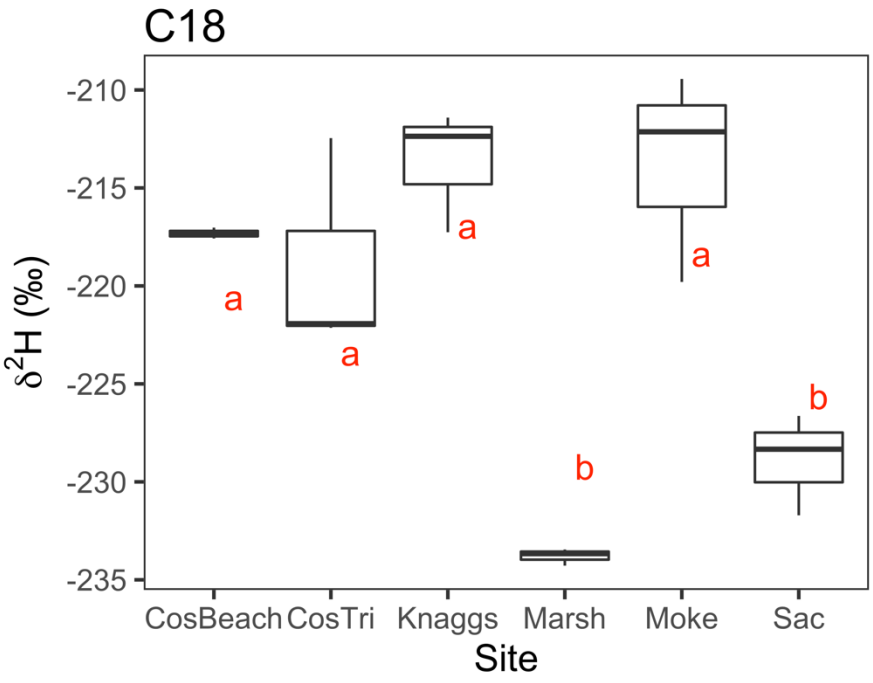

Figure 3.41. Comparison of the hydrogen isotope composition of C18:0 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

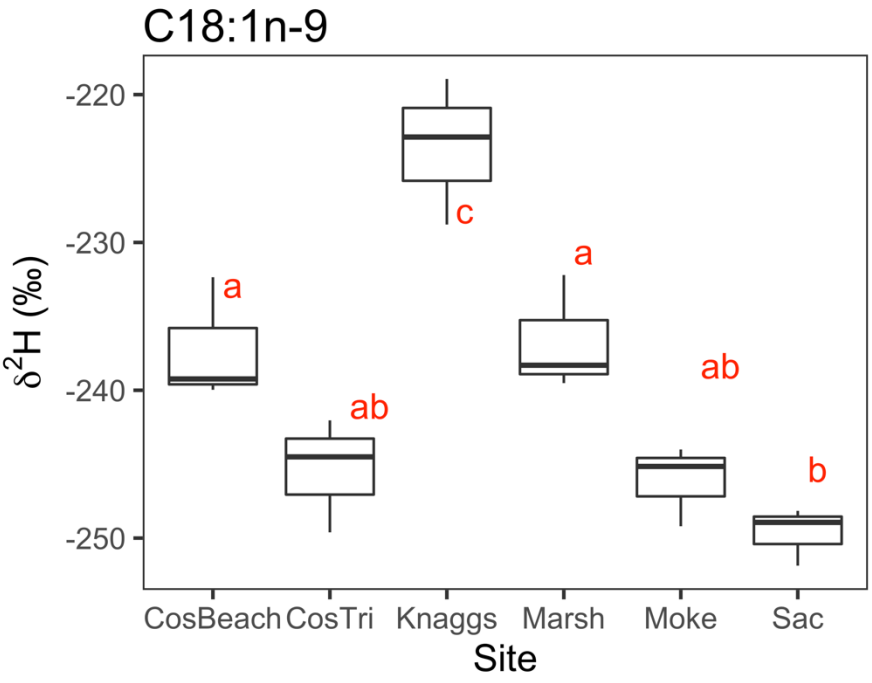

Figure 3.42. Comparison of the hydrogen isotope composition of C18:1n-9 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

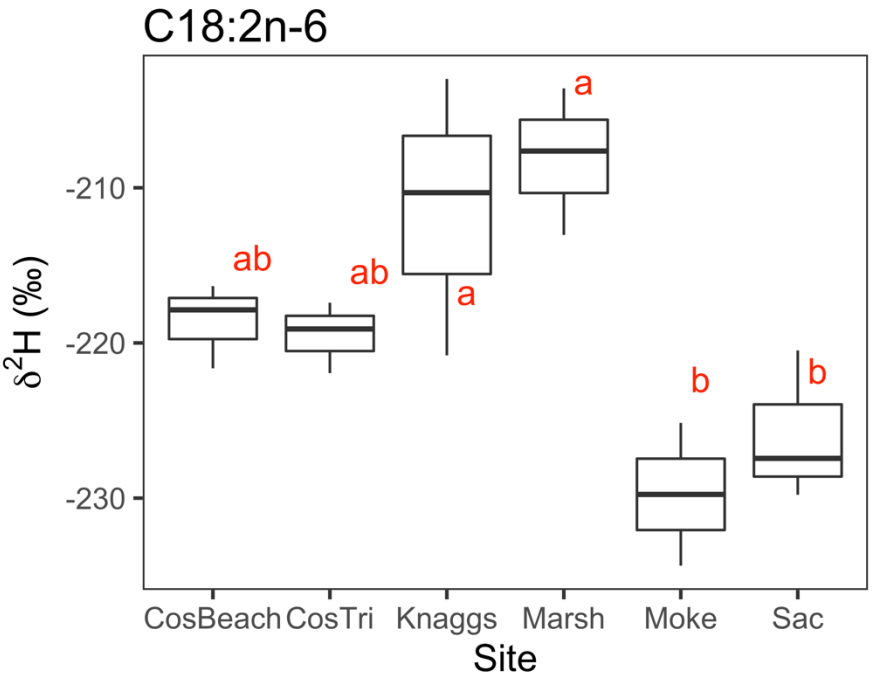

Figure 3.43. Comparison of the hydrogen isotope composition of C18:2n-6 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

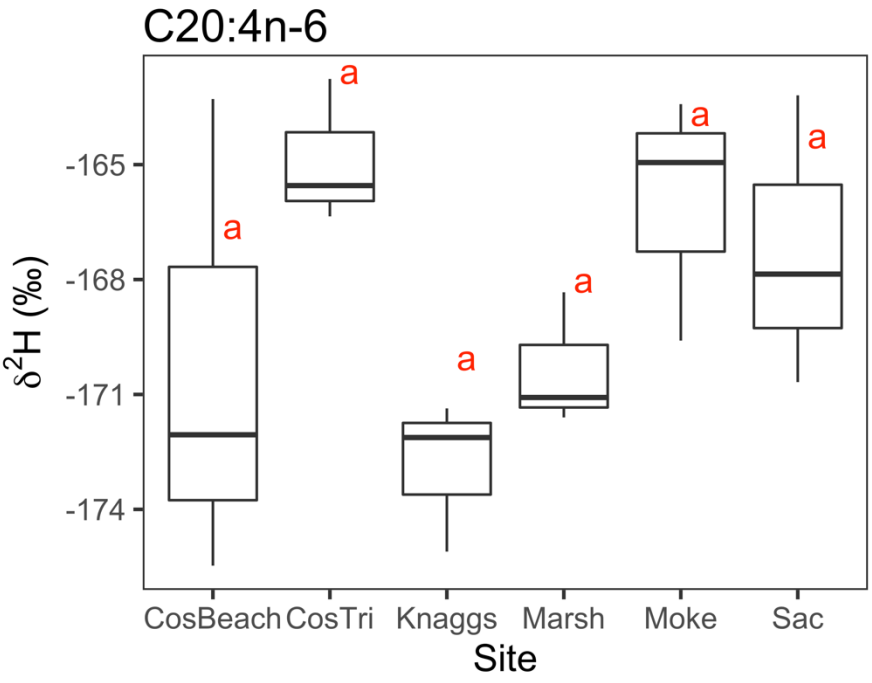

Figure 3.44. Comparison of the hydrogen isotope composition of C20:4n-6 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

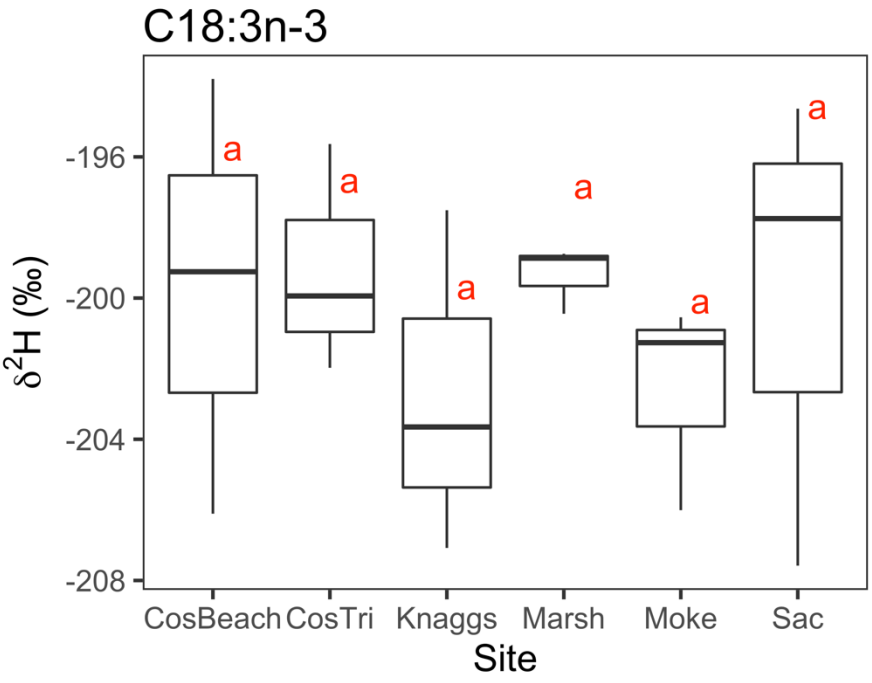

Figure 3.45. Comparison of the hydrogen isotope composition of C18:3n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

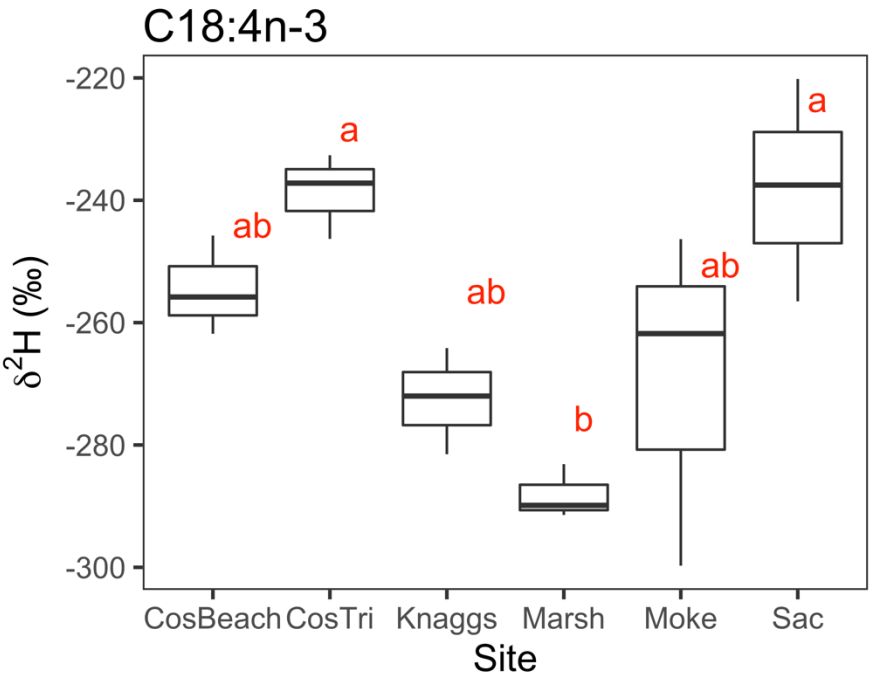

Figure 3.46. Comparison of the hydrogen isotope composition of C18:4n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

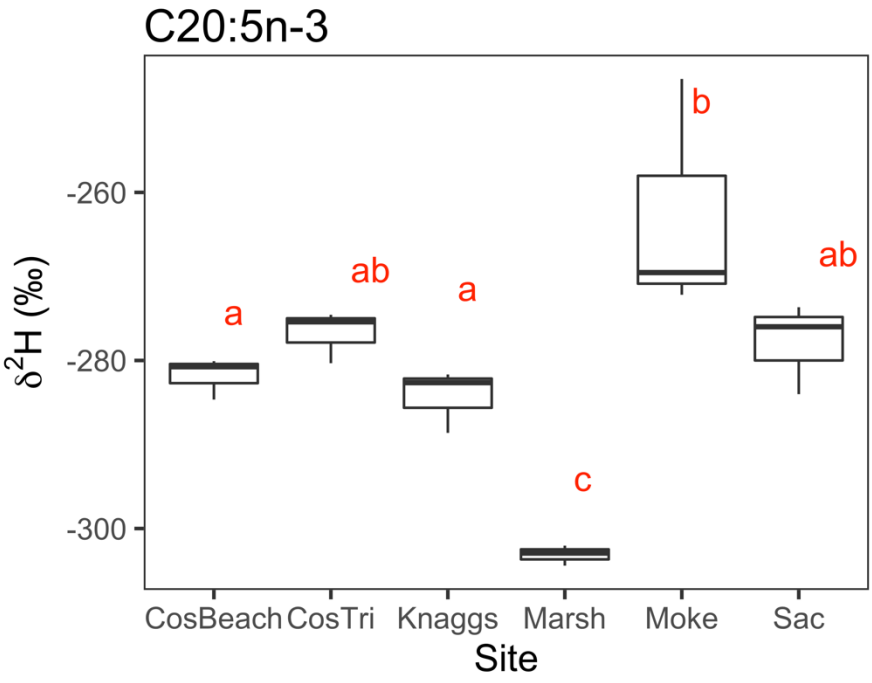

Figure 3.47. Comparison of the hydrogen isotope composition of C20:5n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

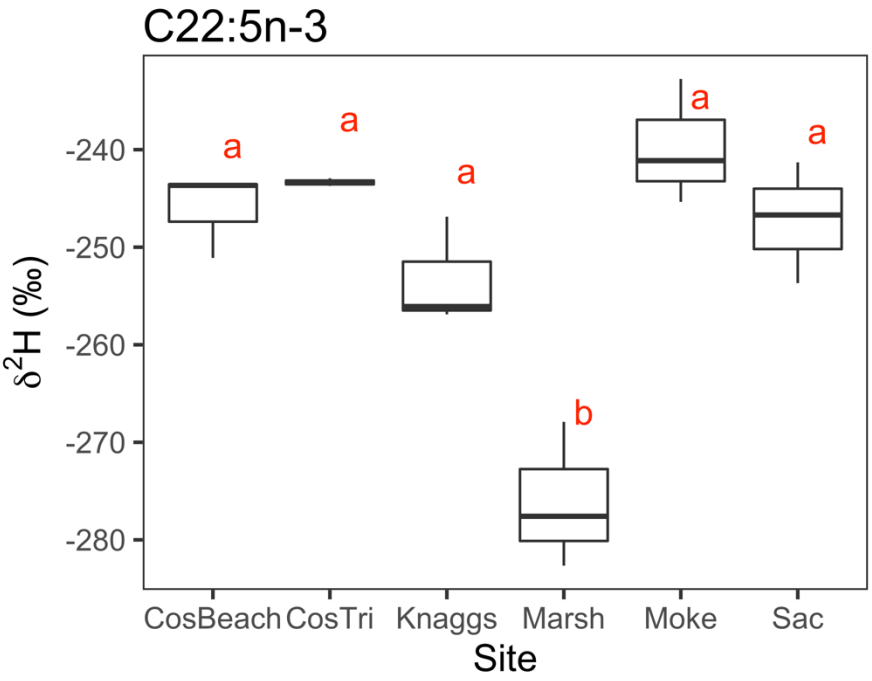

Figure 3.48. Comparison of the hydrogen isotope composition of C22:5n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

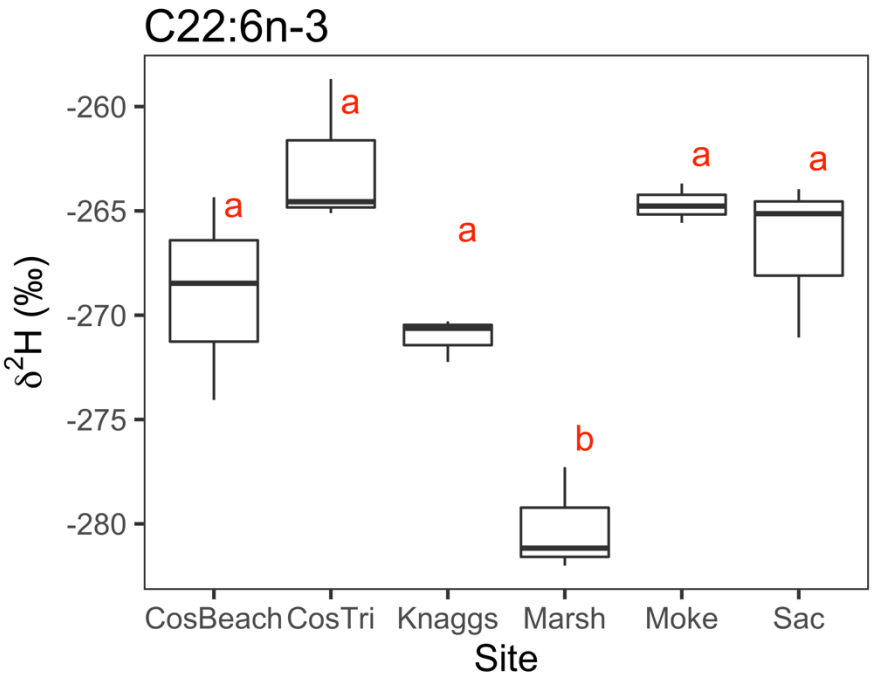

Figure 3.49. Comparison of the hydrogen isotope composition of C22:6n-3 fatty acids between habitat treatments. Letters indicate significant differences ($p < 0.05$; Tukey HSD).

Discussion

Fatty Acid Concentrations

Our results from bulk isotope analysis indicate discretion is necessary in interpreting the FA data. The differences in the FA composition of our experimental Chinook unequivocally point to differences in FA nutrition and/or metabolism among our sites. However, the bulk carbon and nitrogen isotope values for fish were generally too high, relative to available invertebrates. In light of this observation, it seems unlikely that the FA measured in our Chinook

muscle were entirely at steady state with the diet during enclosure. The observed discrepancy between Chinook and SSJD dietary items is consistent with residual influence of marine derived feeds provided at the hatchery. Specifically, it seems that slow growing fish (e.g. Moke and Sac) had bulk isotope compositions most dissimilar from the expectation, while faster growing fish had isotope compositions closer to the expected value. This trend is consistent with either decreasing tissue turnover times being associated with faster growth rates, and/or greater dilution of antecedent biomass with biomass accumulated during enclosure (Jobling, 2004; Robin et al., 2003). Nonetheless, this result indicates that experiments examining FA in juvenile Chinook following a dietary shift should run longer than 45 days. Previous work has demonstrated adequate turnover in fish after a period of 12 weeks (Budge et al., 2012).

Despite incomplete turnover, our results indicate that FA nutrition of Chinook salmon in the SSJD differs among habitats. As a result of a uniform hatchery diet, we assume all the fish in our study had identical FA compositions at the beginning of the experiment. However, after the 45-day enclosure period, we measured significant differences in the concentrations and stable isotope composition of FA in Chinook muscle tissues. Despite differences, all fish analyzed had FA concentrations that were similar and consistent with prior measurements in Chinook (Daly et al., 2010; Kiessling et al., 2005; Mjaavatten et al., 1998). For example, saturated and monounsaturated FA were the most

abundant FA, while n-3 and n-6 PUFA were less abundant. Also, n-3 PUFA had higher concentrations than n-6, primarily due to relatively high concentrations of C22:6n-3. These results are not adequate to fully describe nutritional differences in SSJD prey items between habitats, but they do illustrate that utilization of different habitats has an impact on the FA nutrition of Chinook in the SSJD.

We were surprised to find that, in general, fish from CosTri and CosBeach did not have significantly increased concentrations of FA in their muscle tissue relative to fish from Moke and Sac. However, morphometric results from this experiment indicate that Knaggs and Marsh fish grew the most, followed by fish from CosBeach and CosTri, while fish from Moke and Sac grew very little and had low condition factors (Jeffres et al. in prep). Maintenance of similar FA concentrations whilst putting on significantly more biomass suggests fish from CosBeach and CosTri were more successful foragers than fish from Moke and Sac. Similarly, it seems fish from Knaggs and Marsh were more probably successful foragers than those from CosBeach and CosTri.

Stable Isotopes in Fatty Acids

Our results from carbon and hydrogen isotope analysis of FA indicate that the origin of FA in Chinook muscle was similar among habitats. Overall, differences in the isotope composition of FA among habitat types were small. Taken together with our bulk data showing incomplete turnover of tissues, this

overall result is unsurprising. Nevertheless, the isotope composition of FA across habitats were not homogenous, although, we did not observe consistent, extreme, differences in the isotope composition of FA in Chinook muscle tissue among habitats that might indicate an entirely different source of primary production was supporting fish (e.g. coupled methanogenesis-methanotrophy). It is likely, however, that an extended enclosure, allowing for increased tissue (FA) turnover/accumulation, would increase the magnitude of differences and provide more compelling evidence for habitat specific differences in FA availability.

Overall, we found that our measurements of $\delta^{13}C$ and $\delta^{2}H$ in FA were consistent with prior measurements (Gladyshev et al., 2012; Pilecky et al., 2021). With respect to $\delta^{13}C$, we found a parabolic relationship exists between FA size and saturation vs. the carbon isotope composition. That is to say, moderate length, mildly unsaturated, FA such as C18:3n-3 and C18:2n-3 tend to have more negative $\delta^{13}C$ values than shorter, or more heavily desaturated FA (e.g. C16 or C22:6n-3). Presumably, this is because elongation of FA involves addition of ^{13}C-depleted subunits while desaturation may involve preferential reaction of ^{13}C. The opposite was observed for $\delta^{2}H$. Short, saturated, FA were more negative than moderate length, monounsaturated FA. Conversely, $\delta^{2}H$ of long-chain PUFA (e.g. C22:5n-3) was more negative.

Lipids typically have low $\delta^{13}C$ values, relative to bulk biomass, because formation of acetyl-CoA discriminates strongly against ^{13}C (Hayes, 2001; Monson

& Hayes, 1980). Therefore, inputs of de novo synthesized FA could have lower FA $\delta^{13}C$, relative to stored FA. Our bulk results also indicate residual biomass from before the enclosure began was generally ^{13}C-enriched, relative to biomass accumulated during the experiment. For this reason, we feel confident that either increasing the flux of lipids routed from the diet, or synthesized de novo, would lead to decreases in the $\delta^{13}C$ of FA.

De novo synthesis, or *in situ* alteration, may also introduce FA with lower $\delta^{2}H$. Half of FA hydrogen comes from NADPH. The hydrogen in NADPH is generally derived from dehydrogenase reactions during catabolic central metabolism (i.e. TCA cycle and the oxidative pentose phosphate cycle), although some NADPH is produced via transhydrogenation of NADH; the remaining half of hydrogen atoms in FA are sourced from intracellular water, due to exchange during synthesis, and acetyl-CoA (Seyama et al., 1977; Wijker et al., 2019). Presumably, residual FA from marine derived hatchery foods would have more positive $\delta^{2}H$ than FA accumulated during enclosure as ocean waters $\delta^{2}H$ value is 0‰ while SSJD waters have negative $\delta^{2}H$, closer to -80‰ (Tomkovic et al., 2020).

Saturated and MUFA in fish from Marsh and Knaggs often had low normalized $\delta^{13}C$ and $\delta^{2}H$, relative to other sites. On the other hand, FA from CosTri and CosBeach had relatively high $\delta^{13}C$ in their FA, although $\delta^{2}H$ tended to be similar to other sites. Fish from CosBeach and CosTri may have been well

enough rationed to subsist on a combination of dietary and stored lipids, but not well enough to engage in significant de novo synthesis or deposition, leading to the positive $\delta^{13}C$ values observed in those individuals. Fish from Moke and Sac had $\delta^{13}C$ values more similar to those from Knaggs and Marsh, potentially indicating increased de novo synthesis in those individuals as well. However, given the differences in FA content, the circumstances initiating FA synthesis may have been different. For fish from Marsh and Knaggs, increasing de novo synthesis of FA makes sense in order to stockpile energy and biomass, while fish from other sites may not have had excess energy, and metabolites, to direct towards anabolism. Data on the isotope composition of FA in their original hatchery food sources, as well as local sources, could help disentangle whether differences in isotopes are linked to dietary, or metabolic, differences.

In response to abundant food, fish from Marsh may have been stockpiling excess intake as lipid reserves. Fish from Moke and Sac, on the other hand, may have consumed their lipid reserves during the enclosure period to stave off starvation and began FA synthesis to maintain FA tissue concentrations. Early mobilization of lipid stores would have ramifications for early marine success. In situations where freshwater habitats are low quality, an early escape to marine or estuarine habitats might afford access to better foraging opportunities. Through this means, low foraging success early on in life might be offset by later growth, despite the increased risk of predation due to early emigration (i.e. small size). On the other

hand, accelerated consumption of lipid stores could result in earlier starvation if higher quality foraging opportunities aren't found.

The similarity in lipid concentrations between fish from CosTri, CosBeach, Moke, and Sac despite differences in growth indicate that the observed concentrations may have been maintained at the expense of growth. The high amount of C22:6n-3 in fish from Sac, in contrast to their generally lackluster FA content, also supports this hypothesis, as this PUFA may have been mobilized from lipid stores (i.e. adipose tissue) accumulated during hatchery residence when n-3 PUFA were more common in the diet. The lack of significant biomass accumulation may have helped to concentrate preferentially retained C22:6n-3 in the muscle tissue of these fish. Whether this C22:6n-3 was mobilized to provide energy, or for its bioactive properties, is unknown.

One potential reason for the seeming accumulation of n-3 PUFA in fish from Sac is related to accelerated outmigration. These fish may have initiated signaling pathways to begin smoltification earlier than fish from other sites due to their residence in relatively poor freshwater habitat. During smoltification, Chinook undergo a complex series of biochemical, behavioral, and physical changes to prepare themselves for marine conditions (Hoar, 1988; Stefansson et al., 2008). There is evidence that tissue FA profiles are altered preemptively to include greater proportions of n-3 FA during the transition to seawater and catabolism of lipid stores increases to provide energy for the physiological and

chemical changes taking place (Bell et al., 1996). However, accelerated smoltification seems unlikely, as biophysical factors are thought to be less important than seasonal cues (e.g. water temperature and photoperiod) (Marine & Cech, 2004; Pereira & Adelman, 1985).

We found consistently more positive δ^2H values in the FA C20:4n-6. A potential cause for this is that C20:4n-6 tends to be more abundant in terrestrial resources, which are also likely to have more positive δ^2H. While δ^2H was generally uniform among treatments, δ^{13}C of C20:4n-6 varied approximately 10‰ between habitats. This could be due to increased oxidation of residual C20:4n-6 in some individuals, which may not affect δ^2H and does not necessitate a dietary source of C20:4n-6. This, however, seems unlikely as concentrations of C20:4n-6 were generally similar across treatments. This situation would be impossible to maintain if oxidation were greater in some subjects with no reciprocal increase in supply. Excess C20:4n-6 available in the diet could drive differences in the carbon isotope composition of the FA among treatments. That said, synthesis of C20:4n-6 from precursor FA is still supported by the data. A similar trend among treatments in the δ^{13}C of FA was evident in both C20:4n-6 and its EFA precursor C18:2n-6, suggesting these differences were conserved during biosynthetic alteration. Nonetheless, it remains unclear whether the C20:4n-6 measured in our samples was residual material from hatchery rationing, derived from local dietary items, or synthesized from precursors.

Analysis of other n-6 FA would provide insight into the differences in the FA isotope composition introduced during sequential alteration, however their low abundance in our samples made this infeasible. If differences in the carbon isotope composition of C20:4n-6 were driven primarily by differences in synthesis flux, this result confirms that elongation of C18:3n-6 to C20:3n-6 does involve addition of 13C-depleted carbon subunits since C22:4n-6 had more negative $\delta^{13}C$ than its measured precursor (C18:2n-6). Assuming these differences were driven by biosynthetic flux differences, our data are also consistent with addition of ^{2}H-enriched hydrogen from NADPH as C20:4n-6 had more positive $\delta^{2}H$ than C18:2n-6.

Conclusion

The FA data are complex. We are unable to definitively resolve whether differences were principally driven by differences in the composition of dietary items or availability of similar dietary items. Data on the FA composition of potential food sources and the initial composition of incubated fish could provide more context for the differences observed between treatments. It is also unclear whether wild populations and hatchery derived fish have similar FA requirements. Nonetheless, these analyses indicate that there are differences in the FA nutrition of Chinook salmon rearing in different habitats in the SSJD.

Overall, our results provide support for the importance of off-channel rearing habitats for juvenile Chinook in the SSJD. However, our results also highlight the mixed quality of off-channel habitats for Chinook rearing. Fish from our off-channel treatments, such as the Yolo Bypass (Marsh) and Knaggs Ranch maintained higher tissue FA concentrations than fish in the river channel. On the other hand, fish from other off-channel treatments (i.e., CosTri and CosBeach) did not maintain higher tissue FA concentrations. The reason we did not observe increased FA concentrations in individuals from CosTri and CosBeach is not clear. Evidently, not all off-channel or floodplain habitats, provide equal benefits relative to rearing in the river channel. Regardless of biomass accumulation, the benefits of adequate FA nutrition include both increased somatic growth, healthy development, and potentially greater stored energy reserves (i.e. lipid storage). Continuing to tease apart differences in rearing habitat quality in the SSJD is an important step in managing Chinook populations.

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Works Cited

Ackman, R. G. (1967). Characteristics of the fatty acid composition and biochemistry of some fresh-water fish oils and lipids in comparison with marine oils and lipids. *Comparative Biochemistry and Physiology*, *22*(3), 907–922.

Ahlgren, G., Vrede, T., & Goedkoop, W. (2009). *Lipids in Aquatic Ecosystems* (M. T. Arts, M. J. Kainz, & M. T. Brett, Eds.; pp. 1–395). Springer Science+Business Media.

Alcorn, S. W., Pascho, R. J., Murray, A. L., & Shearer, K. D. (2003). Effects of ration level on immune functions in chinook salmon (Oncorhynchus tshawytscha). *Aquaculture*, *217*(1–4), 529–545.

Beamish, R. J., & Mahnken, C. (2001). A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography*, *49*(1–4), 423–437.

Bell, J. G., Farndale, B. M., Dick, J. R., & Sargent, J. R. (1996). Modification of membrane fatty acid composition, eicosanoid production, and phospholipase a activity in Atlantic Salmon (Salmo salar) gill and kidney by dietary lipid. *Lipids*, *31*(11), 1163–1171.

Bell, M. V., Batty, R. S., Dick, J. R., Fretwell, K., Navarro, J. C., & Sargent, J. R. (1999). Dietary deficiency of docosahexaenoic acid impairs vision at low light intensities in juvenile herring (Clupea harengus L.). *Lipids*, *30*(5), 443.

Bennett, W. A., & Moyle, P. B. (1996). *Where Have All the Fishes Gone? Interactive Factors Producing Fish Declines in the Sacramento-San Joaquin Estuary* (J. T. Hollibaugh, Ed.; pp. 519–542).

Bou, M., Todorčević, M., Torgersen, J., Škugor, S., Navarro, I., & Ruyter, B. (2016). De novo lipogenesis in Atlantic salmon adipocytes. *Biochimica et Biophysica Acta (BBA) - General Subjects*, *1860*(1), 86–96.

Bourret, S. L., Caudill, C. C., & Keefer, M. L. (2016). Diversity of juvenile Chinook salmon life history pathways. *Reviews in Fish Biology and Fisheries*, *26*(3), 375–403.

Bowen, G. J., Wassenaar, L. I., & Hobson, K. A. (2005). Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia*, *143*(3), 337–348.

Brauge, C., Corraze, G., & Médale, F. (1995). Effects of dietary levels of carbohydrate and lipid on glucose oxidation and lipogenesis from glucose in rainbow trout, Oncorhynchus mykiss, reared in freshwater or in seawater. *Comparative Biochemistry and Physiology Part A: Physiology*, *111*(1), 117–124.

Brenner, R. R. (1974). The oxidative desaturation of unsaturated fatty acids in animals. *Molecular and Cellular Biochemistry*, *3*(1), 41–52.

Buchanan, R. A., & Skalski, J. R. (2020). Relating survival of fall-run Chinook Salmon through the San Joaquin Delta to river flow. *Environmental Biology of Fishes*, *103*(5), 389–410.

Budge, S. M., Iverson, S. J., & Koopman, H. N. (2006). STUDYING TROPHIC ECOLOGY IN MARINE ECOSYSTEMS USING FATTY ACIDS: A PRIMER ON ANALYSIS AND INTERPRETATION. *Marine Mammal Science*, *22*(4), 759–801.

Budge, S. M., Penney, S. N., & Lall, S. P. (2012). Estimating diets of Atlantic salmon (Salmo salar) using fatty acid signature analyses; validation with controlled feeding studies. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(6), 1033–1046.

Budge, S. M., Springer, A. M., Iverson, S. J., & Sheffield, G. (2007). Fatty acid biomarkers reveal niche separation in an Arctic benthic food web. *Marine Ecology Progress Series*, *336*, 305–309.

Budge, S. M., Wang, S. W., Hollmen, T. E., & Wooller, M. J. (2011). Carbon isotopic fractionation in eider adipose tissue varies with fatty acid structure: implications for trophic studies. *Journal of Experimental Biology*, *214*(22), 3790–3800.

Budge, S. M., Wooller, M. J., Springer, A. M., Iverson, S. J., McRoy, C. P., & Divoky, G. J. (2008). Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. *Oecologia*, *157*, 117–129.

Burns, C. W., Brett, M. T., & Schallenberg, M. (2011). A comparison of the trophic transfer of fatty acids in freshwater plankton by cladocerans and calanoid copepods. *Freshwater Biology*, *56*(5), 889–903.

Chiapella, A. M., Kainz, M. J., & Strecker, A. L. (2021). Fatty acid stable isotopes add clarity, but also complexity, to tracing energy pathways in aquatic food webs. *Ecosphere*, *12*(2). https://doi.org/10.1002/ecs2.3360

Claiborne, A., Miller, J., Weitkamp, L., Teel, D., & Emmett, R. (2014). Evidence for selective mortality in marine environments: the role of fish migration size, timing, and production type. *Marine Ecology Progress Series*, *515*, 187–202.

Colombo, S. M., Wacker, A., Parrish, C. C., Kainz, M. J., & Arts, M. T. (2017). A fundamental dichotomy in long-chain polyunsaturated fatty acid abundance between and within marine and terrestrial ecosystems. *Environmental Reviews*, *25*(2), 163–174.

Cook, H. W., & McMaster, C. R. (2002). *Biochemistry of Lipids, Lipoproteins and Membranes, 4th Edition* (D. E. Vance & J. E. Vance, Eds.; Vol. 36).

Coulter, D. P., Bowen, G. J., & Höök, T. O. (2017). Influence of diet and ambient water on hydrogen and oxygen stable isotope ratios in fish tissue: patterns within and among tissues and relationships with growth rates. *Hydrobiologia*, *799*(1), 111–121.

Daly, E. A., Benkwitt, C. E., Brodeur, R. D., Litz, M. N. C., & Copeman, L. A. (2010). Fatty acid profiles of juvenile salmon indicate prey selection strategies in coastal marine waters. *Marine Biology*, *157*(9), 1975–1987.

Daly, E. A., Brodeur, R. D., & Weitkamp, L. A. (2009). Ontogenetic Shifts in Diets of Juvenile and Subadult Coho and Chinook Salmon in Coastal Marine Waters: Important for Marine Survival? *Transactions of the American Fisheries Society*, *138*(6), 1420–1438.

Deines, P., Bodelier, P. L. E., & Eller, G. (2007). Methane-derived carbon flows through methane-oxidizing bacteria to higher trophic levels in aquatic systems. *Environmental Microbiology*, *9*(5), 1126–1134.

Deines, P., & Grey, J. (2006). Site-specific methane production and subsequent midge mediation within Esthwaite Water, UK. *Archiv Für Hydrobiologie*, *167*(1), 317–334.

Deines, P., Grey, J., & Richnow, H.-H. (2007). Linking larval chironomids to methane: seasonal variation of the microbial methane cycle and chironomid. *Aquatic Microbial Ecology*, *46*, 273–282.

Deniro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, *42*, 495–506.

Deniro, M. J., & Epstein, S. (1979). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*. 5, 241-251.

Dias, J., Corraze, G., Arzel, J., Alvarez, M. J., Bautista, J. M., Lopez-Bote, C., & Kaushik, S. J. (1999). Nutritional control of lipid deposition in rainbow trout and European seabass: effect of dietary protein/energy ratio. *Cybium*, *27*, 127–137.

Doucett, R. R., Marks, J. C., Blinn, D. W., Caron, M., & Hungate, B. A. (2007). Measuring Terrestrial Subsidies to Aquatic Food Webs Using Stable Isotopes of Hydrogen. *Ecology*, *6*(88), 1587–1592.

Dover, C. L. V., Grassle, J. F., Fry, B., Garritt, R. H., & Starczak, V. R. (1992). Stable isotope evidence for entry of sewage-derived organic material into a deep-sea food web. *Nature*, *360*(6400), 153–156.

Fouilland, E., & Mostajir, B. (2010). Revisited phytoplanktonic carbon dependency of heterotrophic bacteria in freshwaters, transitional, coastal and oceanic waters. *FEMS Microbiology Ecology*, *73*(3), 419–429.

Frøyland, L., Lie, Ø., & Berge, R. K. (2000). Mitochondrial and Peroxisomal b-oxidation capacities in various tissues from Atlantic Salmon (Salmo salar)). *Aquaculture Nutrition*, *6*, 85–89.

Fujibayashi, M., Ogino, M., & Nishimura, O. (2016). Fractionation of the stable carbon isotope ratio of essential fatty acids in zebrafish Danio rerio and mud snails Bellamya chinensis. *Oecologia*, *180*(2), 589–600.

Galloway, A. W. E., Taipale, S. J., Hiltunen, M., Peltomaa, E., Strandberg, U., Brett, M. T., & Kankaala, P. (2014). Diet-specific biomarkers show that high-quality phytoplankton fuels herbivorous zooplankton in large boreal lakes. *Freshwater Biology*, *59*(9), 1902–1915.

Gladyshev, M. I., Makhutova, O. N., Kravchuk, E. S., Anishchenko, O. V., & Sushchik, N. N. (2016). Stable isotope fractionation of fatty acids of Daphnia

fed laboratory cultures of microalgae. *Limnologica - Ecology and Management of Inland Waters*, *56*, 23–29. https://doi.org/10.1016/j.limno.2015.12.001

Gladyshev, M. I., & Sushchik, N. N. (2019). Long-chain Omega-3 Polyunsaturated Fatty Acids in Natural Ecosystems and the Human Diet: Assumptions and Challenges. *Biomolecules*, *9*(9), 485. https://doi.org/10.3390/biom9090485

Gladyshev, M. I., Sushchik, N. N., Kalachova, G. S., & Makhutova, O. N. (2012). Stable Isotope Composition of Fatty Acids in Organisms of Different Trophic Levels in the Yenisei River. *PloS One*, *7*(3), e34059-9.

Glencross, B. D. (2009). Exploring the nutritional demand for essential fatty acids by aquaculture species. *Reviews in Aquaculture*, *1*(2), 71–124.

Graham, C., Oxtoby, L., Wang, S. W., Budge, S. M., & Wooller, M. J. (2014). Sourcing fatty acids to juvenile polar cod (Boreogadus saida) in the Beaufort Sea using compound-specific stable carbon isotope analyses. *Polar Biology*, *37*(5), 697–705.

Grosholz, E., & Gallo, E. (2006). The influence of flood cycle and fish predation on invertebrate production on a restored California floodplain. *Hydrobiologia*, *568*(1), 91–109.

Hanak, E., Lund, J., Arnold, B., Escriva-Bou, A., Gray, B., Green, S., Harter, T., Howitt, R., MacEwan, D., Medellín-Azuara, J., Moyle, P., & Seavy, N. (2017). *Water Stress and a Changing San Joaquin Valley*.

Hastings, N., Agaba, M., Tocher, D. R., Leaver, M. J., Dick, J. R., Sargent, J. R., & Teale, A. J. (2001). A vertebrate fatty acid desaturase withD5 andD6 activities. *Proceedings of the National Academy of Sciences*, *98*, 14304–14309.

Hayes, J. M. (2001). *Fractionation of the Isotopes of Carbon and Hydrogen in Biosynthetic Processes**. National Meeting of the Geological Society of America.

Henderson, R. J. (1996). Fatty acid metabolism in freshwater fish with particular reference to polyunsaturated fatty acids. *Archiv Für Tierernaehrung*, *49*(1), 5–22.

Henderson, R. J., & Sargent, J. R. (1985). Chain-Length Specificities of Mitochondrial and Peroxisomal b-oxidation of fatty acids in livers of Rainbow Trout. *Comparitive Biochemistry and Physiology*, *82*(1), 79–85.

Hertz, E., Trudel, M., Tucker, S., Beacham, T. D., & Mazumder, A. (2016). Overwinter shifts in the feeding ecology of juvenile Chinook salmon. *ICES Journal of Marine Science*, *74*(1), 226–233.

Hoar, W. S. (1988). The Physiology of Smolting Salmonids. *Fish Physiology*, *11*, 275–343.

Hurst, T. P. (2007). Causes and consequences of winter mortality in fishes. *Journal of Fish Biology*, *71*(2), 315–345.

Ishizaki, Y. (2001). The effect of dietary docosahexaenoic acid on schooling behaviour and brain development in larval yellowtail. *Journal of Fish Biology*, *58*(6), 1691–1703.

Jeffres, C. A., Holmes, E. J., Sommer, T. R., & Katz, J. V. E. (2020). Detrital food web contributes to aquatic ecosystem productivity and rapid salmon growth in a managed floodplain. *PLOS ONE*, *15*(9), e0216019. https://doi.org/10.1371/journal.pone.0216019

Jeffres, C. A., Opperman, J. J., & Moyle, P. B. (2008). Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environmental Biology of Fishes*, *83*(4), 449–458.

Jeffres, C. A. (in prep). Experimental enclosure of Chinook Salmon in the Sacramento-San Joaquin River Delta. UC Davis: Center for Watershed Sciences.

Jin, Y., Olsen, R. E., Gillard, G. B., Østensen, M.-A., Korsvoll, S. A., Santi, N., Vik, J. O., Sandve, S. R., & Olsen, Y. (2018). A systemic study of lipid metabolism regulation in salmon fingerlings and early juveniles fed plant oil. *British Journal of Nutrition*, *120*(6), 653–664.

Jobling, M. (2004). 'Finishing' feeds for carnivorous fish and the fatty acid dilution model. *Aquaculture Research*, *35*(7), 706–709.

Kaneda, T. (1991). Iso- and Anteiso-Fatty Acids in Bacteria: Biosynthesis, Function, and Taxonomic Significance. *Microbiological Reviews*, *55*(2), 288–302.

Katz, J., Moyle, P. B., Quiñones, R. M., Israel, J., & Purdy, S. (2013). Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. *Environmental Biology of Fishes*, *96*(10–11), 1169–1186.

Katz, J. V. E., Jeffres, C., Conrad, J. L., Sommer, T. R., Martinez, J., Brumbaugh, S., Corline, N., & Moyle, P. B. (2017). Floodplain farm fields provide novel rearing habitat for Chinook salmon. *PloS One*, *12*(6).

Kiessling, A., Pickova, J., Eales, J. G., Dosanjh, B., & Higgs, D. (2005). Age, ration level, and exercise affect the fatty acid profile of chinook salmon (Oncorhynchus tshawytscha) muscle differently. *Aquaculture*, *243*(1–4), 345–356.

Kraus-Polk, A., & Fulton, J. (2020). California's Sacramento-San Joaquin Delta as an Exemplary Anthropocene Landscape. *Case Studies in the Environment*, *4*(1).

Lai, H.-O., & Yamada, J. (1992). Changes of the Fatty Acid Composition in Smolts of Masu Salmon (Oncorhynchus Masou) Associated with Desmoltification and Sea-Water Transfer). *Comp. Biochem. Physiol.*, *103*(1), 221–226.

Lau, D. C. P., Leung, K. M. Y., & Dudgeon, D. (2009). Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams? *Journal of the North American Benthological Society*, *28*(2), 426–439. https://doi.org/10.1899/07-079.1

Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., Yeager, L. A., Post, D. M., & Bearhop, S. (2011). Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews*, *87*(3), 545–562.

Litz, M. N. C., Miller, J. A., Copeman, L. A., Teel, D. J., Weitkamp, L. A., Daly, E. A., & Claiborne, A. M. (2017). *Ontogenetic shifts in the diets of juvenile Chinook Salmon: new insight from stable isotopes and fatty acids*. 1–24.

Macko, S. A., Estep, M. L. F., & Lee, W. Y. (1983). Stable Hydrogen Isotope Analysis of Foodwebs on Laboratory and Field Populations of Marine Amphipods. *Journal of Experimental Marine Biology and …*, *72*, 243–249.

Macko, S. A., Fogel, M. L., Hare, P. E., & Hoering, T. C. (1987). Isotopic fractionation of nitrogen and carbon in the synthesis of amino acids by

microorganisms. *Chemical Geology: Isotope Geoscience Section*, *65*(1), 79–92.

Makhutova, O. N., Sushchik, N. N., Gladyshev, M. I., Ageev, A. V., Pryanichnikova, E. G., & Kalachova, G. S. (2011). Is the Fatty Acid Composition of Freshwater Zoobenthic Invertebrates Controlled by Phylogenetic or Trophic Factors? *Lipids*, *46*(8), 709–721.

Marine, K. R., & Cech, J. J. (2004). Effects of High Water Temperature on Growth, Smoltification, and Predator Avoidance in Juvenile Sacramento RiverChinook Salmon. *North American Journal of Fisheries Management*, *24*(1), 198–210. https://doi.org/10.1577/m02-142

Marston, D., Mesick, C. W., Hubbard, A., Stanton, D., Fortmann-Roe, S., Tsao, S., & Heyne, T. (2012). Delta Flow Factors Influencing Stray Rate of Escaping Adult San Joaquin River Fall-Run Chinook Salmon (Oncorhynchus tshawytscha). *San Francisco Estuary and Watershed Science*, *10*(4).

Martin-Creuzburg, D., Beck, B., & Freese, H. M. (2011). Food quality of heterotrophic bacteria for Daphnia magna: evidence for a limitation by sterols. *FEMS Microbiology Ecology*, *76*(3), 592–601.

Masuda, R., Takeuchi, T., Tsukamoto, K., Ishizaki, Y., Kanematsu, M., & Imaizumi, K. (1998). Critical involvement of dietary docosohexaenoic acid in the ontogeny of schooling behavior in the yellowtail. *Journal of Fish Biology*, 471–484.

McClure, M. M., Carlson, S. M., Beechie, T. J., Pess, G. R., Jorgensen, J. C., Sogard, S. M., Sultan, S. E., Holzer, D. M., Travis, J., Sanderson, B. L., Power, M. E., & Carmichael, R. W. (2008). Evolutionary consequences of habitat loss for Pacific anadromous salmonids. *Evolutionary Applications*, *1*(2), 300–318.

Mcmeans, B. C., Koussoroplis, A.-M., Arts, M. T., & Kainz, M. J. (2015). Terrestrial dissolved organic matter supports growth and reproduction of Daphnia magna when algae are limiting. *Journal of Plankton Research*, *37*(6), 1201–1209.

Michel, C. J., Ammann, A. J., Lindley, S. T., Sandstrom, P. T., Chapman, E. D., Thomas, M. J., Singer, G. P., Klimley, A. P., & MacFarlane, R. B. (2015). Chinook salmon outmigration survival in wet and dry years in California's

Sacramento River. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(11), 1749–1759. https://doi.org/10.1139/cjfas-2014-0528

Mizuno, S., Urabe, H., Aoyama, T., Omori, H., Iijima, A., Kasugai, K., Torao, M., Misaka, N., Koide, N., & Ueda, H. (2012). Changes in activity and transcript level of liver and gill metabolic enzymes during smoltification in wild and hatchery-reared masu salmon (Oncorhynchus masou). *Aquaculture*, *362*, 109–120.

Mjaavatten, O., Levings, C. D., & Poon, P. (1998). Variation in the fatty acid composition of juvenile chinook and coho salmon from Fraser river estuary determined by multivariate analysis; role of environment and genetic origin. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *120*(2), 291–309.

Monsen, N. E., Cloern, J. E., & Burau, J. R. (2007). Effects of Flow Diversions on Water and Habitat Quality: Examples from Californias Highly Manipulated Sacramento-San Joaquin Delta. *San Francisco Estuary and Watershed Science*, *5*(3).

Monson, K. D., & Hayes, J. M. (1980). Biosynthetic Control of the Natural Abundance of Carbon 13 at Specific Positions within Fatty Acids in Escherichia coli. *The Journal of Biological Chemistry*, *255*(23), 11435–11441.

Mount, J. F., Bennett, W. A., Durand, J. R., & Fleenor, W. E. (2012). Aquatic Ecosystem Stressors in the Sacramento–San Joaquin Delta. *Public Policy Institute of California.*

Newsome, S. D., Wolf, N., Peters, J., & Fogel, M. L. (2014). Amino Acid 13C Analysis Shows Flexibility in the Routing of Dietary Protein and Lipids to the Tissue of an Omnivore. *Integrative and Comparative Biology*, *54*(5), 890–902.

Nicolaides, N., & Woodall, A. N. (1962). Impaired Pigmentation in Chinook Salmon Fed Diets Deficient in Essential Fatty Acids. *Journal of Nutrition*, *78*, 431–437.

Österblom, H., Olsson, O., Blenckner, T., & Furness, R. W. (2008). Junk-food in marine ecosystems. *Oikos*, *117*(7), 967–977.

Pereira, D. L., & Adelman, I. R. (1985). Interactions of Temperature, Size, and Photoperiod on Growth and Smoltification of Chinook Salmon (Oncorhynchus tsawytscha)). *Aquaculture*, *46*, 185–192.

Perry, R. W., Pope, A. C., Romine, J. G., Brandes, P. L., Burau, J. R., Blake, A. R., Ammann, A. J., & Michel, C. J. (2018). Flow-mediated effects on travel time, routing, and survival of juvenile Chinook salmon in a spatially complex, tidally forced river delta. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(11), 1886–1901.

Peterson, B. J., & Fry, B. (1987). STABLE ISOTOPES IN ECOSYSTEM STUDIES. *Annual Review of Ecological Systems*, *18*, 293–320.

Pilecky, M., Winter, K., Wassenaar, L. I., & Kainz, M. J. (2021). Compound-specific stable hydrogen isotope (δ2H) analyses of fatty acids: A new method and perspectives for trophic and movement ecology. *Rapid Communications in Mass Spectrometry*, *35*(16), e9135.

Polakof, S., Panserat, S., Soengas, J. L., & Moon, T. W. (2012). Glucose metabolism in fish: a review. *Journal of Comparative Physiology B*, *182*(8), 1015–1045.

Post, D. M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology*, *83*(3), 703–718.

Ray, P., Wi, S., Schwarz, A., Correa, M., He, M., & Brown, C. (2020). Vulnerability and risk: climate change and water supply from California's Central Valley water system. *Climatic Change*, *161*(1), 177–199.

Robin, J. H., Regost, C., Arzel, J., & Kaushik, S. J. (2003). Fatty acid profile of fish following a change in dietary fatty acid source: model of fatty acid composition with a dilution hypothesis. *Aquaculture*, *225*(1–4), 283–293.

Ruess, L., Tiunov, A., Haubert, D., Richnow, H. H., Häggblom, M. M., & Scheu, S. (2005). Carbon stable isotope fractionation and trophic transfer of fatty acids in fungal based soil food chains. *Soil Biology and Biochemistry*, *37*(5), 945–953.

Sargent, J. R. (1989). *Marine Biogenic Lipids, Fats, and Oils* (R. G. Ackman, Ed.). CRC Press.

Satterthwaite, W., Carlson, S., Allen-Moran, S., Vincenzi, S., Bograd, S., & Wells, B. (2014). Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. *Marine Ecology Progress Series*, *511*, 237–248.

Schulz, H. (1991). Beta oxidation of fatty acids. *Biochimica et Biophysica Acta (BBA) - Lipids and Lipid Metabolism*, *1081*(2), 109–120.

Sessions, A. L., Sylva, S. P., Summons, R. E., & Hayes, J. M. (2004). Isotopic exchange of carbon-bound hydrogen over geologic timescales. *Geochimica et Cosmochimica Acta*, *68*(7), 1545–1559.

Seyama, Y., Kasama, T., Yamakawa, T., Kawaguchi, A., Saito, K., & Okuda, S. (1977). Origin of Hydrogen Atoms in the Fatty Acids Synthesized with Yeast Fatty Acid Synthetase. *Journal of Biochemistry*, *82*, 1325–1329.

Shanab, S. M. M., Hafez, R. M., & Fouad, A. S. (2018). A review on algae and plants as potential source of arachidonic acid. *Journal of Advanced Research*, *11*, 3–13.

Solomon, C. T., Cole, J. J., Doucett, R. R., Pace, M. L., Preston, N. D., Smith, L. E., & Weidel, B. C. (2009). The influence of environmental water on the hydrogen stable isotope ratio in aquatic consumers. *Oecologia*, *161*(2), 313–324.

Stefansson, S. O., Bjornsson, B. T., Ebbesson, L. O., & McCormick, S. D. (2008). Smoltification. In R. N. Finn & B. G. Kapoor (Eds.), *Fish Larval Physiology* (pp. 639–681). Science Publishing.

Stott, A. W., Davies, E., Evershed, R. P., & Tuross, N. (1997). Monitoring the Routing of Dietary and Biosynthesised Lipids Through Compound – Specific Stable Isotope Measurements at Natural Abundance. *Naturwissenschaften*, *84*, 82–86.

Suzuki, Y., Akamatsu, F., Nakashita, R., & Korenaga, T. (2013). Characterization of Japanese Polished Rice by Stable Hydrogen Isotope Analysis of Total Fatty Acids for Tracing Regional Origin. *Analytical Sciences*, *29*, 143–146.

Taipale, S. J., Brett, M. T., Hahn, M. W., Martin-Creuzburg, D., Yeung, S., Hiltunen, M., Strandberg, U., & Kankaala, P. (2014). Differing Daphnia magna assimilation efficiencies for terrestrial, bacterial, and algal carbon and fatty acids. *Ecology*, *95*(2), 563–576.

Taipale, S., Strandberg, U., Peltomaa, E., Galloway, A., Ojala, A., & Brett, M. (2013). Fatty acid composition as biomarkers of freshwater microalgae: analysis of 37 strains of microalgae in 22 genera and in seven classes. *Aquatic Microbial Ecology*, *71*(2), 165–178.

Takata, L., Sommer, T. R., Conrad, J. L., & Schreier, B. M. (2017). Rearing and migration of juvenile Chinook salmon (Oncorhynchus tshawytscha) in a large river floodplain. *Environmental Biology of Fishes*, *100*(9), 1105–1120.

Takeuchi, T. (1997). Essential fatty acid requirements of aquatic animals with emphasis on fish larvae and fingerlings. *Reviews in Fisheries Science*, *5*(1), 1–25.

Tocher, D. R. (2003). Metabolism and Function of Lipids and Fatty Acids in Teleost Fish. *Reviews in Fisheries Science*, *11*(2), 107–184.

Tomkovic, L. A., Gross, E. S., Nakamoto, B., Fogel, M. L., & Jeffres, C. (2020). Source Water Apportionment of a River Network: Comparing Field Isotopes to Hydrodynamically Modeled Tracers. *Water*, *12*(4), 1128.

Twining, C. W., Taipale, S. J., Ruess, L., Bec, A., Martin-Creuzburg, D., & Kainz, M. J. (2020). Stable isotopes of fatty acids: current and future perspectives for advancing trophic ecology. *Philosophical Transactions of the Royal Society B*, *375*(1804), 20190641.

Valentine, D. L., Sessions, A. L., Tyler, S. C., & Chidthaisong, A. (2004). Hydrogen isotope fractionation during H2/CO2 acetogenesis: hydrogen utilization efficiency and the origin of lipid-bound hydrogen. *Geobiology*, *2*, 179–188.

Victoria, R. L., Martinelli, L. A., Trivelin, P. C. O., Matsui, E., Forsberg, B. R., Richey, J. E., & Devol, A. H. (1992). The Use of Stable Isotopes in Studies of Nutrient Cycling: Carbon Isotope Composition of Amazon Varzea Sediments. *Biotropica*, *24*(2B), 240–249.

Wakil, S. J., Stoops, J. K., & Joshi, V. C. (1983). Fatty Acid Synthesis and its Regulation. *Annual Reviews in Biology*, *52*, 537–579.

Waples, R. S., Teel, D. J., Myers, J. M., & Marshall, A. R. (2004). LIFE-HISTORY DIVERGENCE IN CHINOOK SALMON: HISTORIC CONTINGENCY AND PARALLEL EVOLUTION. *Evolution*, *58*(2), 386–403.

Watters, C., Iwamura, S., Ako, H., & Deng, D.-F. (2012). Nutrition Considerations in Aquaculture: The Importance of Omega-3 Fatty Acids in Fish Development and Human Health. *Foods and Nutrition*.

Welch, D. W., Porter, A. D., & Rechisky, E. L. (2021). A synthesis of the coast-wide decline in survival of West Coast Chinook Salmon (Oncorhynchus tshawytscha, Salmonidae). *Fish and Fisheries*, *22*(1), 194–211.

Wetzel, R. G. (1995). Death, detritus, and energy flow in aquatic ecosystems. *Freshwater Biology*, *33*, 83–89.

Whipple, A. A., Viers, J. H., Dahlke, H. E. (2016) Flood regime typology for floodplain ecosystem management as applied to the unregulated Cosumnes River of California, United States. *Ecohydrology,* 10, e1817.

Wijker, R. S., Sessions, A. L., Fuhrer, T., & Phan, M. (2019). H variation in microbial lipids is controlled by NADPH metabolism. *PNAS*, *116*(25), 12173–12182.

Willmes, M., Hobbs, J. A., Sturrock, A. M., Bess, Z., Lewis, L. S., Glessner, J. J. G., Johnson, R. C., Kurth, R., & Kindopp, J. (2018). Fishery collapse, recovery, and the cryptic decline of wild salmon on a major California river. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(11), 1836–1848.

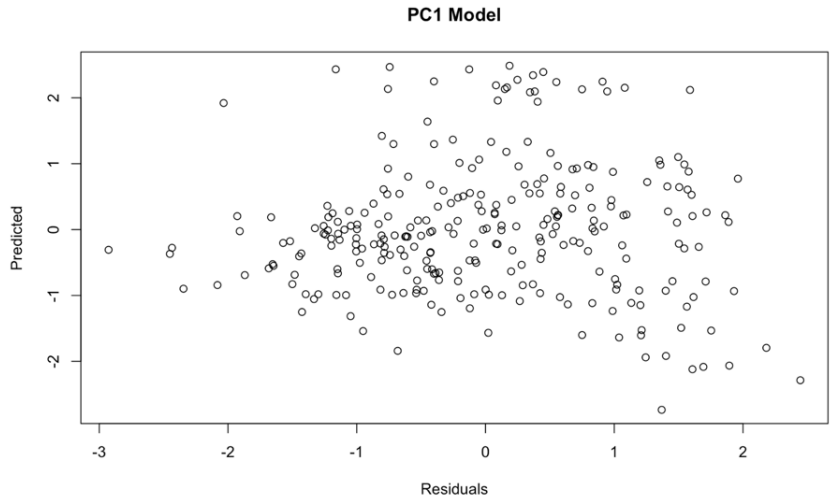
Woodson, L., Wells, B., Weber, P., MacFarlane, R., Whitman, G., & Johnson, R. (2013). Size, growth, and origin-dependent mortality of juvenile Chinook salmon Oncorhynchus tshawytscha during early ocean residence. *Marine Ecology Progress Series*, *487*, 163–175.

Yoshiyama, R. M., Fisher, F. W., & Moyle, P. B. (1998). Historical Abundance and Decline of Chinook Salmon in the Central Valley Region of California. *North American Journal of Fisheries Management*, *18*(3), 487–521

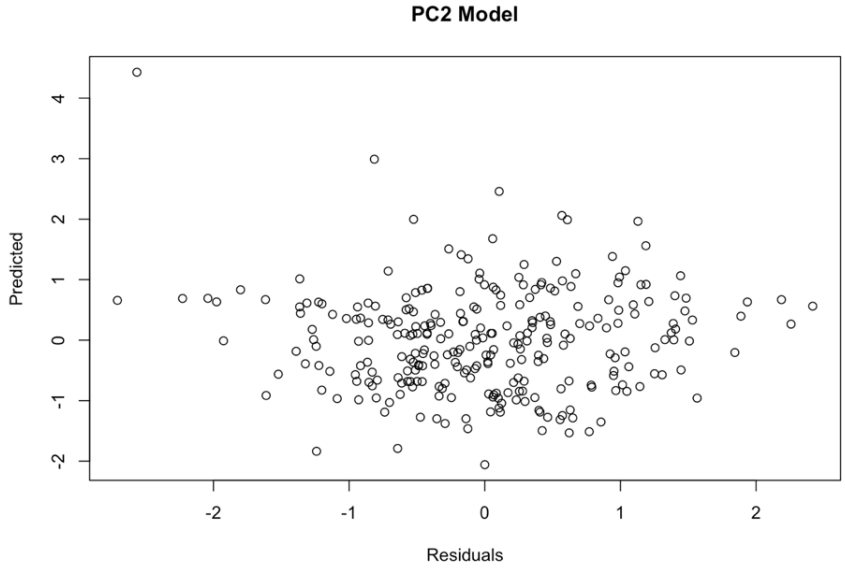
Conclusion

Appendices

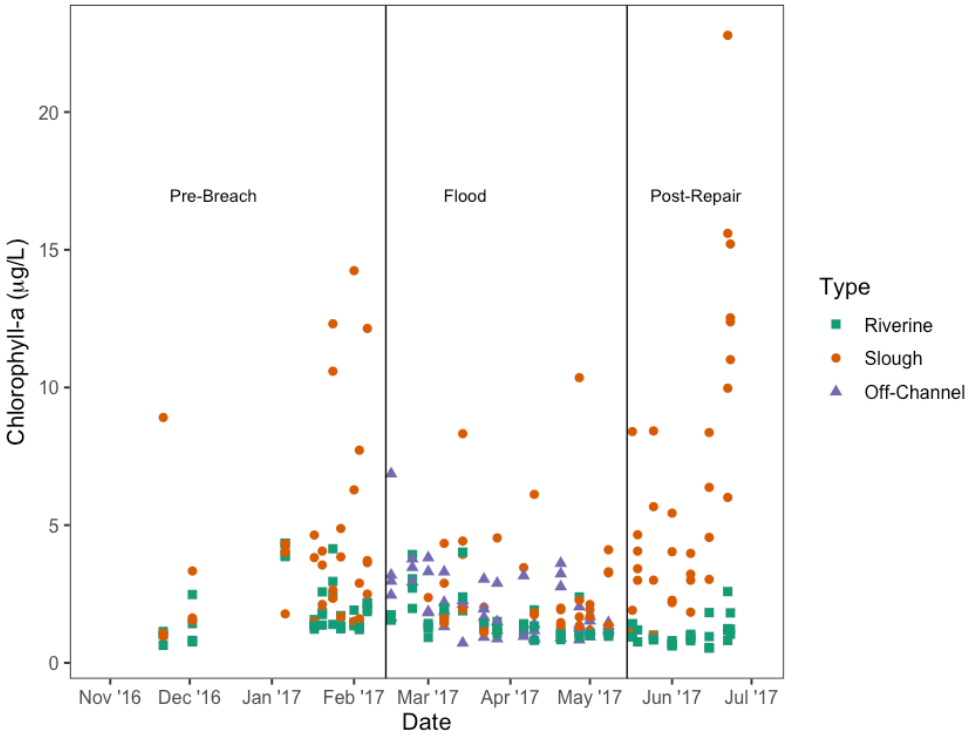
Appendix 1.1. Plot of residuals vs predicted values used to assess model (PC1 Regression) assumptions of homoscedasticity. No systematic patterns are apparent.



Appendix 1.2. Plot of residuals vs predicted values used to assess model (PC2 Regression) assumptions of homoscedasticity. No systematic patterns are apparent.



Appendix 1.3. Chlorophyll-a concentration through time. Different habitat types are shown with different colors and symbols.



Appendix 1.4a. Table of Kendall correlation coefficients for POM and water quality data at river sites. Significance was assessed at $P < 0.05$. Water temperature abbreviated to "W.T."

Riverine: Pre-Breach	C:N Ratio	$\delta^{13}C$	$\delta^{15}N$	W.T. (°C)	Chlorophyll-a (μg/L)	Turbidity (FNU)	Dissolved Oxygen (% Saturation)	Q
C:N Ratio	-	N.S.	-0.42	N.S.	N.S.	N.S.	0.22	N.S.
$\delta^{13}C$	N.S.	-	N.S.	-0.26	0.33	0.42	N.S.	0.53
$\delta^{15}N$	-0.42	N.S.	-	0.23	N.S.	-0.36	N.S.	-0.23
W.T. (°C)	N.S.	-0.26	0.23	-	-0.3	-0.4	N.S.	-0.33
Chlorophyll-a (μg/L)	N.S.	0.33	N.S.	-0.3	-	0.55	N.S.	0.49
Turbidity (FNU)	N.S.	0.42	-0.36	-0.4	0.55	-	-0.24	0.72
Dissolved Oxygen (% Saturation)	0.22	N.S.	N.S.	N.S.	N.S.	-0.24	-	N.S.
Q	N.S.	0.53	-0.23	-0.33	0.49	0.72	N.S.	-

Appendix 1.4b. Table of Kendall correlation coefficients for POM and water quality data at river sites. Significance was assessed at $P < 0.05$. Water temperature abbreviated to "W.T."

Riverine: Flood	C:N Ratio	$\delta^{13}C$	$\delta^{15}N$	W.T. (°C)	Chlorophyll-a (μg/L)	Turbidity (FNU)	Dissolved Oxygen (% Saturation)	Q
C:N Ratio	-	-0.32	-0.38	-0.31	N.S.	0.38	N.S.	0.38
$\delta^{13}C$	-0.32	-	0.23	N.S.	N.S.	-0.27	0.55	N.S.
$\delta^{15}N$	-0.38	0.23	-	0.43	-0.35	-0.5	N.S.	-0.4
W.T. (°C)	-0.31	N.S.	0.43	-	-0.29	-0.36	-0.27	-0.41
Chlorophyll-a (μg/L)	N.S.	N.S.	-0.35	-0.29	-	0.58	N.S.	0.27
Turbidity (FNU)	0.38	-0.27	-0.5	-0.36	0.58	-	N.S.	0.50
Dissolved Oxygen (% Saturation)	N.S.	0.55	N.S.	-0.27	N.S.	N.S.	-	N.S.
Q	0.38	N.S.	-0.4	-0.41	0.27	0.50	N.S.	-

Appendix 1.4c Table of Kendall correlation coefficients for POM and water quality data at river sites. Significance was assessed at $P < 0.05$. Water temperature abbreviated to "W.T."

Riverine: Post-Repair	C:N Ratio	$\delta^{13}C$	$\delta^{15}N$	W.T. (°C)	Chlorophyll-a (μg/L)	Turbidity (FNU)	Dissolved Oxygen (% Saturation)	Q
C:N Ratio	-	-0.34	-0.6	-0.27	N.S.	N.S.	N.S.	0.29
$\delta^{13}C$	-0.34	-	N.S.	N.S.	N.S.	N.S.	0.33	N.S.
$\delta^{15}N$	-0.6	N.S.	-	0.32	N.S.	N.S.	N.S.	-0.44
W.T. (°C)	-0.27	N.S.	0.32	-	N.S.	0.45	-0.54	-0.66
Chlorophyll-a (μg/L)	N.S.	N.S.	N.S.	N.S.	-	N.S.	-0.27	N.S.
Turbidity (FNU)	N.S.	N.S.	N.S.	0.45	N.S.	-	-0.65	N.S.
Dissolved Oxygen (% Saturation)	N.S.	0.33	N.S.	-0.54	-0.27	-0.65	-	N.S.
Q	0.29	N.S.	-0.44	-0.66	N.S.	N.S.	N.S.	-

Slough: Pre-Breach	C:N Ratio	$\delta^{13}C$	$\delta^{15}N$	W.T. (°C)	Chlorophyll-a (μg/L)	Turbidity (FNU)	Dissolved Oxygen (% Saturation)	Q
C:N Ratio	-	N.S.	N.S.	N.S.	N.S.	0.23	N.S.	N.S.
$\delta^{13}C$	N.S.	-	-0.52	-0.36	N.S.	0.34	N.S.	0.44
$\delta^{15}N$	N.S.	-0.52	-	0.22	N.S.	-0.47	N.S.	-0.4
Water Temperature (°C)	N.S.	-0.36	0.22	-	N.S.	-0.4	N.S.	-0.49
Chlorophyll-a (μg/L)	N.S.	N.S.	N.S.	N.S.	-	0.3	-0.26	N.S.
Turbidity (FNU)	0.23	0.34	-0.47	-0.4	0.3	-	N.S.	0.8
Dissolved Oxygen (% Saturation)	N.S.	N.S.	N.S.	N.S.	-0.26	N.S.	-	N.S.
Q	N.S.	0.44	-0.4	-0.49	N.S.	0.8	N.S.	-

Appendix 1.5a. Table of Kendall correlation coefficients for POM and water quality data at slough sites. Significance was assessed at $P < 0.05$. Water temperature abbreviated to “W.T.”

Appendix 1.5b. Table of Kendall correlation coefficients for POM and water quality data at slough sites. Significance was assessed at $P < 0.05$. Water temperature abbreviated to "W.T."

Slough: Post-Repair	C:N Ratio	$\delta^{13}C$	$\delta^{15}N$	W.T. (°C)	Chlorophyll-a (μg/L)	Turbidity (FNU)	D.O.	Q
C:N Ratio	-	-0.27	-0.4	N.S.	N.S.	N.S.	N.S.	N.S.
$\delta^{13}C$	-0.27	-	N.S.	-0.25	N.S.	-0.26	N.S.	N.S.
$\delta^{15}N$	-0.4	N.S.	-	0.33	N.S.	N.S.	N.S.	-0.55
W.T. (°C)	N.S.	-0.25	0.33	-	0.66	0.55	0.25	-0.62
Chlorophyll-a (μg/L)	N.S.	N.S.	N.S.	0.66	-	0.55	N.S.	-0.42
Turbidity (FNU)	N.S.	-0.26	N.S.	0.55	0.55	-	N.S.	-0.38
Dissolved Oxygen (% Saturation)	N.S.	N.S.	N.S.	0.25	N.S.	N.S.	-	-0.33
Q	N.S.	N.S.	-0.55	-0.62	-0.42	-0.38	-0.33	-

Appendix 1.5c. Table of Kendall correlation coefficients for POM and water quality data at slough sites. Significance was assessed at $P < 0.05$. Water temperature abbreviated to "W.T."

Slough: Flood	C:N Ratio	$\delta^{13}C$	$\delta^{15}N$	W.T. (°C)	Chlorophyll-a (μg/L)	Turbidity (FNU)	D.O. (% Saturation)	Q
C:N Ratio	-	N.S.	-0.35	N.S.	N.S.	0.24	N.S.	N.S.
$\delta^{13}C$	N.S.	-	-0.3	-0.3	-0.38	0.3	N.S.	0.32
$\delta^{15}N$	-0.35	-0.3	-	0.35	N.S.	-0.43	N.S.	-0.36
W.T. (°C)	N.S.	-0.3	0.35	-	N.S.	-0.39	N.S.	-0.44
Chlorophyll-a (μg/L)	N.S.	-0.38	N.S.	N.S.	-	N.S.	N.S.	N.S.
Turbidity (FNU)	0.24	0.3	-0.43	-0.39	N.S.	-	N.S.	0.36
Dissolved Oxygen (% Saturation)	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	-	N.S.
Q	N.S.	0.32	-0.36	-0.44	N.S.	0.36	N.S.	-

Off-Channel: Flood	C:N Ratio	$\delta^{13}C$	$\delta^{15}N$	W.T. (°C)	Chlorophyll-a (μg/L)	Turbidity (FNU)	D.O. (% Saturation)	Q
C:N Ratio	-	-0.31	-0.27	-0.27	N.S.	0.33	-0.45	0.44
$\delta^{13}C$	-0.31	-	N.S.	N.S.	0.24	N.S.	N.S.	N.S.
$\delta^{15}N$	-0.27	N.S.	-	0.33	-0.22	-0.36	0.24	-0.4
W.T. (°C)	-0.27	N.S.	0.33	-	N.S.	-0.55	0.31	-0.44
Chlorophyll-a (μg/L)	N.S.	0.24	-0.22	N.S.	-	0.29	N.S.	-0.4
Turbidity (FNU)	0.33	N.S.	-0.36	-0.55	0.29	-	-0.49	-0.47
Dissolved Oxygen Percent Saturation	-0.45	N.S.	0.24	0.31	N.S.	-0.49	-	-0.23
Q	0.44	N.S.	-0.4	-0.44	-0.4	0.47	-0.23	-

Appendix 1.6. Table of Kendall correlation coefficients for POM and water quality data at off-channel sites. Significance was assessed at $P < 0.05$. Water temperature abbreviated to “W.T.”

Appendix 1.7. Tabular summary of principal component analysis variable loadings and proportions of explained variance.

Variable	PC1	PC2	PC3	PC4	PC5
Chlorophyll-a (μg/L)	0.114	-0.736	0.376	-0.073	-0.547
C:N Ratio	0.491	-0.045	-0.725	0.301	-0.375
Carbon-13	0.276	0.617	0.503	0.275	-0.464
Nitrogen-15	-0.577	-0.132	-0.017	0.803	-0.062
Turbidity (FNU)	0.580	-0.243	0.283	0.428	0.584
Standard Deviation	1.42	1.2	0.91	0.68	0.50
Variance Explained	40%	29%	17%	9%	5%
Cumulative Variance	40%	69%	86%	95%	100%

Appendix 1.8 Results from perMANOVA test on POM composition data. Here we test for the effect of time period (as fixed factors), with data grouped by different habitat type(s). A significant result means that POM in that habitat type significantly changed its multivariate centroid location (composition) as a function of time. Significance was determined at $P < 0.01$.

perMANOVA	River Sites Alone	Slough Sites Alone	River + Slough + Off-Channel
Effect of Time	$F_{2, 116} = 4.7$	$F_{2, 106} = 8.4$	$F_{2, 274} = 10.5$

Appendix 2.1a. Coordinates of Sacramento-San Joaquin river delta field collection sites where wild fish were collected for stable isotope analysis.

Wild Fish Collection	Lat.	Lon.
Cosumnes, 2016	38.271953	-121.39596
MWT, 2017	38.271953	-121.489057
Cosumnes, 2018	38.271953	-121.39596

Appendix 2.1b. Coordinates of experimental Chinook salmon enclosures..

Site	Lat.	Lon.
CosBeach	38.26040376	-121.4236662
CosTri	38.27143766	-121.3966422
Knaggs	38.70598537	-121.6436053
Marsh	38.33034535	-121.6722033
Moke	38.25472096	-121.4295373
Sac	38.67367855	-121.6272913

Appendix 2.2a. Coordinates of particulate organic matter collections contributing to the river derived aggregate particulate organic matter sample.

POM "R"	Latitude	Longitude
MOK	38.254617	-121.429978
COS	38.257989	-121.431031
CFL	38.255261	-121.438600
MWT	38.258989	-121.461331

Appendix 2.2b. Coordinates of particulate organic matter collections contributing to the deltaic (i.e. off-channel and intertidal) aggregate particulate organic matter sample.

POM "D"	Latitude	Longitude
LST	38.264542	-121.463408
MST	38.268365	-121.483754
DCC	38.245700	-121.506989
SGS	38.265875	-121.497989

Appendix 2.2c. Coordinates of particulate organic matter collections contributing to the floodplain derived aggregate particulate organic matter sample.

POM "F"	Latitude	Longitude
A2	38.265796	-121.472408
C2	38.247223	-121.483909
SE	38.229917	-121.492504
DC	38.241303	-121.5495154

Appendix 2.3. Description of compound specific carbon isotope data sources.

		Class				
		Algae (n)	Bacteria (n)	Fungi (n)	Plant (n)	Total
Source	Larsen et al. 2009	0	10	13	9	32
	Larsen et al. 2012	2	0	0	0	2
	Larsen et al. 2013	25	0	0	0	25
	Thorp et al. 2016	1	1	1	2	5
Total		28	11	14	11	54

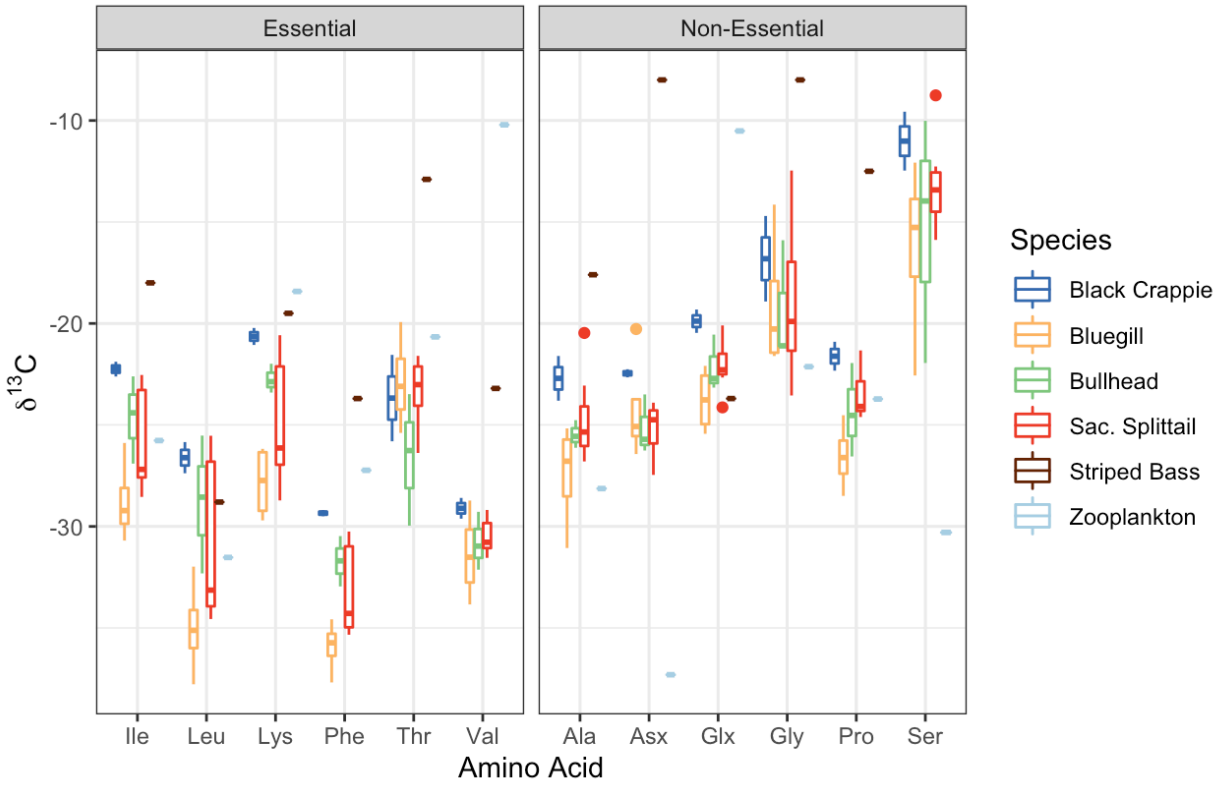
Appendix 2.4a. Carbon isotope composition, and standard deviation, of non-essential amino acids in primary producers.

Simple Name	**Scientific Name**	**Ala**	**alasd**	**Asx**	**asxsd**	**Glx**	**glxsd**	**Gly**	**glysd**	**Pro**	**prosd**	**Ser**	**sersd**
Alder	*Alnus sp.*	-20.2	0.2	-27.5	0.1	-29.0	0.3	-10.0	0.1	-27.6	0.1	-3.6	0.2
Algae	Not Identified	-8.5	0.3	-8.0	0.2	-9.9	0.2	-8.4	0.6	-16.8	0.2	NA	NA
Blackberry	*Rubus sp.*	-23.5	0.1	-24.4	0.1	-28.8	0.1	-10.8	0.2	-25.3	0.1	NA	NA
Egeria	*Egeria sp.*	-24.2	0.2	-20.9	0.4	-29.7	0.3	-16.6	0.1	-29.0	0.2	NA	NA
Hyacinth	*Eichornia crassipes*	-14.4	0.3	-13.7	0.3	-18.6	0.2	-0.5	0.6	-17.8	0.1	NA	NA
Ludwigia	*Ludwigia sp.*	-23.2	0.3	-21.1	0.1	-23.9	0.2	-16.4	0.1	-25.3	0.1	NA	NA

Appendix 2.4b. Carbon isotope composition, and standard deviation, of essential amino acids in primary producers.

Simple Name	Scientific Name	Ile	ilesd	Leu	leusd	Lys	lyssd	Phe	phesd	Thr	thrsd	Val	valsd
Alder	*Alnus sp.*	-30.1	0.2	-40.1	0.3	-25.8	0.1	-30.1	0.1	-10.9	0.2	-28.9	0.2
Algae	Not Identified	-13.0	0.3	-19.6	0.2	NA	NA	-18.4	0.2	NA	NA	-15.2	0.3
Blackberry	*Rubus sp.*	-26.5	1.0	-37.9	0.3	-24.2	0.1	-26.0	0.1	NA	NA	-30.6	0.5
Egeria	*Egeria sp.*	-27.2	NA	-35.6	0.5	NA	NA	-27.9	0.2	NA	NA	-32.2	0.6
Hyacinth	*Eichornia crassipes*	-19.5	0.8	-27.3	0.3	-17.8	0.1	-19.8	0.1	NA	NA	-23.7	0.4
Ludwigia	*Ludwigia sp.*	-26.2	0.1	-36.1	0.1	NA	NA	-27.9	0.2	NA	NA	-30.0	0.2

Appendix 2.5. Carbon isotope composition of essential and nonessential amino acids in fish and invertebrates.



Appendix 2.6. Loadings and explained variance from linear discriminant analysis.

AA/LD	LD1	LD2	LD3
Ile	1.195	1.33	-0.275
Phe	1.927	0.588	2.125
Val	0.493	0.653	-0.086
Leu	-1.826	-0.301	1.714
Gly	0.958	-0.519	0.721
Proportion	0.5181	0.3671	0.1148

Appendix 2.7. Confusion matrix for leave one out validation of our linear discriminant model.

		Predicted			
		Algae	Bacteria	Fungi	Plant
Actual	Algae	28	0	2	1
	Bacteria	2	9	0	0
	Fungi	2	0	11	0
	Plant	1	0	1	10

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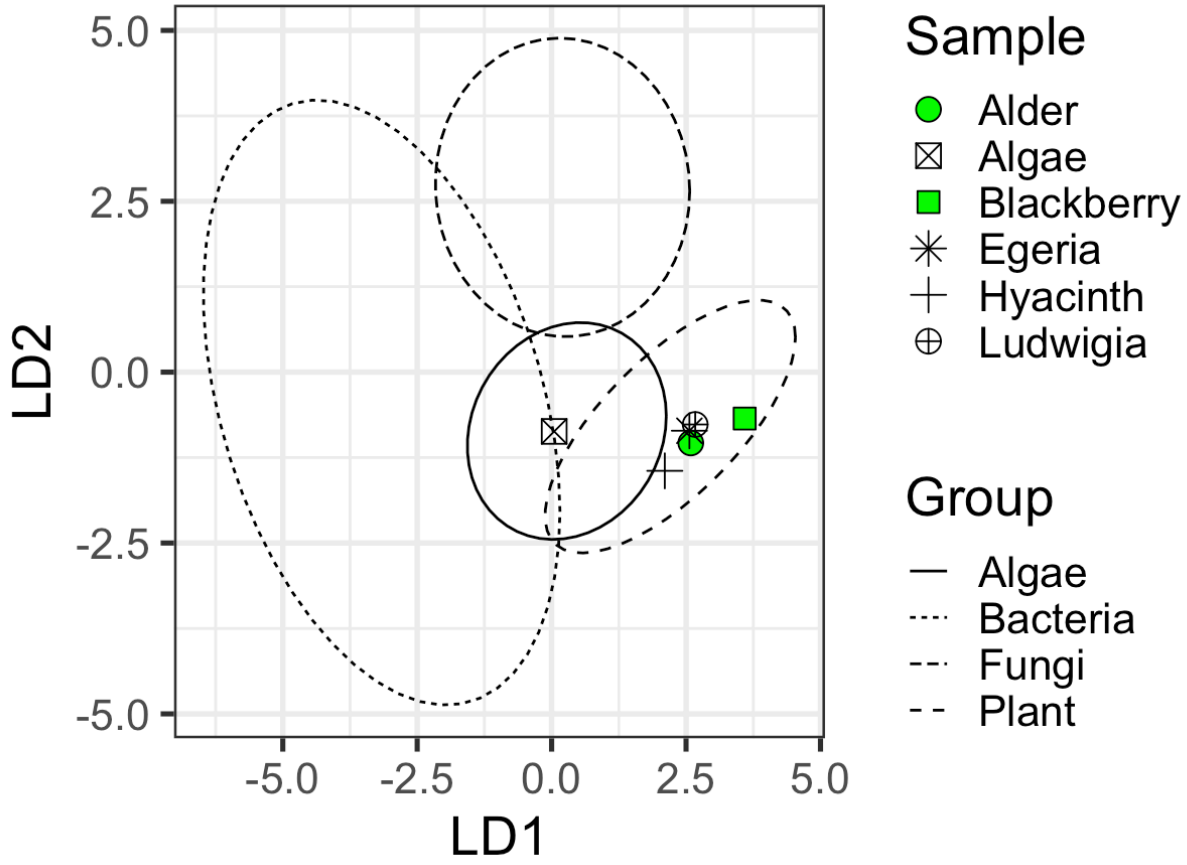
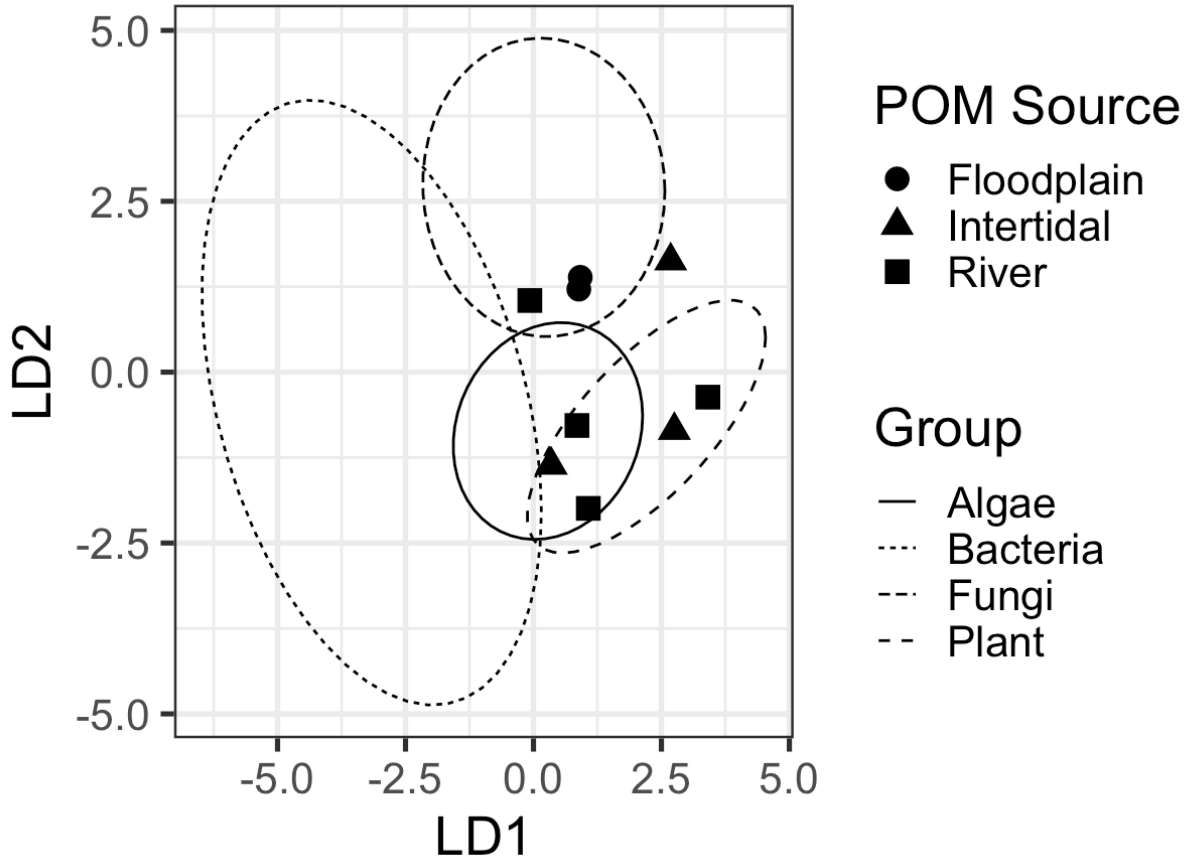
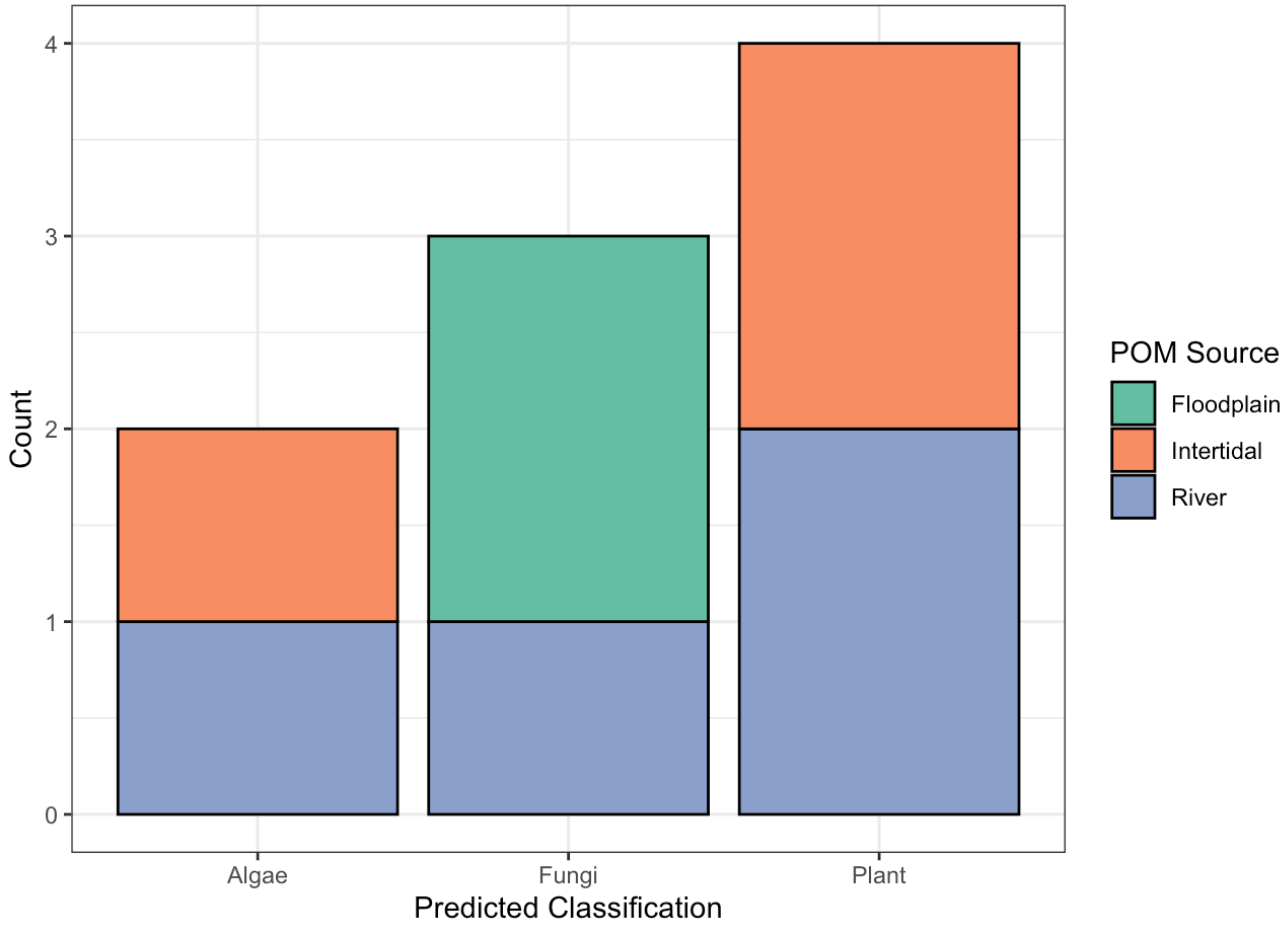
Appendix 2.8. Projection of data from local producers into the linear discriminant space describing variation in the carbon isotope composition.



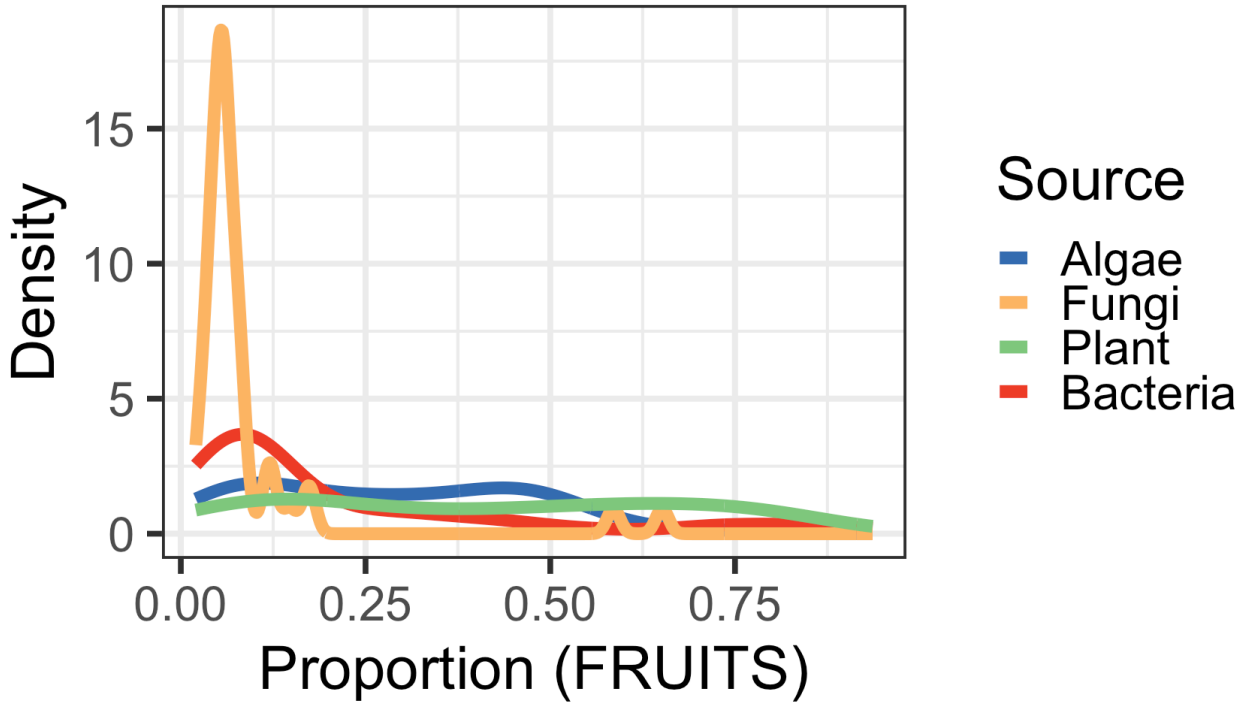
Appendix 2.9. Projection of data from POM into the linear discriminant space describing variation in the carbon isotope composition of amino acids.



Appendix 2.10. Class assignment from linear discriminant analysis of particulate organic matter samples, broken down by habitat of origin for the particulate organic matter.



Appendix 2.11. Distribution of average estimates for source contributions to POM from FRUITS mixing model.



Appendix 3.1. Overview of bulk carbon and nitrogen stable isotope measurements in fish, invertebrates, producers, and litter collected in the Sacramento-San Joaquin Delta. Litter samples are differentiated from live samples with "(L)."

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
5/17/17	-19.8	7.8	Algae	19.6	38.2457	-121.5070
5/17/17	-22.7	5.7	Algae	10.8	38.2517	-121.4888
4/27/17	-18.6	6.9	Algae	16.6	38.2645	-121.4634
4/3/19	-26.8	10.6	Chinook	3.9	38.2604	-121.4237
4/3/19	-27.3	10.8	Chinook	3.9	38.2604	-121.4237
4/3/19	-26.4	10.8	Chinook	3.8	38.2604	-121.4237
4/3/19	-26.4	10.8	Chinook	3.8	38.2604	-121.4237
4/3/19	-27.7	10.8	Chinook	4.0	38.2604	-121.4237
4/3/19	-25.7	10.8	Chinook	3.8	38.2604	-121.4237
4/3/19	-25.6	10.9	Chinook	4.0	38.2604	-121.4237
4/3/19	-25.7	10.9	Chinook	3.9	38.2604	-121.4237
4/3/19	-25.9	10.9	Chinook	3.8	38.2604	-121.4237
4/3/19	-25.4	11.0	Chinook	3.9	38.2604	-121.4237
4/3/19	-26.3	11.0	Chinook	3.8	38.2604	-121.4237
4/3/19	-25.9	11.0	Chinook	3.8	38.2604	-121.4237
4/3/19	-26.5	11.0	Chinook	3.9	38.2604	-121.4237
4/3/19	-25.1	11.1	Chinook	3.9	38.2604	-121.4237
4/3/19	-26.8	11.1	Chinook	3.8	38.2604	-121.4237
4/2/19	-24.6	10.9	Chinook	3.8	38.2714	-121.3966
4/2/19	-24.7	10.9	Chinook	3.8	38.2714	-121.3966
4/2/19	-25.2	11.0	Chinook	4.0	38.2714	-121.3966
4/2/19	-23.7	11.0	Chinook	3.8	38.2714	-121.3966
4/2/19	-24.6	11.0	Chinook	3.8	38.2714	-121.3966
4/2/19	-24.6	11.0	Chinook	3.8	38.2714	-121.3966
4/2/19	-24.2	11.0	Chinook	3.8	38.2714	-121.3966
4/2/19	-24.4	11.2	Chinook	3.8	38.2714	-121.3966
4/2/19	-23.5	11.2	Chinook	3.8	38.2714	-121.3966
4/2/19	-24.9	11.2	Chinook	3.8	38.2714	-121.3966
4/2/19	-23.9	11.2	Chinook	3.8	38.2714	-121.3966
4/2/19	-24.6	11.4	Chinook	3.9	38.2714	-121.3966
NA	-27.5	11.4	Bluegill	3.8	38.2714	-121.3966
NA	-28.4	11.7	Bluegill	3.8	38.2714	-121.3966
NA	-27.3	11.9	Bluegill	3.7	38.2714	-121.3966
NA	-28.8	12.0	Bluegill	3.8	38.2714	-121.3966
NA	-27.1	11.3	Black Bullhead	NA	38.2714	-121.3966
4/12/18	-26.7	11.2	Chinook	NA	38.2714	-121.3966
4/12/18	-26.1	11.2	Chinook	NA	38.2714	-121.3966
4/12/18	-27.0	12.1	Chinook	NA	38.2714	-121.3966
4/13/18	-27.3	10.3	Chinook	NA	38.2714	-121.3966
4/13/18	-27.6	10.6	Chinook	NA	38.2714	-121.3966

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
4/13/18	-27.2	10.7	Chinook	NA	38.2714	-121.3966
4/13/18	-26.8	10.7	Chinook	NA	38.2714	-121.3966
4/13/18	-26.7	10.8	Chinook	NA	38.2714	-121.3966
4/13/18	-28.0	10.8	Chinook	NA	38.2714	-121.3966
4/13/18	-27.4	11.0	Chinook	NA	38.2714	-121.3966
4/13/18	-27.1	11.1	Chinook	NA	38.2714	-121.3966
4/13/18	-26.9	11.1	Chinook	NA	38.2714	-121.3966
4/14/18	-27.1	11.0	Chinook	NA	38.2714	-121.3966
4/14/18	-27.5	11.1	Chinook	NA	38.2714	-121.3966
4/15/18	-28.2	10.6	Chinook	NA	38.2714	-121.3966
4/15/18	-27.8	10.6	Chinook	NA	38.2714	-121.3966
4/15/18	-27.8	10.9	Chinook	NA	38.2714	-121.3966
4/15/18	-26.8	11.0	Chinook	NA	38.2714	-121.3966
4/16/18	-26.5	11.3	Chinook	NA	38.2714	-121.3966
4/16/18	-27.0	11.5	Chinook	NA	38.2714	-121.3966
4/24/18	-28.4	11.0	Chinook	NA	38.2714	-121.3966
4/24/18	-27.5	11.4	Chinook	NA	38.2714	-121.3966
4/25/18	-28.1	11.3	Chinook	NA	38.2714	-121.3966
4/27/18	-26.7	11.0	Chinook	NA	38.2714	-121.3966
4/28/18	-27.7	10.5	Chinook	NA	38.2714	-121.3966
4/30/18	-28.4	9.6	Chinook	NA	38.2714	-121.3966
5/1/18	-27.7	10.3	Chinook	NA	38.2714	-121.3966
5/1/18	-28.4	11.0	Chinook	NA	38.2714	-121.3966
5/2/18	-29.1	10.3	Chinook	NA	38.2714	-121.3966
5/2/18	-27.5	10.4	Chinook	NA	38.2714	-121.3966
5/2/18	-27.8	10.6	Chinook	NA	38.2714	-121.3966
5/4/18	-27.6	10.5	Chinook	NA	38.2714	-121.3966
4/2/19	-27.9	10.2	Chinook	3.8	38.7060	-121.6436
4/2/19	-27.2	10.2	Chinook	3.8	38.7060	-121.6436
4/2/19	-27.9	10.4	Chinook	3.9	38.7060	-121.6436
4/2/19	-28.5	10.5	Chinook	3.9	38.7060	-121.6436
4/2/19	-28.0	10.5	Chinook	3.9	38.7060	-121.6436
4/2/19	-28.0	10.5	Chinook	3.8	38.7060	-121.6436
4/2/19	-28.3	10.5	Chinook	3.7	38.7060	-121.6436
4/2/19	-28.1	10.5	Chinook	3.8	38.7060	-121.6436
4/2/19	-28.0	10.5	Chinook	3.8	38.7060	-121.6436
4/2/19	-27.5	10.5	Chinook	3.9	38.7060	-121.6436
4/2/19	-28.9	10.7	Chinook	3.9	38.7060	-121.6436
4/2/19	-28.1	10.8	Chinook	4.0	38.7060	-121.6436
4/2/19	-28.4	10.8	Chinook	4.2	38.7060	-121.6436
4/2/19	-28.5	10.8	Chinook	4.0	38.7060	-121.6436
4/2/19	-28.9	10.8	Chinook	3.9	38.7060	-121.6436
4/2/19	-28.2	10.9	Chinook	3.8	38.7060	-121.6436
5/10/16	-19.4	18.1	American Shad	3.6	38.3131	-121.3788

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
4/28/16	-29.4	11.1	Black Bullhead	3.7	38.3131	-121.3788
4/28/16	-26.9	12.3	Black Bullhead	3.5	38.3131	-121.3788
5/10/16	-23.2	13.6	Black Bullhead	3.5	38.3131	-121.3788
5/10/16	-25.6	13.6	Black Bullhead	3.8	38.3131	-121.3788
5/24/16	-30.3	9.1	Black Crappie	3.7	38.3131	-121.3788
5/24/16	-27.8	9.7	Bluegill	3.6	38.3131	-121.3788
5/12/16	-23.7	9.2	Chinook	3.6	38.3131	-121.3788
5/12/16	-22.9	9.9	Chinook	3.6	38.3131	-121.3788
5/13/16	-24.1	9.6	Chinook	3.5	38.3131	-121.3788
5/13/16	-24.0	9.9	Chinook	3.8	38.3131	-121.3788
5/13/16	-23.9	10.0	Chinook	3.6	38.3131	-121.3788
5/13/16	-24.0	10.3	Chinook	3.7	38.3131	-121.3788
5/13/16	-23.8	10.4	Chinook	3.5	38.3131	-121.3788
5/17/16	-23.0	9.2	Chinook	3.6	38.3131	-121.3788
5/17/16	-23.8	9.4	Chinook	3.7	38.3131	-121.3788
5/18/16	-24.2	9.6	Chinook	3.6	38.3131	-121.3788
5/18/16	-22.9	9.6	Chinook	3.5	38.3131	-121.3788
5/18/16	-24.1	9.8	Chinook	3.8	38.3131	-121.3788
5/18/16	-24.4	9.9	Chinook	3.6	38.3131	-121.3788
5/18/16	-22.8	10.3	Chinook	3.6	38.3131	-121.3788
5/18/16	-23.9	10.4	Chinook	3.6	38.3131	-121.3788
5/19/16	-23.6	9.8	Chinook	3.6	38.3131	-121.3788
5/19/16	-22.8	9.8	Chinook	3.6	38.3131	-121.3788
5/19/16	-23.9	10.2	Chinook	3.6	38.3131	-121.3788
5/20/16	-22.9	9.6	Chinook	3.7	38.3131	-121.3788
5/24/16	-23.6	9.8	Chinook	3.7	38.3131	-121.3788
5/24/16	-24.1	10.2	Chinook	3.6	38.3131	-121.3788
5/25/16	-25.0	10.2	Chinook	3.7	38.3131	-121.3788
5/24/16	-25.0	12.0	Log Perch	3.7	38.3131	-121.3788
4/6/16	-23.0	9.1	Pikeminnow	3.8	38.3131	-121.3788
3/25/16	-22.4	7.2	Rainbow Trout	3.5	38.3131	-121.3788
3/30/16	-25.1	15.2	Red Ear Sunfish	3.8	38.3131	-121.3788
3/30/16	-20.6	15.3	Red Ear Sunfish	3.9	38.3131	-121.3788
3/30/16	-26.9	15.4	Red Ear Sunfish	3.7	38.3131	-121.3788
4/6/16	-28.4	12.3	Red Ear Sunfish	3.7	38.3131	-121.3788
4/6/16	-24.5	13.8	Red Ear Sunfish	3.7	38.3131	-121.3788
4/6/16	-30.5	14.1	Red Ear Sunfish	3.6	38.3131	-121.3788
3/25/16	-25.7	15.3	Sacramento Sucker	3.8	38.3131	-121.3788
5/6/16	-26.2	15.3	Striped Bass	3.8	38.3131	-121.3788
5/6/16	-25.2	16.7	Striped Bass	3.6	38.3131	-121.3788
5/19/16	-26.3	14.2	Striped Bass	3.5	38.3131	-121.3788
5/19/16	-23.4	15.8	Striped Bass	3.7	38.3131	-121.3788
5/19/16	-19.3	17.6	Striped Bass	3.6	38.3131	-121.3788
4/28/16	-25.6	11.6	White Catfish	3.7	38.3131	-121.3788

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
4/28/16	-26.9	14.2	White Catfish	3.7	38.3131	-121.3788
5/5/16	-26.0	13.2	White Catfish	3.5	38.3131	-121.3788
5/11/16	-27.5	11.3	White Catfish	3.8	38.3131	-121.3788
5/11/16	-26.1	12.6	White Catfish	3.8	38.3131	-121.3788
5/20/16	-23.9	12.2	White Catfish	3.8	38.3131	-121.3788
5/20/16	-25.3	12.5	White Catfish	3.5	38.3131	-121.3788
5/20/16	-27.5	13.0	White Catfish	3.7	38.3131	-121.3788
5/20/16	-23.6	13.6	White Catfish	3.6	38.3131	-121.3788
5/20/16	-26.8	16.5	White Catfish	2.2	38.3131	-121.3788
4/3/19	-22.9	10.0	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-24.4	10.0	Chinook Salmon	3.8	38.2547	-121.4295
4/3/19	-23.1	10.1	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-23.0	10.2	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-22.7	10.2	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-23.1	10.2	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-23.2	10.3	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-23.8	10.3	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-23.6	10.4	Chinook Salmon	3.8	38.2547	-121.4295
4/3/19	-23.1	10.4	Chinook Salmon	3.8	38.2547	-121.4295
4/3/19	-23.4	10.4	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-22.9	10.6	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-23.0	10.6	Chinook Salmon	3.8	38.2547	-121.4295
4/3/19	-22.8	10.9	Chinook Salmon	3.9	38.2547	-121.4295
4/3/19	-22.0	11.0	Chinook Salmon	3.8	38.2547	-121.4295
2017	-27.9	10.6	Splittail	3.8	38.2590	-121.4613
2017	-28.4	10.8	Splittail	4.4	38.2590	-121.4613
2017	-26.2	10.9	Splittail	3.8	38.2590	-121.4613
2017	-29.7	11.3	Splittail	5.6	38.2590	-121.4613
2017	-26.7	11.3	Splittail	3.9	38.2590	-121.4613
2017	-26.6	11.3	Splittail	3.9	38.2590	-121.4613
2017	-28.4	11.4	Splittail	4.8	38.2590	-121.4613
2017	-28.0	11.5	Splittail	4.4	38.2590	-121.4613
2017	-27.0	11.8	Splittail	4.0	38.2590	-121.4613
2017	-28.1	11.9	Splittail	3.7	38.2590	-121.4613
1/24/16	-34.7	10.0	Black Crappie	3.6	38.2992	-121.3848
1/24/16	-33.4	10.6	Black Crappie	3.8	38.2992	-121.3848
1/24/16	-29.3	10.7	Black Crappie	3.8	38.2992	-121.3848
2/24/16	-34.0	10.2	Black Crappie	3.7	38.2992	-121.3848
2/24/16	-32.9	10.4	Black Crappie	3.7	38.2992	-121.3848
2/24/16	-31.8	11.8	Black Crappie	3.9	38.2992	-121.3848
2/24/16	-24.5	7.8	Bluegill	3.9	38.2992	-121.3848
2/24/16	-22.0	8.0	Bluegill	3.6	38.2992	-121.3848
2/24/16	-25.9	8.3	Bluegill	3.7	38.2992	-121.3848
3/3/16	-30.8	8.1	Golden Shiner	4.0	38.2992	-121.3848
3/3/16	-29.7	8.7	Golden Shiner	4.0	38.2992	-121.3848

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
3/3/16	-30.1	8.9	Golden Shiner	3.7	38.2992	-121.3848
4/26/16	-22.5	15.2	Largemouth Bass	3.7	38.2992	-121.3848
1/29/16	-25.7	13.1	Red Ear Sunfish	3.8	38.2992	-121.3848
1/29/16	-27.7	13.5	Red Ear Sunfish	3.6	38.2992	-121.3848
2/28/19	-31.9	6.2	Zooplankton	5.9	38.3304	-121.6722
2/28/19	-31.7	6.3	Zooplankton	6.0	38.3304	-121.6722
3/27/19	-33.2	8.8	Zooplankton	5.2	38.3304	-121.6722
4/9/19	-32.3	8.9	Zooplankton	5.0	38.3304	-121.6722
12/23/15	-26.8	1.5	Annelida	5.0	38.2992	-121.3848
12/23/15	-27.0	2.5	Annelida	6.4	38.2992	-121.3848
12/23/15	-27.8	1.4	Arthropoda	7.1	38.2992	-121.3848
12/23/15	-26.3	4.4	Nematoda	5.8	38.2992	-121.3848
2/3/17	-31.4	8.1	Copepoda	6.0	38.2553	-121.4386
7/7/17	-28.6	4.3	Zooplankton	9.5	38.2553	-121.4386
2/15/17	-32.9	5.9	Cladocera	5.9	38.2580	-121.4310
4/10/17	-32.3	6.0	Cladocera	5.3	38.2580	-121.4310
4/27/17	-36.8	15.3	Cladocera	4.9	38.2580	-121.4310
2/1/17	-33.9	6.7	Cladocera	6.5	38.2580	-121.4310
2/3/17	-33.4	6.1	Cladocera	6.3	38.2580	-121.4310
2/6/17	-34.2	6.3	Cladocera	6.6	38.2580	-121.4310
2/1/17	-31.4	9.1	Copepoda	6.6	38.2580	-121.4310
2/3/17	-32.0	9.1	Copepoda	6.3	38.2580	-121.4310
2/6/17	-30.4	9.3	Copepoda	5.8	38.2580	-121.4310
2/15/17	-32.3	9.4	Copepoda	5.3	38.2580	-121.4310
7/7/17	-29.8	4.4	Zooplankton	8.8	38.2580	-121.4310
12/10/18	-28.3	8.8	Zooplankton	5.1	38.2604	-121.4237
12/26/18	-30.0	5.9	Zooplankton	4.8	38.2604	-121.4237
1/17/19	-34.2	8.0	Zooplankton	5.0	38.2604	-121.4237
2/1/19	-32.9	8.1	Zooplankton	5.5	38.2604	-121.4237
2/14/19	-32.9	7.9	Zooplankton	5.8	38.2604	-121.4237
2/27/19	-34.0	7.1	Zooplankton	5.5	38.2604	-121.4237
2/27/19	-33.0	8.5	Zooplankton	5.5	38.2604	-121.4237
3/14/19	-34.5	6.9	Zooplankton	5.5	38.2604	-121.4237
3/26/19	-32.2	8.9	Zooplankton	5.4	38.2604	-121.4237
2/1/19	-34.1	9.1	Zooplankton	4.5	38.2714	-121.3966
2/13/19	-33.4	8.7	Zooplankton	5.5	38.2714	-121.3966
2/26/19	-33.3	9.6	Zooplankton	5.2	38.2714	-121.3966
NA	-31.2	13.9	Amphipod	6.4	38.2714	-121.3966
2/3/17	-37.0	5.8	Cladocera	6.9	38.2457	-121.5070
2/6/17	-38.1	8.3	Cladocera	5.7	38.2457	-121.5070
4/20/17	-33.1	6.0	Cladocera	NA	38.2457	-121.5070
5/25/17	-32.5	5.2	Cladocera	8.8	38.2457	-121.5070
4/27/17	-33.1	6.0	Cladocera	5.4	38.2457	-121.5070
2/3/17	-36.3	8.6	Copepoda	7.0	38.2457	-121.5070
2/6/17	-35.5	11.3	Copepoda	5.6	38.2457	-121.5070

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
4/27/17	-33.1	9.3	Copepoda	5.4	38.2457	-121.5070
5/25/17	-32.3	7.6	Copepoda	9.1	38.2457	-121.5070
7/7/17	-29.4	2.6	Zooplankton	7.6	38.2457	-121.5070
4/27/17	-32.3	10.3	Cladocera	5.5	38.2316	-121.4952
5/11/17	-30.5	8.8	Cladocera	5.1	38.2316	-121.4952
11/21/16	-27.3	10.4	Zooplankton	7.6	38.2316	-121.4952
1/6/17	-27.4	7.1	Zooplankton	8.5	38.2316	-121.4952
1/17/17	-27.8	6.1	Zooplankton	8.9	38.2316	-121.4952
1/20/17	-27.3	7.6	Zooplankton	8.3	38.2316	-121.4952
1/24/17	-27.7	5.5	Zooplankton	10.0	38.2316	-121.4952
1/27/17	-27.8	6.8	Zooplankton	9.3	38.2316	-121.4952
2/1/17	-27.6	6.7	Zooplankton	9.6	38.2316	-121.4952
2/3/17	-27.6	6.4	Zooplankton	9.2	38.2316	-121.4952
2/6/17	-27.6	9.6	Zooplankton	8.2	38.2316	-121.4952
3/7/17	-27.9	8.2	Zooplankton	8.6	38.2316	-121.4952
3/14/17	-27.2	5.3	Zooplankton	7.4	38.2316	-121.4952
3/22/17	-27.0	5.3	Zooplankton	8.0	38.2316	-121.4952
3/27/17	-27.4	4.7	Zooplankton	7.5	38.2316	-121.4952
4/6/17	-26.9	6.5	Zooplankton	7.1	38.2316	-121.4952
4/10/17	-27.4	4.6	Zooplankton	7.9	38.2316	-121.4952
4/20/17	-27.4	6.0	Zooplankton	7.5	38.2316	-121.4952
4/27/17	-27.4	5.6	Zooplankton	7.8	38.2316	-121.4952
5/1/17	-27.4	5.7	Zooplankton	7.6	38.2316	-121.4952
5/8/17	-27.4	4.8	Zooplankton	8.5	38.2316	-121.4952
5/17/17	-27.1	4.9	Zooplankton	7.7	38.2316	-121.4952
5/19/17	-27.4	3.8	Zooplankton	8.0	38.2316	-121.4952
5/25/17	-27.4	4.0	Zooplankton	8.2	38.2316	-121.4952
6/1/17	-27.2	5.3	Zooplankton	8.3	38.2316	-121.4952
6/7/17	-27.2	5.6	Zooplankton	NA	38.2316	-121.4952
6/8/17	-27.2	4.1	Zooplankton	8.1	38.2316	-121.4952
6/15/17	-27.4	3.5	Zooplankton	8.0	38.2316	-121.4952
6/22/17	-27.8	4.3	Zooplankton	8.7	38.2316	-121.4952
6/23/17	-27.5	5.3	Zooplankton	8.2	38.2316	-121.4952
7/7/17	-27.9	5.1	Zooplankton	8.7	38.2316	-121.4952
12/2/17	-28.2	9.7	Zooplankton	NA	38.2316	-121.4952
12/23/15	-26.6	6.3	Annelida	8.4	38.2992	-121.3848
12/23/15	-28.2	1.9	Arthropoda	10.6	38.2992	-121.3848
4/10/17	-32.6	5.0	Cladocera	5.6	38.2517	-121.4888
2/15/17	-24.9	10.6	Copepoda	5.9	38.2517	-121.4888
4/27/17	-31.0	6.1	Zooplankton	5.7	38.2517	-121.4888
2/15/17	-30.4	7.5	Cladocera	5.9	38.2517	-121.4888
1/9/19	-31.3	6.2	Zooplankton	5.7	38.7060	-121.6436
1/17/19	-27.9	5.5	Zooplankton	6.7	38.7060	-121.6436
1/17/19	-28.5	5.6	Zooplankton	5.7	38.7060	-121.6436
1/19/19	-33.6	7.1	Zooplankton	5.7	38.7060	-121.6436

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
1/29/19	-31.5	6.7	Zooplankton	5.4	38.7060	-121.6436
1/29/19	-31.3	6.7	Zooplankton	5.6	38.7060	-121.6436
1/29/19	-28.9	7.3	Zooplankton	5.9	38.7060	-121.6436
2/12/19	-30.5	7.3	Zooplankton	7.8	38.7060	-121.6436
2/12/19	-28.8	7.8	Zooplankton	5.8	38.7060	-121.6436
2/26/19	-30.5	7.2	Zooplankton	5.3	38.7060	-121.6436
3/27/19	-35.0	8.9	Zooplankton	5.6	38.7060	-121.6436
4/10/19	-35.8	11.1	Zooplankton	5.7	38.7060	-121.6436
4/10/19	-34.4	11.1	Zooplankton	5.8	38.7060	-121.6436
12/23/15	-26.0	4.4	Annelida	6.4	38.3131	-121.3788
12/23/15	-26.0	6.4	Arthropoda	5.4	38.3131	-121.3788
3/10/16	-30.2	6.7	Cladocera	5.8	38.3131	-121.3788
3/10/16	-32.2	8.8	Copepoda	5.6	38.3131	-121.3788
3/10/16	-26.2	3.2	Insecta	5.4	38.3131	-121.3788
3/10/16	-25.0	4.2	Insecta	6.1	38.3131	-121.3788
3/10/16	-24.2	9.8	Polychaeta	8.7	38.3131	-121.3788
2/3/17	-31.0	7.1	Cladocera	5.7	38.2645	-121.4634
2/6/17	-33.3	5.3	Cladocera	6.5	38.2645	-121.4634
2/6/17	-32.8	7.2	Cladocera	6.3	38.2645	-121.4634
4/10/17	-31.0	6.5	Cladocera	5.5	38.2645	-121.4634
4/20/17	-28.5	6.5	Cladocera	6.0	38.2645	-121.4634
2/3/17	-29.1	9.5	Copepoda	4.9	38.2645	-121.4634
2/6/17	-30.2	8.9	Copepoda	6.2	38.2645	-121.4634
5/1/17	-31.0	9.1	Copepoda	5.3	38.2645	-121.4634
7/7/17	-30.7	4.2	Unknown	9.3	38.2645	-121.4634
2/19/19	-30.5	5.4	Zooplankton	6.1	NA	NA
4/27/17	-32.0	9.0	Cladocera	6.4	NA	NA
4/27/17	-32.7	10.6	Cladocera	5.0	NA	NA
4/27/17	-32.0	10.6	Cladocera	5.2	NA	NA
5/11/17	-29.6	7.4	Cladocera	6.2	NA	NA
2/6/17	-33.3	6.3	Cladocera	6.2	38.2547	-121.4295
2/6/17	-32.9	8.9	Copepoda	6.2	38.2547	-121.4295
5/1/17	-29.0	6.3	Copepoda	8.0	38.2547	-121.4295
7/7/17	-27.8	4.9	Zooplankton	8.7	38.2547	-121.4295
3/26/19	-31.3	4.9	Zooplankton	5.4	38.2547	-121.4295
4/27/17	-30.4	13.5	Copepoda	5.1	38.2547	-121.4295
5/11/17	-30.0	9.5	Zooplankton	5.0	38.2547	-121.4295
11/21/16	-28.5	8.1	Zooplankton	8.9	38.2524	-121.4795
1/6/17	-27.5	6.3	Zooplankton	8.8	38.2524	-121.4795
1/17/17	-27.4	7.7	Zooplankton	9.2	38.2524	-121.4795
1/20/17	-27.3	8.0	Zooplankton	9.0	38.2524	-121.4795
1/24/17	-27.6	7.5	Zooplankton	9.0	38.2524	-121.4795
1/27/17	-27.5	6.8	Zooplankton	9.0	38.2524	-121.4795
2/1/17	-27.5	7.8	Zooplankton	10.0	38.2524	-121.4795
2/3/17	-27.7	6.3	Zooplankton	9.3	38.2524	-121.4795

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
2/6/17	-27.5	8.0	Zooplankton	9.0	38.2524	-121.4795
7/7/17	-30.2	5.4	Zooplankton	NA	38.2684	-121.4838
7/7/17	-28.2	4.2	Zooplankton	9.3	38.2590	-121.4613
1/31/16	-27.2	7.3	Acarina	6.7	38.3131	-121.3788
1/31/16	-29.5	1.2	Insecta	5.7	38.3131	-121.3788
2/3/17	-29.9	6.6	Cladocera	5.9	38.2911	-121.3813
2/3/17	-30.5	11.9	Copepoda	5.2	38.2911	-121.3813
7/7/17	-28.6	3.8	Zooplankton	9.2	38.2911	-121.3813
12/23/15	-27.3	3.4	Annelida	6.9	38.3059	-121.3832
12/23/15	-29.0	3.8	Arthropoda	18.3	38.3059	-121.3832
1/31/16	-30.6	2.9	Cladocera	6.6	38.3059	-121.3832
12/23/15	-29.9	2.3	Insecta	12.1	38.3059	-121.3832
12/23/15	-28.6	2.9	Insecta	50.9	38.3059	-121.3832
1/31/16	-27.1	2.1	Insecta	5.1	38.3059	-121.3832
1/31/16	-31.1	3.1	Insecta	6.4	38.3059	-121.3832
1/31/16	-19.3	5.4	Insecta	4.5	38.3059	-121.3832
2/1/17	-35.4	7.2	Cladocera	6.6	38.2659	-121.4980
2/1/17	-35.6	6.6	Cladocera	6.8	38.2659	-121.4980
2/1/17	-34.0	10.0	Copepoda	6.4	38.2659	-121.4980
2/1/17	-34.2	10.9	Copepoda	6.4	38.2659	-121.4980
2/1/17	-28.2	11.7	Insecta	8.1	38.2659	-121.4980
2/1/17	-27.2	9.7	Mollusca	5.5	38.2659	-121.4980
7/7/17	-29.3	6.6	Zooplankton	7.2	38.2659	-121.4980
11/21/16	-27.6	8.7	Zooplankton	7.8	38.2514	-121.5004
1/6/17	-27.7	5.4	Zooplankton	9.4	38.2514	-121.5004
1/17/17	-27.6	7.6	Zooplankton	9.4	38.2514	-121.5004
1/20/17	-27.7	6.1	Zooplankton	8.7	38.2514	-121.5004
1/24/17	-27.3	6.9	Zooplankton	8.5	38.2514	-121.5004
1/27/17	-28.2	6.5	Zooplankton	8.5	38.2514	-121.5004
2/1/17	-29.4	9.3	Zooplankton	7.5	38.2514	-121.5004
2/3/17	-28.4	9.2	Zooplankton	7.8	38.2514	-121.5004
2/6/17	-28.7	9.5	Zooplankton	8.2	38.2514	-121.5004
12/2/17	-28.4	9.6	Zooplankton	NA	38.2514	-121.5004
12/23/15	-27.2	2.5	Annelida	15.0	38.2992	-121.3848
12/23/15	-27.4	4.1	Arthropoda	6.0	38.2992	-121.3848
3/10/16	-29.5	5.9	Cladocera	6.1	38.2992	-121.3848
3/10/16	-31.9	7.7	Copepoda	6.2	38.2992	-121.3848
12/23/15	-21.9	5.7	Insecta	5.8	38.2992	-121.3848
1/31/16	-28.7	2.5	Insecta	14.8	38.2992	-121.3848
3/10/16	-25.0	4.3	Insecta	6.8	38.2992	-121.3848
1/25/16	-26.6	10.1	Arachnida	4.4	38.2727	-121.3952
1/31/16	-31.2	3.6	Cladocera	6.4	38.2727	-121.3952
1/25/16	-33.0	4.9	Copepoda	7.4	38.2727	-121.3952
1/31/16	-28.8	3.4	Insecta	6.0	38.2727	-121.3952
1/31/16	-25.5	7.6	Acarina	4.9	38.2992	-121.3848

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
1/31/16	-25.8	2.6	Annelida	5.6	38.2992	-121.3848
1/31/16	-30.7	3.9	Cladocera	6.1	38.2992	-121.3848
3/15/16	-31.0	4.8	Cladocera	5.6	38.2992	-121.3848
1/31/16	-29.0	5.8	Copepoda	6.4	38.2992	-121.3848
1/31/16	-24.8	3.6	Insecta	6.1	38.2992	-121.3848
1/31/16	-31.9	5.7	Insecta	6.6	38.2992	-121.3848
3/15/16	-29.0	3.4	Insecta	5.8	38.2992	-121.3848
12/23/15	-28.0	1.0	Annelida	7.6	38.2727	-121.3952
12/23/15	-30.8	2.5	Arthropoda	11.2	38.2727	-121.3952
3/10/16	-29.8	4.8	Cladocera	6.9	38.2727	-121.3952
3/10/16	-33.2	7.6	Copepoda	5.9	38.2727	-121.3952
3/10/16	-31.2	4.3	Gastropod	6.5	38.2727	-121.3952
3/10/16	-28.8	5.0	Insecta	7.6	38.2727	-121.3952
12/23/15	-28.4	5.3	Annelida	10.6	38.2727	-121.3952
12/23/15	-28.4	5.2	Arthropoda	7.4	38.2727	-121.3952
1/25/16	-28.8	2.6	Cladocera	10.2	38.2727	-121.3952
3/7/16	-30.7	4.2	Cladocera	6.4	38.2727	-121.3952
3/10/16	-30.2	5.9	Cladocera	5.9	38.2727	-121.3952
3/15/16	-29.5	5.3	Cladocera	6.1	38.2727	-121.3952
1/25/16	-32.0	6.1	Copepoda	9.2	38.2727	-121.3952
3/7/16	-31.7	8.8	Copepoda	6.1	38.2727	-121.3952
3/10/16	-32.5	7.5	Copepoda	6.1	38.2727	-121.3952
3/15/16	-31.9	8.7	Copepoda	5.9	38.2727	-121.3952
1/25/16	-29.6	3.9	Insecta	8.9	38.2727	-121.3952
3/7/16	-27.4	2.7	Insecta	15.8	38.2727	-121.3952
3/7/16	-25.7	3.9	Insecta	5.6	38.2727	-121.3952
3/8/16	-27.4	5.8	Insecta	7.6	38.2727	-121.3952
3/8/16	-26.2	6.9	Insecta	11.6	38.2727	-121.3952
3/10/16	-27.6	3.7	Insecta	6.1	38.2727	-121.3952
3/10/16	-28.2	4.5	Insecta	6.5	38.2727	-121.3952
3/10/16	-27.5	5.4	Insecta	5.9	38.2727	-121.3952
3/15/16	-27.8	4.5	Insecta	6.5	38.2727	-121.3952
3/15/16	-26.6	7.3	Insecta	7.1	38.2727	-121.3952
2/13/19	-33.5	8.9	Zooplankton	5.6	NA	NA
2/26/19	-30.5	8.7	Zooplankton	5.2	NA	NA
3/26/19	-32.6	9.8	Zooplankton	5.2	NA	NA
2/1/17	-35.2	4.4	Cladocera	6.7	38.2252	-121.4915
2/1/17	-31.9	5.5	Cladocera	6.4	38.2252	-121.4915
2/6/17	-33.5	6.7	Cladocera	6.1	38.2252	-121.4915
2/1/17	-32.0	10.4	Copepoda	5.6	38.2252	-121.4915
2/6/17	-31.8	9.1	Copepoda	5.9	38.2252	-121.4915
7/7/17	-27.9	4.6	Zooplankton	9.6	38.2252	-121.4915
1/21/19	-30.2	4.8	Zooplankton	5.8	38.6737	-121.6273
1/28/19	-30.2	5.2	Zooplankton	5.5	38.6737	-121.6273

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
2/11/19	-31.8	5.1	Zooplankton	5.8	38.6737	-121.6273
2/25/19	-31.6	5.0	Zooplankton	5.6	38.6737	-121.6273
12/23/15	-28.9	-1.8	Quercus sp. (L)	76.9	NA	NA
12/15/15	-29.7	0.2	Cirsium sp. (L)	271.8	38.2992	-121.3848
12/23/15	-31.5	-1.0	Unidentified Tree (L)	32.2	38.2992	-121.3848
12/23/15	-27.0	0.0	Quercus sp. (L)	57.7	38.2992	-121.3848
12/15/15	-29.2	-2.2	Populus sp. (L)	62.8	38.3131	-121.3788
12/15/15	-29.2	-1.2	Quercus sp. (L)	66.4	38.3131	-121.3788
12/15/15	-27.9	-1.1	Unknown (L)	105.2	38.3131	-121.3788
12/15/15	-28.8	0.0	Populus sp. (L)	134.5	38.3131	-121.3788
12/15/15	-29.7	0.1	Cirsium sp. (L)	135.1	38.3131	-121.3788
12/15/15	-28.0	4.3	Salix sp. (L)	74.0	38.3131	-121.3788
1/6/17	-29.2	-2.0	Woody Debris (L)	189.7	38.2645	-121.4634
1/6/17	-25.9	1.2	Woody Debris (L)	373.3	38.2645	-121.4634
1/6/17	-27.4	4.5	Woody Debris (L)	126.3	38.2645	-121.4634
12/15/15	-30.4	0.4	Populus sp. (L)	89.0	38.2992	-121.3848
12/15/15	-30.3	0.9	Cirsium sp. (L)	49.1	38.2992	-121.3848
12/15/15	-30.1	0.9	Quercus sp. (L)	75.9	38.2992	-121.3848
12/15/15	-31.6	1.6	Salix sp. (L)	117.8	38.2992	-121.3848
12/15/15	-25.5	6.8	Rumex sp. (L)	31.8	38.2992	-121.3848
12/23/15	-26.3	-1.4	Unidentified Tree (L)	53.9	38.2992	-121.3848
12/23/15	-29.5	-0.7	Unidentified Tree (L)	39.0	38.2992	-121.3848
12/23/15	-29.2	-0.2	Quercus sp. (L)	53.2	38.2992	-121.3848
1/27/17	-25.6	2.8	Egeria sp.	9.9	38.2580	-121.4310
1/27/17	-27.7	3.4	Egeria sp.	11.4	38.2580	-121.4310
5/17/17	-28.8	4.8	Ludwigia sp.	19.9	38.2457	-121.5070
5/17/17	-28.3	9.7	Eichornia sp.	13.3	38.2457	-121.5070
1/6/17	-28.3	6.8	Ludwigia sp.	16.9	38.2645	-121.4634
1/6/17	-30.0	-2.7	Ludwigia sp.	51.5	38.2645	-121.4634
1/6/17	-29.6	1.4	Ludwigia sp.	67.4	38.2645	-121.4634
1/6/17	-29.7	2.1	Ludwigia sp.	33.9	38.2645	-121.4634
1/6/17	-30.0	3.7	Eichornia sp.	22.0	38.2645	-121.4634
1/6/17	-27.3	4.8	Eichornia sp.	36.1	38.2645	-121.4634
1/6/17	-28.3	5.9	Eichornia sp.	31.0	38.2645	-121.4634
1/6/17	-28.0	6.6	Eichornia sp.	27.8	38.2645	-121.4634
1/6/17	-29.1	3.7	Egeria sp.	14.6	38.2645	-121.4634
1/6/17	-31.3	17.0	Egeria sp.	9.5	38.2645	-121.4634
5/17/17	-27.2	10.9	Eichornia sp.	27.4	38.2645	-121.4634
1/27/17	-29.2	3.8	Egeria sp.	9.3	38.2547	-121.4295
1/27/17	-28.3	5.2	Egeria sp.	8.8	38.2547	-121.4295
4/27/17	-29.1	7.2	Periphyton	9.3	38.2517	-121.4888
12/23/15	-27.0	1.9	Phytoplankton	7.9	38.2992	-121.3848
12/23/15	-27.0	-1.4	Phytoplankton	12.7	38.2992	-121.3848

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
12/23/15	-26.7	1.7	Phytoplankton	33.5	38.2992	-121.3848
5/11/17	-31.4	12.6	Phytoplankton	7.0	38.2580	-121.4310
5/11/17	-30.1	11.0	Phytoplankton	5.7	38.2316	-121.4952
3/10/16	-26.4	4.4	Phytoplankton	12.2	38.2992	-121.3848
3/10/16	-27.6	2.7	Phytoplankton	15.8	38.2992	-121.3848
12/23/15	-26.8	-0.8	Phytoplankton	8.5	38.2992	-121.3848
12/23/15	-26.9	-3.6	Phytoplankton	8.5	38.2992	-121.3848
12/23/15	-26.7	-2.6	Phytoplankton	10.9	38.2992	-121.3848
12/23/15	-27.1	-2.9	Phytoplankton	4.6	38.3131	-121.3788
12/23/15	-26.4	1.5	Phytoplankton	8.2	38.3131	-121.3788
3/10/16	-26.8	3.4	Phytoplankton	14.7	38.3131	-121.3788
3/10/16	-30.5	3.3	Phytoplankton	65.3	38.3131	-121.3788
3/10/16	-28.2	2.7	Phytoplankton	15.1	38.3131	-121.3788
5/11/17	-28.4	10.4	Phytoplankton	4.1	38.2547	-121.4295
1/31/16	-27.9	1.4	Phytoplankton	17.2	38.3131	-121.3788
1/31/16	-28.0	0.9	Phytoplankton	19.0	38.3131	-121.3788
12/23/15	-26.0	1.7	Phytoplankton	9.9	38.3059	-121.3832
12/23/15	-26.3	1.1	Phytoplankton	11.0	38.3059	-121.3832
1/31/16	-28.2	3.3	Phytoplankton	15.2	38.3059	-121.3832
1/31/16	-28.1	3.2	Phytoplankton	15.6	38.3059	-121.3832
2/1/17	-33.7	7.4	Phytoplankton	6.9	38.2659	-121.4980
2/1/17	-31.0	7.5	Phytoplankton	9.7	38.2659	-121.4980
12/23/15	-25.1	-4.2	Phytoplankton	6.2	38.2992	-121.3848
12/23/15	-25.8	1.5	Phytoplankton	7.2	38.2992	-121.3848
1/25/16	-24.6	5.0	Phytoplankton	5.7	38.2992	-121.3848
3/10/16	-25.0	5.4	Phytoplankton	13.6	38.2992	-121.3848
3/10/16	-29.8	4.0	Phytoplankton	46.2	38.2992	-121.3848
3/15/16	-28.4	1.7	Phytoplankton	11.5	38.2992	-121.3848
1/25/16	-27.8	2.2	Phytoplankton	20.8	38.2992	-121.3848
3/10/16	-26.1	6.1	Phytoplankton	15.1	38.2992	-121.3848
3/10/16	-30.8	5.9	Phytoplankton	64.1	38.2992	-121.3848
3/15/16	-28.1	3.1	Phytoplankton	12.6	38.2992	-121.3848
1/25/16	-27.8	1.7	Phytoplankton	16.2	38.2727	-121.3952
1/25/16	-30.4	5.0	Phytoplankton	79.4	38.2727	-121.3952
1/31/16	-28.1	1.5	Phytoplankton	17.7	38.2727	-121.3952
1/31/16	-28.4	1.0	Phytoplankton	20.8	38.2727	-121.3952
1/25/16	-27.5	1.7	Phytoplankton	13.4	38.2727	-121.3952
1/25/16	-27.8	1.7	Phytoplankton	17.1	38.2727	-121.3952
1/25/16	-31.1	4.7	Phytoplankton	68.1	38.2727	-121.3952
1/25/16	-30.7	1.0	Phytoplankton	123.7	38.2727	-121.3952
1/25/16	-30.8	3.9	Phytoplankton	139.1	38.2727	-121.3952
1/31/16	-28.3	0.5	Phytoplankton	20.8	38.2727	-121.3952
1/31/16	-27.5	0.9	Phytoplankton	18.6	38.2992	-121.3848
3/15/16	-28.1	3.6	Phytoplankton	6.9	38.2992	-121.3848
3/15/16	-28.1	0.0	Phytoplankton	16.1	38.2992	-121.3848

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
1/31/16	-27.8	0.5	Phytoplankton	21.1	38.2992	-121.3848
3/15/16	-28.8	3.6	Phytoplankton	7.4	38.2992	-121.3848
3/15/16	-28.3	-0.3	Phytoplankton	17.6	38.2992	-121.3848
12/23/15	-28.5	5.4	Phytoplankton	5.5	38.2727	-121.3952
1/25/16	-29.2	3.1	Phytoplankton	11.1	38.2727	-121.3952
3/10/16	-29.6	5.3	Phytoplankton	10.3	38.2727	-121.3952
1/25/16	-29.7	3.5	Phytoplankton	12.7	38.2727	-121.3952
1/25/16	-29.8	3.9	Phytoplankton	13.2	38.2727	-121.3952
3/10/16	-30.1	5.0	Phytoplankton	10.8	38.2727	-121.3952
12/23/15	-27.0	0.1	Phytoplankton	11.2	38.2727	-121.3952
12/23/15	-27.7	1.1	Phytoplankton	12.3	38.2727	-121.3952
12/23/15	-28.2	-3.7	Phytoplankton	13.9	38.2727	-121.3952
12/23/15	-27.6	-1.5	Phytoplankton	14.6	38.2727	-121.3952
1/25/16	-28.4	1.7	Phytoplankton	11.5	38.2727	-121.3952
3/7/16	-28.0	2.8	Phytoplankton	16.4	38.2727	-121.3952
3/8/16	-27.4	2.8	Phytoplankton	14.5	38.2727	-121.3952
3/10/16	-27.9	5.4	Phytoplankton	12.6	38.2727	-121.3952
3/15/16	-27.7	1.8	Phytoplankton	16.6	38.2727	-121.3952
1/25/16	-27.0	2.0	Phytoplankton	13.8	38.2727	-121.3952
3/7/16	-27.8	1.9	Phytoplankton	16.7	38.2727	-121.3952
3/8/16	-27.8	2.3	Phytoplankton	16.5	38.2727	-121.3952
3/10/16	-27.4	4.9	Phytoplankton	14.2	38.2727	-121.3952
3/10/16	-30.6	3.0	Phytoplankton	174.1	38.2727	-121.3952
3/15/16	-28.1	1.7	Phytoplankton	17.5	38.2727	-121.3952
3/10/16	-30.9	2.0	Phyto Lipid	155.2	38.3131	-121.3788
1/31/16	-30.4	1.7	Phyto Lipid	97.4	38.2992	-121.3848
1/31/16	-31.0	2.3	Phyto Lipid	222.1	38.2992	-121.3848
3/10/16	-33.1	4.3	Phyto Lipid	110.3	38.2727	-121.3952
3/10/16	-33.4	2.8	Phyto Lipid	169.2	38.2727	-121.3952
12/15/15	-31.8	4.3	Cirsium sp.	6.9	38.2992	-121.3848
12/23/15	-17.2	-1.2	Grass	40.1	38.2992	-121.3848
1/27/17	-28.2	0.2	Betulaceae sp.	51.7	38.2580	-121.4310
12/23/15	-29.6	-2.5	Quercus sp.	40.9	NA	NA
12/15/15	-25.8	3.8	Cirsium sp.	103.4	38.2992	-121.3848
12/15/15	-27.0	9.5	Rumex sp.	48.6	38.2992	-121.3848
12/15/15	-32.6	10.0	Cirsium sp.	13.6	38.2992	-121.3848
12/15/15	-31.8	-2.2	Populus sp.	12.3	38.3131	-121.3788
1/6/17	-29.5	-1.4	Rubis sp.	30.8	38.2645	-121.4634
1/6/17	-30.4	-0.6	Betulaceae sp.	25.5	38.2645	-121.4634
1/27/17	-28.0	0.7	Betulaceae sp.	30.4	38.2547	-121.4295
12/15/15	-28.4	2.5	Litter	76.0	38.3131	-121.3788
1/31/16	-31.2	-1.9	Litter	44.6	38.3131	-121.3788
1/31/16	-29.1	-0.5	Litter	83.5	38.3131	-121.3788
12/15/15	-32.4	2.8	Quercus sp.	10.2	38.3131	-121.3788
1/31/16	-13.9	5.4	Grass	51.6	38.3131	-121.3788

Date	$\delta^{13}C$	$\delta^{15}N$	Info	C:N	Lat.	Lon.
12/23/15	-27.4	6.4	Unidentified Seed	5.9	38.3059	-121.3832
12/15/15	-28.1	-1.0	Moss	8.5	38.2992	-121.3848
12/15/15	-32.3	2.4	Moss	8.8	38.2992	-121.3848
12/15/15	-26.4	2.6	Moss	9.3	38.2992	-121.3848
12/15/15	-32.8	2.8	Moss	10.4	38.2992	-121.3848
12/15/15	-27.0	3.1	Moss	10.9	38.2992	-121.3848
12/15/15	-33.8	4.8	Moss	7.1	38.2992	-121.3848
3/10/16	-31.5	1.0	Seed	65.3	38.2992	-121.3848
3/10/16	-33.7	1.2	Grass	16.4	38.2992	-121.3848
12/23/15	-33.5	-0.4	Unidentified Tree	19.2	38.2727	-121.3952
12/23/15	-30.1	0.0	Quercus sp.	58.4	38.2727	-121.3952
12/23/15	-30.7	0.4	Unidentified Tree	50.9	38.2727	-121.3952
12/23/15	-28.4	0.6	Unidentified Tree	54.4	38.2727	-121.3952
12/23/15	-31.2	0.8	Salix sp.	71.1	38.2727	-121.3952
12/23/15	-27.6	-0.3	Unidentified Seed	157.4	38.2727	-121.3952
12/23/15	-30.5	2.5	Quercus sp.	6.8	38.2727	-121.3952
1/31/16	-30.0	1.0	Quercus sp.	40.3	38.2727	-121.3952
3/10/16	-32.9	1.7	Salix sp.	37.5	38.2727	-121.3952
12/23/15	-30.9	3.6	Grass	8.3	38.2727	-121.3952

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Appendix 4.1. Summary of compound specific carbon and hydrogen isotope measurements of muscular fatty acids extracted from experimentally enclosed Chinook Salmon. Fatty acid concentrations are reported as mg/g of muscle tissue (wet weight).

Code	FA	mg FA / g	σ (mg)	$\delta^{13}C$	σ ($\delta^{13}C$)	$\delta^{2}H$	σ ($\delta^{2}H$)	Treatment
BM1	14	1.9	0.1	-32.2	0.9	-255.1	2.8	Marsh
BM2	14	1.4	0.0	-31.2	0.2	-256.5	2.7	Marsh
BM3	14	1.5	0.1	-31.4	0.1	-258.8	4.5	Marsh
CB1	14	0.6	0.0	-28.6	0.2	-226.8	11.8	CosBeach
CB2	14	0.2	0.0	-26.5	0.2	-210.2	3.5	CosBeach
CB3	14	0.6	0.0	-28.8	0.4	-220.8	11.8	CosBeach
CT1	14	0.4	0.0	-27.3	0.3	-221.7	17.8	CosTri
CT2	14	0.9	0.1	-25.6	0.0	-220.4	6.1	CosTri
CT3	14	0.3	0.0	-26.4	0.4	-226.3	6.9	CosTri
KR1	14	0.6	0.0	-32.5	0.7	-223.8	14.3	Knaggs
KR2	14	1.3	0.1	-30.6	0.1	-239.6	1.5	Knaggs
KR3	14	1.4	0.4	-31.1	0.1	-230.1	5.7	Knaggs
MR1	14	0.2	0.0	-25.6	0.7	-204.0	6.2	Moke
MR2	14	0.4	0.0	-24.2	0.8	-231.6	7.7	Moke
MR3	14	0.3	0.0	-25.2	0.2	-205.3	12.6	Moke
XS1	14	0.3	0.0	-28.1	0.6	-255.4	3.4	Sac
XS2	14	0.2	0.0	-25.4	0.1	-216.6	3.5	Sac
XS3	14	0.1	0.0	-25.9	0.3	-218.0	18.7	Sac
BM1	16	8.4	0.6	-29.6	0.7	-241.6	1.3	Marsh
BM2	16	6.2	0.2	-28.5	0.1	-240.5	0.5	Marsh
BM3	16	6.7	0.4	-28.9	0.2	-242.4	0.8	Marsh
CB1	16	5.0	0.1	-24.7	0.5	-232.7	0.8	CosBeach
CB2	16	3.2	0.1	-23.8	0.1	-232.2	3.3	CosBeach
CB3	16	5.2	0.2	-25.6	0.2	-228.1	1.0	CosBeach
CT1	16	4.7	0.0	-23.7	0.2	-234.7	0.9	CosTri
CT2	16	6.5	0.2	-22.1	0.2	-232.1	0.9	CosTri
CT3	16	4.7	0.3	-23.0	0.3	-235.0	3.4	CosTri
KR1	16	4.4	0.2	-29.5	0.3	-216.5	3.7	Knaggs
KR2	16	7.1	0.1	-27.3	0.1	-228.9	0.3	Knaggs
KR3	16	6.7	0.1	-27.8	0.0	-221.8	1.2	Knaggs
MR1	16	3.6	0.3	-23.9	0.8	-230.9	1.3	Moke
MR2	16	5.8	0.1	-21.3	0.6	-237.1	1.5	Moke
MR3	16	4.3	0.2	-22.3	0.1	-225.7	1.7	Moke
XS1	16	3.7	0.1	-24.7	0.5	-250.0	1.4	Sac
XS2	16	3.4	0.0	-23.1	0.1	-244.0	3.7	Sac
XS3	16	3.9	0.1	-24.0	0.2	-243.9	2.1	Sac
BM1	18	2.4	0.3	-29.8	1.1	-208.8	2.3	Marsh
BM2	18	1.7	0.1	-28.8	0.3	-208.2	2.8	Marsh
BM3	18	1.9	0.2	-29.6	0.3	-207.9	8.0	Marsh
CB1	18	1.5	0.1	-25.4	0.4	-190.5	3.2	CosBeach
CB2	18	0.9	0.1	-24.5	0.0	-190.7	8.4	CosBeach
CB3	18	1.3	0.1	-26.1	0.2	-190.1	1.3	CosBeach
CT1	18	1.1	0.0	-24.7	0.2	-195.7	4.3	CosTri
CT2	18	1.3	0.1	-22.9	0.2	-185.2	2.5	CosTri

Code	FA	mg FA / g	σ (mg)	$\delta^{13}C$	σ ($\delta^{13}C$)	$\delta^{2}H$	σ ($\delta^{2}H$)	Treatment
CT3	18	1.0	0.1	-23.8	0.2	-195.4	1.0	CosTri
KR1	18	1.2	0.1	-30.2	0.5	-184.0	4.1	Knaggs
KR2	18	1.6	0.1	-29.4	0.1	-190.4	2.3	Knaggs
KR3	18	1.5	0.1	-29.4	0.3	-185.1	5.0	Knaggs
MR1	18	1.1	0.0	-23.1	0.4	-184.8	1.9	Moke
MR2	18	1.7	0.1	-21.3	0.6	-193.1	3.9	Moke
MR3	18	1.4	0.1	-21.2	0.3	-181.9	1.7	Moke
XS1	18	1.2	0.1	-25.2	0.6	-206.0	5.2	Sac
XS2	18	1.1	0.0	-23.8	0.2	-202.4	4.1	Sac
XS3	18	1.2	0.0	-24.7	0.4	-200.5	2.3	Sac
BM1	16:1n7	5.5	1.0	-31.5	0.1	-227.6	3.8	Marsh
BM2	16:1n7	3.7	0.1	-31.0	0.2	-226.4	4.1	Marsh
BM3	16:1n7	4.2	0.2	-31.1	0.1	-229.8	1.2	Marsh
CB1	16:1n7	1.9	0.2	-27.0	0.1	-227.3	4.5	CosBeach
CB2	16:1n7	0.7	0.1	-26.5	0.2	-222.2	3.1	CosBeach
CB3	16:1n7	1.7	0.1	-27.1	0.2	-225.7	1.6	CosBeach
CT1	16:1n7	1.2	0.1	-27.7	0.2	-227.1	3.8	CosTri
CT2	16:1n7	1.5	0.1	-26.7	0.7	-226.5	1.6	CosTri
CT3	16:1n7	0.9	0.1	-28.1	1.0	-227.2	1.7	CosTri
KR1	16:1n7	2.4	0.2	-30.4	0.3	-202.9	1.4	Knaggs
KR2	16:1n7	3.0	0.1	-28.9	0.3	-208.0	1.6	Knaggs
KR3	16:1n7	3.0	0.2	-29.4	0.5	-199.0	2.2	Knaggs
MR1	16:1n7	0.8	0.0	-28.8	0.5	-192.3	4.9	Moke
MR2	16:1n7	1.5	0.1	-27.5	0.9	-210.1	2.8	Moke
MR3	16:1n7	1.6	0.1	-29.5	0.3	-170.4	2.0	Moke
XS1	16:1n7	1.1	0.0	-28.6	0.8	-237.1	3.5	Sac
XS2	16:1n7	0.5	0.0	-28.4	0.3	-226.5	2.9	Sac
XS3	16:1n7	0.5	0.0	-28.9	0.6	-222.5	3.4	Sac
BM1	18:1n9	4.0	1.3	-25.4	3.1	-205.1	5.6	Marsh
BM2	18:1n9	3.0	0.1	-27.8	1.5	-211.7	3.1	Marsh
BM3	18:1n9	2.8	0.1	-22.9	3.8	-213.0	4.4	Marsh
CB1	18:1n9	3.4	0.2	-20.6	2.8	-213.5	5.4	CosBeach
CB2	18:1n9	2.1	0.1	-18.1	4.2	-212.7	6.5	CosBeach
CB3	18:1n9	2.1	0.2	-22.3	1.2	-205.2	2.0	CosBeach
CT1	18:1n9	2.4	0.2	-21.4	0.5	-218.4	8.3	CosTri
CT2	18:1n9	3.6	0.3	-21.8	0.4	-215.8	1.9	CosTri
CT3	18:1n9	2.0	0.0	-22.1	0.2	-224.0	7.0	CosTri
KR1	18:1n9	1.7	0.5	-25.9	2.2	-190.6	2.3	Knaggs
KR2	18:1n9	2.8	0.0	-25.5	3.1	-201.3	0.9	Knaggs
KR3	18:1n9	2.5	0.1	-24.9	4.1	-194.9	2.9	Knaggs
MR1	18:1n9	2.5	0.1	-20.1	2.7	-217.9	0.9	Moke
MR2	18:1n9	3.1	0.1	-20.9	2.4	-219.1	1.1	Moke
MR3	18:1n9	2.9	0.1	-19.6	1.3	-223.6	29.5	Moke
XS1	18:1n9	2.7	0.1	-23.7	0.2	-222.4	2.1	Sac
XS2	18:1n9	2.9	0.1	-21.9	1.0	-226.4	4.3	Sac
XS3	18:1n9	2.8	0.1	-22.6	1.3	-223.3	2.1	Sac
BM1	18:2n6	1.7	0.6	-29.5	2.7	-172.1	5.0	Marsh
BM2	18:2n6	1.4	0.1	-26.1	0.3	-182.4	2.1	Marsh
BM3	18:2n6	1.3	0.0	-26.5	1.1	-176.5	0.8	Marsh

Code	FA	mg FA / g	σ (mg)	$\delta^{13}C$	σ ($\delta^{13}C$)	$\delta^{2}H$	σ ($\delta^{2}H$)	Treatment
CB1	18:2n6	1.4	0.1	-23.6	0.3	-187.7	7.1	CosBeach
CB2	18:2n6	0.7	0.0	-24.8	0.2	-191.8	6.2	CosBeach
CB3	18:2n6	0.8	0.1	-24.1	0.6	-186.0	0.7	CosBeach
CT1	18:2n6	0.8	0.1	-24.2	1.4	-187.2	6.6	CosTri
CT2	18:2n6	1.4	0.2	-23.3	0.1	-192.1	5.7	CosTri
CT3	18:2n6	0.6	0.0	-24.4	1.5	-189.0	8.2	CosTri
KR1	18:2n6	0.5	0.2	-32.0	3.1	-171.4	14.7	Knaggs
KR2	18:2n6	1.6	0.1	-26.0	0.3	-190.9	3.7	Knaggs
KR3	18:2n6	1.4	0.1	-24.9	0.5	-179.4	3.7	Knaggs
MR1	18:2n6	0.6	0.0	-27.7	0.8	-205.7	3.9	Moke
MR2	18:2n6	1.1	0.1	-23.2	1.0	-200.7	2.3	Moke
MR3	18:2n6	0.7	0.0	-25.5	0.2	-195.6	1.2	Moke
XS1	18:2n6	1.1	0.1	-27.1	0.6	-198.1	4.8	Sac
XS2	18:2n6	1.0	0.0	-25.9	0.1	-190.5	13.5	Sac
XS3	18:2n6	1.0	0.1	-25.7	0.1	-200.7	7.5	Sac
BM1	18:3n3	1.2	0.4	-43.4	1.6	-164.6	0.7	Marsh
BM2	18:3n3	0.7	0.0	-40.8	0.5	-166.5	1.0	Marsh
BM3	18:3n3	0.8	0.0	-41.6	1.1	-164.8	0.9	Marsh
CB1	18:3n3	0.3	0.0	-37.9	0.8	-165.2	1.8	CosBeach
CB2	18:3n3	0.1	0.0	-39.2	0.6	-159.2	3.3	CosBeach
CB3	18:3n3	0.3	0.0	-36.5	0.2	-172.7	2.3	CosBeach
CT1	18:3n3	0.1	0.0	-34.3	1.4	-168.2	14.7	CosTri
CT2	18:3n3	0.2	0.0	-31.9	0.6	-161.2	3.0	CosTri
CT3	18:3n3	0.1	0.0	-33.9	2.1	-166.0	1.7	CosTri
KR1	18:3n3	0.5	0.1	-46.8	0.8	-163.3	4.2	Knaggs
KR2	18:3n3	0.6	0.0	-43.0	0.5	-170.0	3.9	Knaggs
KR3	18:3n3	0.7	0.0	-42.0	0.2	-173.8	3.7	Knaggs
MR1	18:3n3	0.1	0.0	-41.7	1.5	-166.6	4.7	Moke
MR2	18:3n3	0.1	0.0	-37.3	0.6	-172.6	9.6	Moke
MR3	18:3n3	0.2	0.2	-35.8	5.7	-167.4	5.5	Moke
XS1	18:3n3	0.2	0.0	-41.1	1.6	-174.4	5.5	Sac
XS2	18:3n3	0.1	0.0	-42.0	0.8	-160.1	6.2	Sac
XS3	18:3n3	0.2	0.0	-40.8	1.3	-163.5	18.7	Sac
BM1	18:4n3	0.9	0.3	-40.2	3.1	-263.1	3.0	Marsh
BM2	18:4n3	0.5	0.0	-36.3	1.6	-255.6	12.3	Marsh
BM3	18:4n3	0.6	0.0	-37.8	1.5	-264.8	1.2	Marsh
CB1	18:4n3	0.1	0.0	-41.8	1.0	-225.4	1.8	CosBeach
CB2	18:4n3	0.0	0.0	-42.0	1.2	-214.3	16.9	CosBeach
CB3	18:4n3	0.1	0.0	-39.8	0.8	-232.0	7.1	CosBeach
CT1	18:4n3	0.03	0.0	-40.4	1.4	-204.8	0.9	CosTri
CT2	18:4n3	0.1	0.0	-34.3	0.4	-199.7	9.7	CosTri
CT3	18:4n3	0.04	0.0	-41.1	0.4	-214.9	6.9	CosTri
KR1	18:4n3	0.2	0.0	-44.4	1.7	-243.3	2.5	Knaggs
KR2	18:4n3	0.3	0.0	-43.1	2.1	-234.6	24.2	Knaggs
KR3	18:4n3	0.4	0.0	-41.5	1.9	-253.8	0.4	Knaggs
MR1	18:4n3	0.05	0.0	-45.9	0.9	-232.0	102.1	Moke
MR2	18:4n3	0.03	0.0	-44.6	2.2	-214.9	1.9	Moke
MR3	18:4n3	0.03	0.0	-46.8	1.0	-274.0	103.1	Moke
XS1	18:4n3	0.06	0.0	-44.2	0.9	-226.2	3.2	Sac

Code	FA	mg FA / g	σ (mg)	$\delta^{13}C$	σ ($\delta^{13}C$)	$\delta^{2}H$	σ ($\delta^{2}H$)	Treatment
XS2	18:4n3	0.05	0.0	-42.7	1.0	-185.9	33.7	Sac
XS3	18:4n3	0.05	0.0	-42.5	1.9	-205.1	5.6	Sac
BM1	20:4n6	0.7	0.2	-32.4	0.5	-136.5	1.3	Marsh
BM2	20:4n6	0.5	0.0	-30.8	0.2	-137.1	4.3	Marsh
BM3	20:4n6	0.5	0.0	-31.2	0.8	-133.5	3.3	Marsh
CB1	20:4n6	0.5	0.1	-26.2	1.0	-137.6	5.1	CosBeach
CB2	20:4n6	0.4	0.0	-25.7	0.7	-128.0	2.6	CosBeach
CB3	20:4n6	0.4	0.1	-26.3	0.4	-141.3	2.3	CosBeach
CT1	20:4n6	0.3	0.0	-24.5	0.6	-130.4	3.4	CosTri
CT2	20:4n6	0.5	0.0	-23.8	0.3	-131.3	13.1	CosTri
CT3	20:4n6	0.5	0.5	-22.5	0.6	-127.4	3.7	CosTri
KR1	20:4n6	0.4	0.1	-30.9	1.3	-136.8	0.9	Knaggs
KR2	20:4n6	0.4	0.0	-31.7	0.2	-140.9	2.4	Knaggs
KR3	20:4n6	0.4	0.0	-32.2	0.2	-137.6	2.8	Knaggs
MR1	20:4n6	0.4	0.0	-26.2	0.2	-134.9	4.5	Moke
MR2	20:4n6	0.3	0.0	-25.6	1.8	-129.8	4.0	Moke
MR3	20:4n6	0.3	0.0	-25.4	0.6	-128.1	11.9	Moke
XS1	20:4n6	0.4	0.1	-28.8	0.7	-136.0	2.1	Sac
XS2	20:4n6	0.7	0.0	-27.3	0.8	-133.0	2.9	Sac
XS3	20:4n6	0.8	0.0	-27.3	0.3	-127.9	3.6	Sac
BM1	20:5n3	2.5	0.5	-36.3	2.0	-278.2	1.7	Marsh
BM2	20:5n3	1.7	0.1	-34.6	0.3	-279.2	1.3	Marsh
BM3	20:5n3	1.9	0.1	-35.2	0.8	-280.8	1.2	Marsh
CB1	20:5n3	1.1	0.1	-29.5	1.2	-254.8	3.0	CosBeach
CB2	20:5n3	0.8	0.0	-29.1	0.4	-254.1	3.3	CosBeach
CB3	20:5n3	1.0	0.1	-28.6	0.4	-259.1	2.3	CosBeach
CT1	20:5n3	0.7	0.0	-26.3	1.2	-248.9	3.2	CosTri
CT2	20:5n3	0.9	0.0	-25.1	0.3	-254.3	25.8	CosTri
CT3	20:5n3	0.5	0.0	-24.1	0.2	-248.0	1.9	CosTri
KR1	20:5n3	1.0	0.1	-34.0	0.6	-255.8	2.6	Knaggs
KR2	20:5n3	1.2	0.0	-35.2	0.4	-256.9	1.6	Knaggs
KR3	20:5n3	1.2	0.0	-35.2	0.2	-263.5	1.1	Knaggs
MR1	20:5n3	0.6	0.0	-29.0	0.8	-242.5	6.5	Moke
MR2	20:5n3	0.5	0.0	-26.8	1.4	-245.4	4.8	Moke
MR3	20:5n3	0.5	0.0	-27.0	0.3	-217.1	46.1	Moke
XS1	20:5n3	0.9	0.1	-34.3	1.0	-258.4	2.3	Sac
XS2	20:5n3	1.3	0.0	-29.8	0.1	-247.0	4.3	Sac
XS3	20:5n3	1.8	0.0	-29.5	0.2	-249.6	1.2	Sac
BM1	22:5n3	0.9	0.1	-32.6	1.9	-254.4	5.6	Marsh
BM2	22:5n3	0.6	0.0	-31.5	0.3	-243.9	8.4	Marsh
BM3	22:5n3	0.6	0.0	-32.6	1.0	-259.9	3.2	Marsh
CB1	22:5n3	0.5	0.1	-27.0	2.0	-217.3	5.3	CosBeach
CB2	22:5n3	0.3	0.0	-25.5	0.3	-217.5	9.3	CosBeach
CB3	22:5n3	0.3	0.0	-27.3	0.3	-225.6	6.7	CosBeach
CT1	22:5n3	0.3	0.0	-24.7	1.1	-217.6	15.4	CosTri
CT2	22:5n3	0.5	0.1	-24.8	0.7	-217.2	14.4	CosTri
CT3	22:5n3	0.3	0.0	-22.8	0.4	-216.7	2.1	CosTri
KR1	22:5n3	0.5	0.0	-29.8	0.3	-231.9	7.1	Knaggs
KR2	22:5n3	0.5	0.0	-32.6	0.1	-221.0	10.4	Knaggs

Code	FA	mg FA / g	σ (mg)	$\delta^{13}C$	σ ($\delta^{13}C$)	$\delta^{2}H$	σ ($\delta^{2}H$)	Treatment
KR3	22:5n3	0.5	0.0	-32.5	0.9	-231.0	6.3	Knaggs
MR1	22:5n3	0.3	0.0	-26.4	1.0	-205.7	6.5	Moke
MR2	22:5n3	0.3	0.0	-24.1	1.2	-219.4	4.1	Moke
MR3	22:5n3	0.6	0.4	-23.0	0.9	-214.8	8.4	Moke
XS1	22:5n3	0.4	0.0	-28.0	0.6	-228.4	4.0	Sac
XS2	22:5n3	0.5	0.0	-26.4	0.4	-215.0	7.9	Sac
XS3	22:5n3	0.6	0.0	-26.2	0.6	-220.8	8.5	Sac
BM1	22:6n3	1.9	0.2	-30.8	2.4	-252.6	7.5	Marsh
BM2	22:6n3	1.5	0.0	-28.8	0.5	-256.9	3.2	Marsh
BM3	22:6n3	1.3	0.1	-30.0	0.2	-257.8	0.2	Marsh
CB1	22:6n3	2.6	0.2	-25.7	0.2	-243.0	0.5	CosBeach
CB2	22:6n3	2.5	0.0	-25.2	0.1	-238.5	8.7	CosBeach
CB3	22:6n3	2.4	0.3	-27.0	0.2	-249.1	1.1	CosBeach
CT1	22:6n3	2.3	0.0	-25.2	0.2	-238.7	1.0	CosTri
CT2	22:6n3	2.7	0.2	-24.0	0.1	-232.3	3.0	CosTri
CT3	22:6n3	2.3	0.2	-24.0	0.1	-239.3	2.1	CosTri
KR1	22:6n3	1.8	0.1	-29.5	0.5	-247.1	2.5	Knaggs
KR2	22:6n3	1.9	0.1	-29.3	0.7	-245.0	0.2	Knaggs
KR3	22:6n3	1.9	0.1	-29.5	0.4	-245.4	2.8	Knaggs
MR1	22:6n3	2.7	0.1	-25.1	0.4	-239.8	2.0	Moke
MR2	22:6n3	2.4	0.2	-23.1	1.5	-239.0	1.2	Moke
MR3	22:6n3	2.3	0.1	-23.3	0.3	-237.8	0.6	Moke
XS1	22:6n3	2.7	0.5	-26.3	0.8	-245.8	0.7	Sac
XS2	22:6n3	5.1	0.0	-24.1	0.1	-239.4	0.7	Sac
XS3	22:6n3	7.0	0.0	-25.3	0.1	-238.1	1.3	Sac