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Peruvian Pinnipeds as Archivists of ENSO Effects

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Mickie Rae Edwards

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

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Halmos College of Natural Sciences and Oceanography

December 2018

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

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By:
Mickie Rae Edwards

Submitted to the Faculty of
Halmos College of Natural Sciences and Oceanography
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Marine Biology

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ABSTRACT

Environmental fluctuations in the eastern Pacific Ocean are reflected in the tissues of some of its most vulnerable apex predators, the Peruvian fur seal (PFS) *Arctocephalus australis ssp.* and the South American sea lion (SASL) *Otaria byronia.* These large pinnipeds live in sympatry along the Pacific coastline of South America and forage within the neritic waters over the continental shelf. The coastal waters off Peru are a region of great environmental fluctuations due to periodic, oscillating El Niño- La Niña-Southern Oscillation (ENSO) events, which result in ecosystem-wide food web changes. Pinniped vibrissae (whiskers) are continuously growing keratinous tissues and reflect the incorporation of prey from the region. Fine resolution sampling along their length provided trophic information on a weekly to monthly time scale over several years. Vibrissae were obtained from 2010-2016 from female (n=47), male (n=17) and newborn pup (n=6) fur seals and male (n=6) sea lions collected during pinniped rookery health assessments. Stable isotope ratios (δ^{13}C and δ^{15}N) in vibrissae infer temporal primary production and dietary variations in individuals. ENSO conditions were dictated by the sea surface temperature anomaly (SSTA) recordings from the Niño 1+2 Index region over 12 years. Fluctuations in vibrissae δ^{15}N were correlated to varying SSTA readings ($p<0.001$) in both species, indicating that ENSO conditions may alter the foraging of these apex predators over time. Anomalous warm phase temperatures corresponded to depleted δ^{15}N ($p<0.001$); whereas, cold phase anomalous conditions corresponded to the most enriched δ^{15}N signatures ($p<0.001$). Although both male and female PFS vibrissae δ^{13}C revealed minor fluctuations ranging from -18.13 to -13.17‰ over the 12-year period, δ^{13}C did reveal a significant depletion and enrichment oscillation during specific points in time, such as the 2014-2016 El Niño event, which ranged from -15.09 to -13.83‰ ($p=0.040$). Stable isotope signatures varied between genders, but not by species. Female fur seal stable isotope signatures were significantly more depleted in both δ^{13}C and δ^{15}N than males ($p<0.001$, $p<0.001$, respectively). Male SASL and PFS showed no significant difference between mean stable isotope signatures. In PFS, both δ^{13}C and δ^{15}N were inversely correlated to each other from 2014 to 2016; this was during the strongest El Nino-Southern Oscillation event on record ($p=0.002$). As δ^{13}C signatures became more enriched, δ^{15}N signatures depleted from 2014 until 2016. This suggests that when ENSO warm phase conditions occur, the environments resources change in historic foraging grounds, possibly forcing pinnipeds to travel farther distances offshore to forage or altering what they feed on throughout these stressful conditions. This study serves to help understand of the impact of oceanographic influences on these pinnipeds. ENSO conditions influence the trophic dynamics and resultant survival adaptations in both of these vulnerable Peruvian marine mammals.

Key words: South American sea lion · Peruvian fur seal · Stable isotope ratios · Peru · ENSO · δ^{13}C · δ^{15}N

INTRODUCTION

Preface

Large-scale climatic anomalies associated with periodic, alternating El Niño-Southern Oscillation (ENSO) conditions, are recorded globally through a combination of atmospheric and oceanic teleconnections, resulting in significant, ecosystem-wide impacts (Ropelewski & Halpert 1987, Trenberth et al. 1998, McPhaden et al. 2006, Sulca et al. 2017). The Humboldt Current Upwelling Ecosystem, a cold, nutrient-rich coastal current that supports ecologically and economically important species, is dramatically impacted by strong ENSO events (Barber & Chavez 1983, Niquen & Bouchon 2004). In Peru pinnipeds such as the Peruvian fur seal and the South American sea lion forage along and within the Humboldt Current and feed predominantly on anchoveta (Vásquez 1995, Zavalaga et al. 1998, Arias-Schreiber 2000, 2003). Peruvian anchoveta comprise the largest single-species fishery in the world, although it experienced severe stock collapses during the 1982/83, 1997/98 and the recent 2015/16 ENSO events (Alheit & Niquen 2004, Niquen & Bouchon 2004, Espinoza-Morriberon et al. 2017). South American pinniped mortality events and anchoveta abundance declines coincided with these ENSO periods, though no definitive cause for these mortality events have been determined (Arias-Shreiber & Rivas 1998, Cardenas-Alayza 2012).

Both Peruvian pinniped species are vulnerable during these strong magnitude ENSO episodes. The feeding ecology and movements of these pinnipeds are of substantial interest as ENSO events continue to intensify in both frequency and magnitude (Sepúlveda et al. 2014). Through a combined analysis of stable isotope profiles and abiotic recordings from Niño indices, the feeding ecologies of two sympatric species of otariid were investigated in Punta San Juan, Peru (Figure 1) over a time series of various ENSO conditions. Stable isotopes were used to depict the trophic fluctuations of both seal and sea lion individuals and their populations. Abiotic recordings from the Niño 1+2 index (Figure 1) are reflective of environmental changes due to alternating ENSO conditions along the coast of Peru. By using continuously growing, inert vibrissae (whiskers) from Peruvian pinnipeds (i.e., apex predators), it is possible to obtain valuable multi-year dietary information from their foraging environment across fluctuating environmental conditions (i.e., overlapping multiple ENSO events).

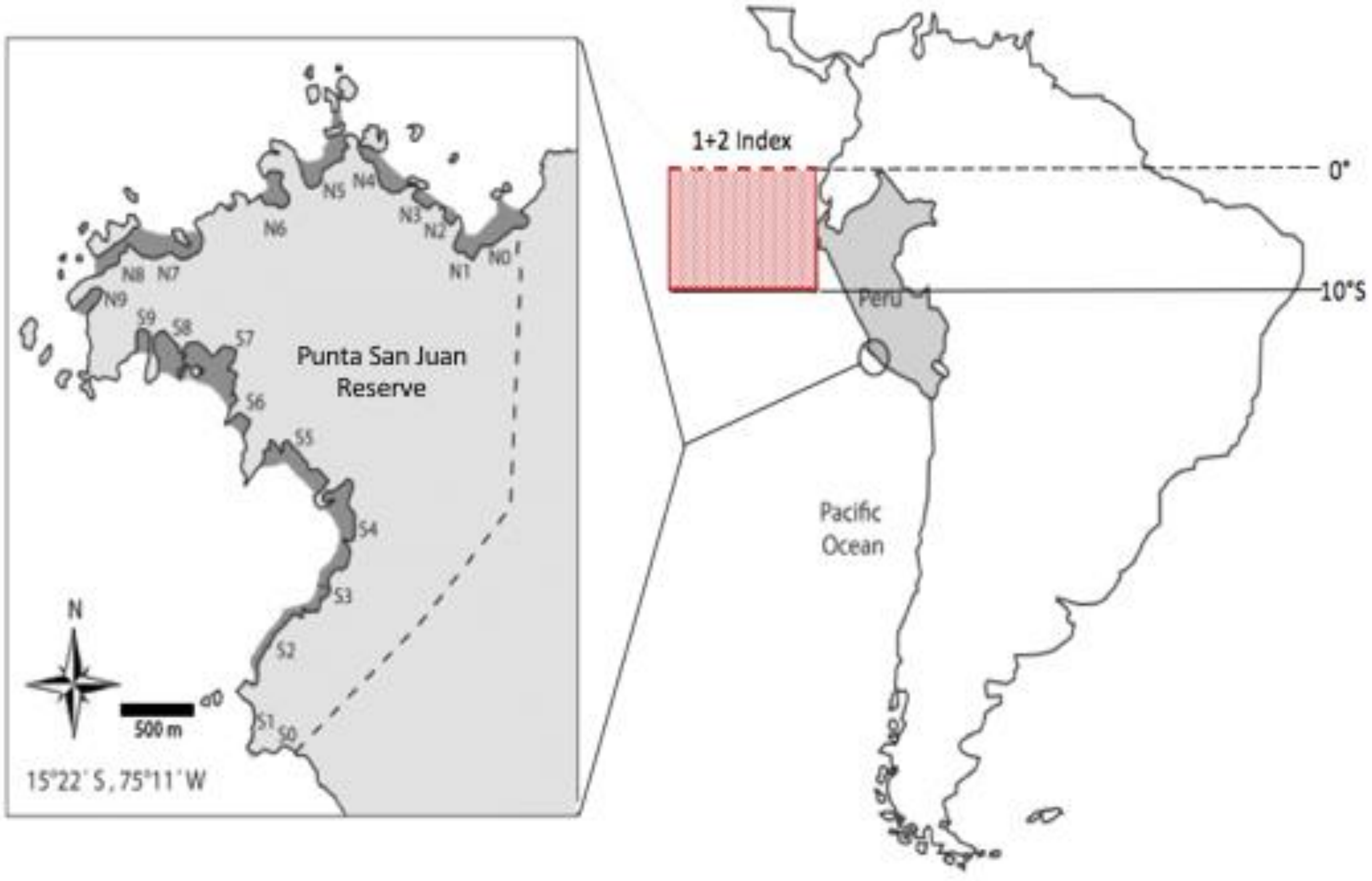

Figure 1. Map of the Punta San Juan Reserve and its beaches, relative to its location in Peru and South America. Red square shows the region of coastal waters of El Niño index 1+2 region. (Map adapted from Cárdenas-Alayza 2012).

Peruvian Marine Ecosystem

The coastal marine ecosystem along the arid margin of western South America is supported by the Humboldt Current System (HCS), one of the world's four major eastern boundary upwelling systems (EBUS) and the largest meridional extent of all EBUSs, ranging from 4 to 42° S (Berger 1988, Strub et al. 1998, Daneri et al. 2000, Vargas et al. 2007). Eastern boundary currents form highly productive regions due to strong air-sea-land physical interactions (Berger 1988, Strub et al. 1998). The productive waters along this coast are the result of longshore winds, which bring cold, nutrient-rich waters from the Equatorial Subsurface waters (ESSW) into the euphotic zone where they are available for primary producers (Sverdrup 1938, Wooster 1963, Huyer et al. 1987, Berger 1988, Strub et al. 1998, Vargas et al. 2007, Bakun et al. 2015).

The coastal margin off western South America is symmetrically sinuous though the width of the continental shelf is variable - narrow off Ecuador, wider off Peru, and then narrow again off northern Chile - which affects how upwellings occur along the coastline. Additionally, due to their low-latitude proximity, the coast of Peru experiences a weakened Coriolis Effect, which allows for persistent, equatorward winds that drive larger Ekman transport and upwelling than other regions found at higher latitudes with similar wind patterns (Strub et al. 1998). The near-coast, northward flowing HCS comprises the surface and subsurface flows of the EBCS along the Peruvian coast. The HCS hosts several major currents, among them are two equatorward-flowing and two poleward-flowing currents, each having a surface and subsurface flow, respectively. The offshore, equatorward flow is the Humboldt Current and the nearshore equatorward flow comprises the Peru-Chile Coastal Current. The poleward surface-flowing current is the Peru-Chile Countercurrent while the poleward subsurface-flowing current is the Peru-Chile Undercurrent (Karstensen & Ulloa 2009). The linkage of the coastal and equatorial upwelling regions extends to the poleward undercurrent and the offshore Peru-Chile Countercurrent, both of which receive input from the Equatorial Undercurrent and extend from the tropics to the mid-latitudes of Chile (Figure 2) (Bakun et al. 2015).

Powered by the southeast trade winds, which blow equatorward and parallel to the coast at a speed of 3-10 m/s, coastal upwelling in the HCS is continuous with little variability in normal (i.e., average) climatic states (Huyer et al. 1987, Tarazona & Arntz

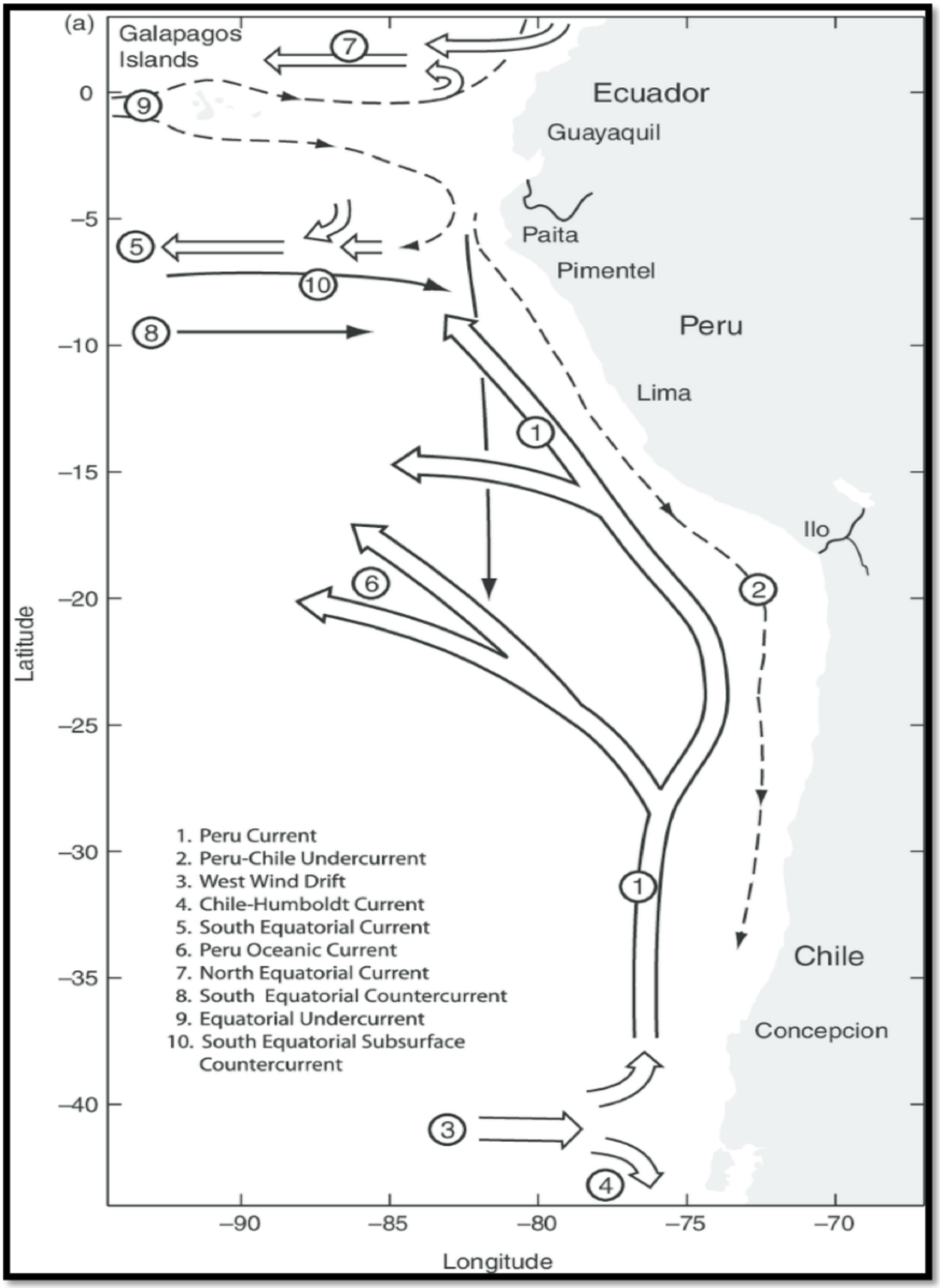

Figure 2. Coastal region current circulation (Checkley et al. 2009). The study site, Punta San Juan, Peru was located at 15°22’ S, 75°11’ W.

2001, Pennington et al. 2006, Espinoza-Morriberon et al. 2017). Resultant phytoplankton blooms from these nutrient-rich waters nourish productive zooplankton communities that feed small pelagic fish populations, such as anchovy and sardine, that are vital to the world's fisheries (Chavez et al. 2003, Weise et al. 2006, Barth et al. 2007, Bakun et al. 2015). A substantial portion of animal biomass in the HCS is comprised of these small, pelagic planktivorous fish species, making coastal Peru a vital fishery ecosystem, which supports approximately 20% of the world's fish catches (Chavez et al. 2003, Bakun et al. 2015). Historical evidence of pelagic fish and apex predator abundances, such as during the 1982/83 ENSO event, illustrate how these fish populations control the trophic dynamics of marine mammals and sea birds (Schwartzlose et al. 1999, Bakun et al. 2015).

Approximately every 2-7 years, the Humboldt Current Upwelling Ecosystem is impacted by El Niño phases, which experience increased sea surface temperatures and reduced primary productivity due to stratified waters. This stratification of waters is believed to directly influence the depth distribution and abundance of the Peruvian anchovy (Barber & Chavez 1983, Huyer et al. 1987, Luna-Jorquera & Culik 2000). Ecosystem productivity in coastal ocean upwelling systems is threatened due to increased frequency and intensity of ENSO events. Apex predators, such as marine mammals and sea birds that cluster at key rookery sites and nesting grounds, experience difficulties in prey acquisition in response to intensifying climatic anomalies (Bakun et al. 2015).

El Niño- La Niña- Southern Oscillations

The eastern Pacific Ocean is subject to strong environmental fluctuations in the form of alternating El Niño-Southern Oscillation (ENSO) events. El Niño-Southern Oscillations are alternating cycles of warm and cold sea surface temperature (SST) in the tropical central and eastern Pacific Ocean which can last upwards of 18 months with re-occurrence approximately every 2-7 years (Gutierrez et al. 2007, Taylor et al. 2008, Grandi et al. 2012). ENSO events are classified by magnitude and are quantified using sea surface temperature anomalies (SSTA) in degrees Celsius (i.e., temperatures that are not within average conditions) (Oliveira 2011). Sea surface temperatures off the coast of Peru have seasonal dependent averages, acknowledged as "normal conditions" for that time of year. Anomalies are deviations from the average conditions for that period and are anything greater than +/-1° C (Waluda et al. 2006, Grandi et al. 2012). Magnitudes of ENSO range from Weak (+/-1 to 1.5°C) to Extreme (+/-2.5 to 3.0° C) (Waluda et al. 2006, Grandi et al. 2012). Regional average SST anomaly data are collected within Niño indices that are compiled from buoy recordings from specific regions (Trenberth & Stepaniak 2001). Currently, five indices are monitored in the tropical Pacific Ocean; these include the Niño 1+2 (10° S-0°, 80-90° W) (Figure 1), Niño 3 (5° S5° N, 90-150° W), Niño 3.4, also known as the Oceanic Nino Index (ONI) (5° S-5° N, 120-170° W), Niño 4 (5° S-5° N, 150° W-160° E) and Trans- Niño Index (TNI) which is the difference in normalized SST anomalies between the Niño 1+2 and Niño 4 regions (Trenberth & Stepaniak 2001, Yu & Lau 2007, Kao & Yu 2009, Kug & Jin 2009, Trenberth 2016). The Niño 3.4 Index (ONI) is the most commonly used index to define ENSO events; however, the Niño region along the South American coastline is the Niño-1+2 region. The Niño 1+2 region is the smallest and eastern-most of the indices, and it tends to have the largest variance of all the Niño SST indices (Trenberth & Stepaniak 2001).

The warm SST phase of ENSO is referred to as El Niño and the cooler SST phase is known as the La Niña. The precursor to ocean temperature changes begins when the southeast trade winds weaken over the equatorial Pacific Ocean, which allows for the eastward displacement of the warm pool, thereby decreasing the upwelling strength of cold, nutrient-rich water (Barber & Kogelschatz 1990, Picaut et al. 1996). Under such decreased upwelling, the surface waters along the coasts of Peru, Ecuador, and Chile are instead warmer and relatively nutrient-poor (Taylor & Wolff 2007, Oliveira 2011). El Niño events can increase SST in the central and eastern Pacific Ocean by up to 9º C, resulting in depleted surface chlorophyll (Chavez et al. 2003, Arntz et al. 2006, Graco et al. 2007, 2017). Eventually, a renewal in the southeast trade winds pushes the warmer surface waters towards the central Pacific basin, thus resuming the upwelling of coastal waters along the coast of South America (Barber & Kogelschatz 1990).

In contrast with El Niño, La Niña events are evidenced by shallow thermoclines, cooler than average sea surface temperatures, and increased marine productivity (Ordinola 2002a, 2002b). Physical indications of La Niña events include unusually cold temperatures in the central and eastern equatorial Pacific Ocean, stronger than normal easterlies (i.e., westward blowing trade winds), stronger upwelling, and conditions that are generally more arid. La Niña impacts on HCS ecosystems are still unclear; however, higher commercial landings and greater fishery exports occur during these events (Ordinola 2002a, 2002b).

Pronounced bottom-up mechanisms, which decrease primary production, occur off the coast of Peru during El Niño events (Tam et al. 2008, Espinoza-Morriberon et al. 2017). Among these mechanisms are downwelling equatorial Kelvin waves (deepening nearshore thermocline and nutricline), changes in equatorial circulation, and high intensity mesoscale eddies (increasing offshore transport and subduction of nutrients) (Barber and Chavez 1983, Kessler and McPhaden 1995, Chaigneau et al. 2008, Lathuiliere et al. 2010, Gruber et al. 2011, Calienes 2014, Echevin et al. 2014). However, throughout La Niña events, the coastal ecosystem encounters intensified upwelling favorable winds, cooler SST, shallow thermo- and nutriclines, and increased primary production (Bouchon and Pena 2008, Calienes 2014).

Chlorophyll concentrations (Chl_a), which are a proxy for phytoplankton biomass, were recorded at historic lows during strong/extreme El Niño events (i.e., the 1997/1998 event) (Calienes 2014, Gutierrez et al. 2016, Espinoza-Morriberon et al. 2017). During these events of SST and sea level rise, the thermocline and nutricline deepen significantly. In conjunction, the passing of coastal-trapped waves cause the nutrient concentration in coastal waters to decrease. Impact on nutrient concentrations and upwelling strength is dependent on the magnitude of the ENSO events (Espinoza-Morriberon et al. 2017).

Eight El Niño-Southern Oscillation events had been recorded from 1950-2003 (Wang & Feidler 2006) with the 1982/83 and the 1997/98 events considered to be the most severe (Gutierrez et al. 2007, Taylor et al. 2008). NOAA (2015) speculated 2015/16 would be a strong magnitude El Niño event, which proved to be correct. In fact, the 2015/16 ENSO event is by some measures (i.e., SSTA); one of the strongest magnitude events on record, and it has triggered widespread ecosystem changes, such as strong decreases in phytoplankton productivity within the coastal Pacific Ocean (Jacox et al. 2016, Espinoza-Morriberon et al. 2017). Climate change models are predicting stronger and more frequent ENSO events in the future (NCDC-NOOA 2004, Oliveira 2011).

Inter-annual environmental fluctuations are frequently observed in the highly unpredictable marine environments off the coasts of South America; these cyclical fluctuations in turn affect all types of marine organisms throughout the ecosystem, often changing the trophic dynamics of large areas of the ocean. Shifts in available food, beginning with primary producers, have long-ranging implications both for commercial fisheries and for apex predators like Peruvian fur seals and South American sea lions. The higher the trophic level at which the animal feeds, the more production becomes necessary to sustain it. During periods of lower productivity, environments become resource limited, which can have damaging effects on reproduction and species viability (Benson & Trites 2002, Hanson et al. 2009, Coyle et al. 2011).

Peruvian Pinnipeds

South America was once a source of significant trade for pinniped blubber and fur throughout the 18th century. Targeted hunting and trade decimated South American otariid species' (sea lions and fur seals) historical population sizes by nearly 80% by the late 20th century (Bonavia 1982, Reeves et al. 1992, Riedman 1990, Webber et al. 2004). By the mid-1940s, South American fur seal distribution range in Peru had been reduced to a few isolated sites (Kostrisky 1963, Piazza 1969, Majluf & Trillmich 1981, Muck and Fuentes 1987, Cardenas-Alayza 2012). Much like fur seals, South American sea lions suffered heavy direct exploitation during the early 20th century throughout their range due to the commercial uses of pinnipeds for fur, oil and food (Rodriguez & Bastida 1998, Oliveira 2011, Dassis et al. 2012, Saporiti et al. 2014, Zenteno et al. 2015). With a recognized risk of pinniped extinction in Peru, legislation in 1959 banned all sealing in Peruvian waters in an effort to save these pinniped species, although some illegal poaching continues (Majluf 1984, Oliveira 2011, Cardenas-Alayza 2012). However, despite protection Peruvian populations have struggled to recover to previous population sizes due to ecological and anthropogenic stressors (Majluf & Apaza 1998, Majluf 1998, Oliveira 2011).

Home to the largest colonies of Peruvian fur seal and South American sea lion, Punta San Juan is a 133-acre peninsula located in southern Peru, 15° S of the equator Cárdenas-Alayza & Cardeña-Mormontoy 2012). This reserve is part of a marine protected network of reserves known as the National Reserve System of Guano Islands, Islets and Points (RNSIIPG). The RNSIIPG, managed by the National Service of Protected Natural Areas of Peru (SERNANP), serves as a protection to all marine wildlife with a focus on the protection of guano producing sea birds (Cárdenas-Alayza & Cardeña-Mormontoy 2012). Among the 21,000 individuals along their entire distribution range, over 70% of the total PFS population is found in Peru clustered into the RNSIIPG system, with the majority found in Punta San Juan, Peru (Cárdenas-Alayza & Oliveira 2016).

Peruvian Fur Seals

Peruvian fur seals (*Arctocephalus australis* unnamed ssp.) (PFS), a subspecies of the South American fur seal (SAFS), are found along the eastern Pacific coastline of South America (Berta & Churchill 2012, Oliveira & Brownell 2014, Cárdenas-Alayza & Oliveira 2016). Distributed between breeding colonies and haul-out areas, fur seals can be found year-round at coastal sites due to their strong site-fidelity (Majluf 1987a, Oliveira 2011, Cardenas-Alayza 2012). Females will travel distances of 70 to 150 km in order to forage, whereas males will travel an average of 200 km (Cardenas-Alayza & Oliveira 2016). Fur seal colonies are ordinarily found along rocky coastlines, on ledges, in caves, and around beaches covered in large boulders so that they can utilize the ocean access, tidal pools, shade and protection these environments provide (Stevens & Boness 2003). Geographical isolation between breeding colonies has led to the genetic variation between the South American fur seal and the Peruvian fur seal (Berta & Churchill 2012, Nyakatura & Bininda-Emonds 2012, Oliveira & Brownell 2014). Additionally, the 1997/98 ENSO caused such a severe decline in effective population size that it might have compromised the evolutionary potential of the Peruvian fur seal to respond to environmental changes (Oliveira et al. 2006). Distribution of these genetically isolated subspecies ranges from Peru southward into northern Chile, with approximately 21,000 individuals along this distribution (Torres 1985, Guerra & Torres 1987, Oliveira et al. 2012, IMARPE 2014). The majority of the breeding population resides in Peru between 15-17° S; over 50% of the entire Peruvian fur seal population is only found among five sites in Peru (Cárdenas-Alayza & Oliveira 2016). Population declines and fewer breeding colonies have led to classification of the Peruvian fur seal as

“Vulnerable” species in the International Union for Conservation of Nature red list (IUCNRL) (Oliveira & Brownell 2014, CSA-UPCH 2016, 2017, 2018).

Both fur seal subspecies are sexually dimorphic (Cárdenas-Alayza & Oliveira 2016, Oliveira et al. 2005, 2008). Adult Peruvian fur seal males reach lengths of 1.7 m and can weigh between 90–140 kg, while females are approximately 1.3 m in length and weigh between 30-90 kg. Newborn pups are 50-65 cm in length and weigh 3.5-7.5 kg (Cárdenas-Alayza & Oliveira 2016). Peruvian subspecies males are smaller in body size than that of SAFS males while conversely, PFS females are larger in body size than SAFS females (Cárdenas-Alayza & Oliveira 2016, Oliveira et al. 2005, 2008).

The life history of PFS varies between genders, where adult bull males become sexually mature at approximately 8 years old, in contrast to females who become sexually mature as early as 4 years old (Lima & Páez 1995, 1997, Vales et al. 2015). Adult bulls are polygynous and territorial; in fact only a few large, strong bulls out of the total population mate each season (Cardenas-Alayza et al. 2016). In Punta San Juan, bulls will occupy territories for an average of 23 days and mate with 6-20 females within their territory (Majluf 1987a, Cappozzo 1995, Cárdenas-Alayza & Oliveira 2016). Breeding season for Peruvian fur seals takes place during austral summer between the months of October and December (Majluf 1987a). The gestation duration is normally 11 months, with a 3 to 4-month embryonic diapause (Vaz Ferreira et al. 1982a, Katz et al. 2013). Pupping peaks during mid- to late November (Majluf 1992, Cardenas-Alayza 2012). Pregnant females normally come ashore roughly 1-4 days before the birth of the pup and then stay with the newborn pup for a perinatal period lasting around 11 days (Franco-Trecu 2010). After this period, fur seal dams enter a brief estrus, copulate, and then depart to sea to forage (Majluf 1987b, Cardenas-Alayza 2012).

Following mating, females alternate between foraging trips at sea between 1-8 days and then suckling pups in the rookery for 1-3 days, food source availability depending (Majluf 1987b, Cardenas-Alayza 2012). Throughout the initial three months of maternal care, female foraging trip durations are highly variable, which can affect the survivability of offspring (Franco-Trecu et al. 2010). The seals tend to have flexible and adaptive pup rearing strategies, such as flexible weaning duration, to accommodate for environmental stressors (i.e., ENSO events), (Trillmich & Ono 1991). Prolonged, simultaneous maternal care of multiple offspring at various life stages has enhanced survival of Peruvian fur seals during mild ENSO events, and can explain extraordinary growth rates of fur seals when food sources are in abundance (Trillmich et al. 1986, Cárdenas-Alayza 2012). Dams wean offspring anywhere between 6 months to 3 years of age and can nurse multiple-aged offspring simultaneously. Female fur seals have been observed nursing both a newborn pup and a yearling, and on rare occasion, nursing a pup, yearling, and a 2 to 3 years old juvenile (Majluf 1987a). This cumulative maternal contribution generates enormous metabolic needs and can lead to competition for milk among suckling young, with a risk of starvation for all as well spontaneous abortion of a fetus (Trillmich 1990, Cardenas-Alayza 2012).

In 1987, the Punta San Juan, Peru rookery experienced its highest recorded early pup mortality percentages (31-49%); other rookeries experienced anywhere from 3 to 28% early pup mortality (Majluf 1987b, 1989, Harcourt 1992). This early pup mortality in Peru does not appear to be related to food availability, except for during ENSO conditions when mortality increases dramatically (Limberger et al. 1983, Trillmich et al. 1986, Majluf 1989, Harcourt 1992). El Niño years have a negative impact on these seals, causing females to spend extended durations foraging at sea, upwards of 20 days, which affects offspring growth and survival (Trillmich et al. 1986, Majluf 1987b). Adult females reveal patterns of site fidelity for pupping and are known to give birth within 20 m of a previous birth site (Gentry & Holt 1986, Majluf 1987b, Lunn & Boyd 1991, Harcourt 1992). This strong site fidelity makes both pups and adult females more vulnerable to environmental changes and anthropogenic influences that occur at rookery sites (Gentry & Holt 1986, Majluf 1987b, Lunn & Boyd 1991, Harcourt 1992).

Fur seal nourishment varies with prey source abundance and location; their diet is comprised of fish, crustaceans and mollusks. Peruvian fur seals are specialized foragers; their main prey sources include anchoveta (*Engraulis ringens*), red squat lobster (*Galathea squamifera*), and cephalopods (Vasquez 1995, Zavalaga et al. 1998, Arias-Schreiber 2000, 2003). However, other pelagic and demersal fish species like sardines (*Sardinops sagax*), mote sculpin (*Normanichthys crockeri*), chub mackerel (*Scomber japonicus*), Pacific jack mackerel (*Trachurus symmertricus*) and lanternfish species (*Myctophidae*) are consumed in smaller proportions (Arias-Schreiber 2003).

Additionally, a study by Vales et al. (2015) revealed that demersal and benthic prey are rarely in male fur seal diets.

Fishermen frequently complain that fur seals damage their nets and reduce their catches, especially in gillnet fisheries (Arias-Schreiber 1993, 2003), although studies by observers of artisanal fisheries in northern Chile never registered interaction with this species (Sepulveda et al. 2007, Bartheld et al. 2008). Fishermen have been known to occasionally kill fur seals with shotguns, harpoons, dynamite, and poison (Arias-Schreiber 1993). Arias-Schreiber (1993) reported that it is common for some fishermen to kill and use pinnipeds as bait to catch saltwater snails or winkles in Peru. Bycatch mortality is present from fishing nets also entangle and kill fur seals that are transiting between land and their feeding grounds (Majluf et al. 2002). Mortalities are also recorded in the Punta San Juan area due to hooks used by longline fisheries during the 2015-2016 ENSO (Colchao-Claux 2016). The overall impact of intentional and incidental fur seal mortality related to fishery activities is unknown. Additionally, industrial fishing fleets along the coast of Peru threaten the pelagic resources on which fur seals depend. These fisheries started in the 1950s and contributed to several declines in biomass of anchoveta upon which the fur seals depend on as their primary prey source (Pauly & Tsukayama 1987, Pauly & Palomares 1989).

South American Sea Lions

South American sea lions (*Otaria byronia*) reside along the South American coastlines from Brazil to Peru, including coastal islands like the Falkland and Galapagos islands (Vaz-Ferreira 1982b, Alonso et al. 2000, Dans et al. 2004, Perrin et al. 2009, Dassis et al. 2012). These sea lions are considered a non-migratory species, although individuals make seasonal movements away from rookeries abandoned over winter months (Pinedo 1990, Rosas et al. 1994). South American sea lions have two significant genetic differentiations between the Pacific and Atlantic coast populations due to prolonged geographical isolation (Gehara 2009, Committee on Taxonomy 2015). The species is monitored along its entire range around South America and its population status is of Least Concern (Túnez et al. 2007, Gehara 2009, Oliveira & Brownell 2014, Cardenas-Alayza et al. 2016), although, after the 1997/98 100% pup mortality event, sea lions along Peru were classified as “Vulnerable” by the Peruvian government, contradictory to the IUCN red list “Least Concern” classification (Oliveira 2011). The total population of South American sea lions is estimated at 445,000 individuals along its entire distribution, with the Peruvian population estimated at approximately 105,000 (IMARPE 2013, Cardenas-Alayza et al. 2016).

South American sea lions are sexually dimorphic with females reaching lengths of 2 m and weighing up to 170 kg, while males can reach 3 m and weigh upwards of 350 kg (Vaz-Ferreira 1982b, Rosas et al. 1993, Cappozzo & Perrin 2009, Perrin et al. 2009, Grandi et al. 2012, Riet-Sapriza et al. 2013). Sexual maturity is reached at approximately 4-5 years for females and 4-7 years for males (Vaz-Ferreira 1982b, Perrin et al. 2009, Grandi et al. 2012). Congregations of sea lions on rookeries occurs in early December for breeding and pupping, with breeding seasons lasting into late February (Sepúlveda et al. 2007, Perrin et al. 2009). The gestation period for this species lasts for approximately one year; pups are born in January and nursed for 8-12 months (Vaz-Ferreira 1982b, Perrin et al. 2009). Newborn pups weigh between 11-15 kg and are 75-85 cm long. (Vaz-Ferreira 1975). Following the birth of the pup, female sea lions generally breed within one week (Soto et al. 2004). Therefore, mature females can be in a perpetual state of pregnancy and nursing, both metabolically taxing processes. Successful foraging on energetically rich prey is key to the survivability of this species; extreme environmental fluctuations such as strong inter-annual ENSO events can place these sea lions in jeopardy.

South American sea lions are considered a neritic species and are commonly found foraging in the shallower water over the continental shelf and slope (Vaz-Ferreira 1982b, Campagna et al. 2001, Crespo et al 2007, Hückstädt et al. 2014). Females with nursing pups spend 53% of their time foraging at sea and the rest at rookeries or haul out sites (Perrin et al. 2009). However, diet and maternal care patterns suggest inter-annual fluctuations in food availability. In the variable Peruvian upwelling ecosystem, females adjust their diets and maternal attendance patterns in response to changes in the abundance and distribution of prey (Soto et al. 2006). During ENSO events when prey are less abundant near the rookeries, female sea lions are observed spending less time onshore nursing and more time foraging at sea. As a result, the fasting ability of pups was exceeded, causing higher mortality rates due to starvation (Soto et al. 2004, 2006).

Female sea lions primarily feed in shallow, coastal waters on benthic species, whereas males tend to feed predominantly on demersal-pelagic species (Crespo et al. 1997, Koen Alonso et al. 2000, Campagna et al. 2001, Drago et al. 2009). Female dives are typically shallow (19-60 m), and their dive profiles are flat-bottomed, indicating extended foraging at specific depths (Campagna et al. 2001). This dive profile pattern may be due to the shallow thermocline (< 50 m) found in the waters off the coastline of Peru during the normal state of upwelling (Morales et al. 1999). Male sea lions spend more time at sea than females, approximately 4-9 days versus 1-4 days, and travel greater distances, up to 300 km for males compared to 200 km for females. Considering the maximum width of the continental shelf along northern Peru is 130 km, it could be assumed that some sea lions may be foraging in pelagic waters off the continental shelf as well further north and south along the shelf (Vaz-Ferreira 1982b, Alonso et al. 2000, Campagna et al. 2001). Distinctions between foraging habits of male and female sea lions are not constant over time and are exemplified during pre-breeding periods (Drago et al. 2009, 2015). During this time, both males and females increase their consumption of pelagic prey versus benthic prey, although prey preference between males and females does not overlap This indicates that during the pre-breeding season, when areas around the rookeries are crowded and resource availability declines, sexual foraging segregation still takes place but normal foraging behavior is altered (Drago et al. 2015).

South American sea lions are considered generalist foragers that feed on a variety of prey which varies with geographical location. Prey types include benthic and pelagic fish, squid, crustaceans, birds, and, on rare occasions, marine mammals (Vaz-Ferreira 1982b, Harcourt 1993, Alonso et al. 2000, Soto et al. 2006, Perrin et al. 2009). A small percentage of subadult and adult male South American sea lions regularly attack, kill and eat South American fur seal pups, juveniles and sometimes, although rare, adult females in Peru (Harcourt 1992, 1993).

Little is known about the specific foraging habits of the sea lions along the Peruvian coast, and although they are known to feed on Peruvian anchoveta when the waters are rich in nutrients and highly productive, they are known to be generalist foragers. Besides targeted anchoveta prey consumption, Peruvian sea lions prey upon mote sculpin, lumptail sea robin, Peruvian hake, red squat lobster, and cephalopods

(Paredas & Arias-Schreiber 1999). During an ENSO event when anchoveta and squat lobster were not in high abundance, a larger diversity of prey species, particularly demersal fishes, were consumed. This indicates that when target prey are less available, sea lions respond to variation in prey abundance and accessibility by modifying their diet (Muñoz et al. 2011, Sepúlveda et al. 2015). Conversely, even though this species has been observed modifying forage habits, this seems to have little effect on their survival during strong enough ENSO events. With little known about the region's trophic structure during the productivity-challenging phases of El Niño, this leaves this species vulnerable to increased frequency and strengthened ENSO events in the future (Soto et al. 2004, 2006, Hückstädt et al. 2007).

Sea lions along the Peruvian coastline suffer frequent population declines due to prey loss during inter-annual-ENSO events (Grandi et al. 2012). The Peruvian sea lions suffered massive losses during the 1997/98 El Niño event with the population declining approximately 81% from 144,000 individuals in 1996 to 28,000 in 1998 (Arias-Schreiber & Rivas 1998, Arias-Schreiber 1998, Grandi et al. 2012, Oliveira 2011). This decline was most likely due to a combined effect of both mortality and dispersal from historically surveyed breeding and haul out sites. This strong magnitude ENSO (1997/98) also caused 100% pup mortality during the pupping season (Soto et al. 2004). Increases in foraging time have been linked to lower prey availability (Womble et al. 2014). Consistent with decreased prey availability, female Peruvian sea lions' forage trips lasted 10 to 20 days during an El Niño versus the usual 1 to 4 days, which presumably contributed to starvation of nursing pups (Oliveira 2011).

Stable Isotope Ratios

Stable isotopes are forms of the same elements that have an increased atomic mass due to the addition of one or two extra neutrons in the nucleus. Dissimilarities in the relative abundance of the light isotope (fewer neutrons) and heavy isotope (more neutrons) can be measured and expressed as a ratio, which is reported as parts per thousand (‰) (Fry 2006The stable carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotope ratios in an organism's tissue can be used to investigate their trophic ecology (DeNiro & Epstein 1978, 1981, Kelly 2000, Bearhop et al. 2002). Stable isotope studies are a valuable implement for examining the life history, diet, and habitat use in marine mammals (Peterson & Fry 1987, Kelly 2000). In fact, Hobson et al. (1997), Hirons (2001), Kurle and Worthy (2001), and Hückstädt et al. (2007) have all demonstrated that phocid and otariid tissues reflected trophic dynamics in their respective waters utilizing $\delta^{13}C$ and $\delta^{15}N$. Pinniped tissues can be used as biological recorders for temperature, salinity, and pH as well as being indicators of feeding history, trophic level, and metabolic rate (Peterson & Fry 2016).

Marine environments contain stable isotope ratios of carbon ($^{13}C/^{12}C$ or $\delta^{13}C$), which result from fractionation differences originating at the base of the food web. Stable carbon experiences a small fractionation generally less than 1‰ during assimilation; and therefore, carbon signatures can be used to trace the importance of different carbon pools to a consumer or determine the source of carbon at the base of the food web (O'Leary 1981, France 1995, Gannes et al. 1998, Kelly 2000). Variations in $\delta^{13}C$ values are indicative of plants (i.e., phytoplankton, algae) utilizing either the C_3, C_4, or crassulacean acid metabolism (CAM) photosynthetic pathways (DeNiro & Epstein 1978). An animal's diet and the primary production at the base of the food web, as well as geographic variability, can be detected in $\delta^{13}C$ (DeNiro & Epstein 1978, Hirons et al. 2001, Dehn et al. 2007, Newsome et al. 2007).

Marine environments contain naturally occurring stable nitrogen isotope ratios ($^{15}N/^{14}N$ or $\delta^{15}N$), which provide information on potential food sources as well as trophic position. Throughout assimilation of proteins, ^{14}N is preferentially used due to its lighter nature, which increases the ratio of ^{15}N to ^{14}N in the tissues of the consumer relative to its food source (Gannes et al. 1998), creating a step-wise enrichment of 3-5‰ per trophic level (DeNiro & Epstein 1981, Fry 1988, Hobson et al. 1997). The comparison of consumer tissue $\delta^{13}C$ and $\delta^{15}N$ with those of their potential prey items provide information regarding food web linkages and ocean productivity (France & Peters 1997, Hirons 2001, Kurle & Worthy 2001). Pinnipeds are apex predators; this requires them to eat more prey items to sustain themselves, thus making them susceptible to changes in food web production. Periods when production is very high or very low alters the length of the food webs and may change the trophic level of the marine mammals' prey. The comparison of pinniped $\delta^{13}C$ and $\delta^{15}N$ with their potential prey items provides information regarding food web linkages and ocean productivity as well as geographic location (Polovina et al. 1995, France & Peters 1997, Hirons 2001, Kurle & Worthy 2001).

Vibrissae (whiskers) are continuously growing, inert tissue composed of proteinaceous keratin (Rubenstein and Hobson 2004, Hall-Aspland et al. 2005). Metabolically inert tissues preserve information from the moment they develop, thereby allowing the study of dietary change (Darimont et al. 2002, Bearhop et al. 2004, Hall-Aspland et al. 2005, Rosas-Hernandez 2018). The most recent growth of a whisker is located at the base, and a single whisker can provide one or more years of information, making this tissue suitable for various types of foraging studies (Rubenstein and Hobson 2004, Lewis et al. 2006, Hirons 2001, Hirons et al. 2001, Ginter et al. 2012, Rosas-Hernandez 2018). While there are currently no published data on the growth rates of South American fur seal and South American sea lion vibrissae, otariids show great variability in their whisker growth rates, ranging from 0.02 to 0.16 mm/day in adults. This highlighting the importance of assessing growth rates on a species to species basis (Mote-Herrera 2011, Kernaleguen 2012, Kernaleguen 2015, McHuron et al. 2016, Rosas-Hernandez 2018). Some Otariidae species evaluated for whisker growth rates include Antarctic fur seal (*Arctocephalus gazella*), Steller sea lion (*Eumetopias jubatus*), California sea lion (*Zalophus californianus*) and the northern fur seal (*Callorhinus ursinus*) (Hirons et al. 2001, Cherel et al. 2009, Rea et al. 2015, Kelleher 2016, McHuron et al. 2016).

Stable nitrogen and carbon isotope ratios (δ^{15}N and δ^{13}C) were used to evaluate the impact the environment has on the seals' diet on a time scale represented along the vibrissae. The δ^{13}C indicated the changes in primary production, likely due to changes in upwelling strength, in foraging locations within that individual's environment (Fry 1988, Hobson et al. 1997), while the δ^{15}N revealed changes in the length of the marine food web (Minigawa & Wada 1984, Hobson et al. 1997, Hirons 2001). The δ^{15}N can detect shifts in the trophic levels of marine organisms, which, in tandem with δ^{13}C, is an indication of periods of very low or high production (Fry & Sherr 1984, Hobson & Welch 1992, Hirons 2001). Since δ^{15}N and δ^{13}C can define differences in foraging locations and trophic levels, we can relate inter-annual variability of the ecosystem, such as an ENSO event, to the respective time-periods along the whisker (Lowther & Goldsworthy 2011).

METHODS

Permits

All samples were collected following methods approved under research permits Resolución Jefatural No. 009-2010-, No.023-2011-, No. 022-2012-, No. 008-2015-, and 019-2016-SERNANP-RNSIIPG issued by the Peruvian National Service of Natural Protected Areas (Spanish acronym SERNANP) and the Peruvian Ministry of the Environment (Spanish acronym MINAM). SERNANP. Personnel of the Punta San Juan Program and the Chicago Zoological Society collected all tissue samples.

Sample Collection

Vibrissae were collected annually between the years 2010 and 2016 as part of population health monitoring program at the Punta San Juan guano reserve (PSJ) in the province of Ica in southern Peru (15°22’ S, 75°11’ W) (Figure 1). This reserve is one of the largest Peruvian fur seal and sea lion rookeries in Peru, serving as an ideal location to assess both of these pinniped populations. Animals were anesthetized for sample collection under the supervision and direction of Dr. Michael Adkesson of the Chicago Zoological Society.

Veterinarians removed Peruvian fur seal whiskers from live animals every November/December during 2010, 2011, 2012, 2014, 2015, and 2016 (Table 1). Vibrissae from twenty-nine adult female fur seals were collected and analyzed in 2010. Six adult male and six adult female fur seal vibrissae (n=12) were analyzed in 2011, and in 2012 five male and six adult female fur seal vibrissae (n=11) were analyzed for stable carbon and nitrogen isotope ratios. Vibrissae from six mother (dam)-pup pairs (n=12) were analyzed in 2015 and in 2016 vibrissae from six adult males were analyzed. Vibrissae from six subadult male South American sea lions, a sympatric species to the Peruvian fur seal within this rookery, were collected in February/March 2011.

Table 1. Total number of pinniped vibrissae analyzed in this study, including year sampled, mean vibrissae length, and associated gender and species. Aa = Arctocephalus australis unnamed ssp., Ob = Otaria byronia.

SPECIES	**SAMPLE YEAR**	**TOTAL N**	**LENGTH x ± SD; cm**	**FEMALE N**	**MALE N**	**PUP N**
Aa	2010	29	11.73 ± 2.69	29	-	-
	2011	12	15.21 ± 4.24	6	6	-
	2012	11	12.79 ± 2.61	6	5	-
	2015	12	8.21 ± 2.75	6	-	6
	2016	6	10.33 ± 1.92	-	6	-
Ob	2011	6	17.33 ± 4.60	-	6	-

Laboratory Analyses

Pinniped vibrissae (whiskers) were scrubbed using a scrubbing pad and rinsed with deionized water to remove any surface contaminants. Once thoroughly dried at 60° C for at least 24 hours, whiskers were cut into 2.5 mm sections from base to tip, each section representing 0.6-0.8 mg, and placed in individual tin capsules. Approximately 20 samples were analyzed per vibrissae, using alternating segments as pseudo-replicates in case of loss during mass spectrometer analysis. All vibrissae techniques followed the methods of Hirons (2001). Samples were combusted and analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the Smithsonian Institution's Museum Conservation Institute (Suitland, MD) using a Thermo Delta V Advantage mass spectrometer in continuous flow mode coupled to a Costech 4010 Elemental Analyzer (EA) via a Thermo Conflo IV (CF-IRMS). A set of standards were run for every 10-12 samples. The standards included USGS40 and USGS41 (L-glutamic acid) as well as Costech acetanilide. All samples and standards were run with the same parameters; this included an expected reproducibility of the standards $\leq 0.2‰$ (1σ) for both $\delta^{13}C$ and $\delta^{15}N$. Stable isotope values were expressed in terms of δ and were reported relative to the standard reference material, Vienna Pee Dee Belemnite (VPDB) standard for $\delta^{13}C$ and atmospheric air (N_2) for $\delta^{15}N$.

Stable isotope values were reported with the standard parts per thousand notation (‰):

$$\delta = [R_{sample} / R_{standard} - 1] * 1000$$

Environmental data such as sea surface temperature (SST) and sea surface temperature anomaly (SSTA) were obtained from the National Oceanographic and Atmospheric Administration's (NOAA) Teleconnections ENSO website (http://www.cpc.ncep.noaa.gov/data/indices/sstoi.indices). NOAA_ERSST_V5 data were obtained from NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, (https://www.esrl.noaa.gov/psd/). Sea surface temperature anomaly (SSTA) (º C) was used as our proxy for ENSO conditions. Data were collected from Extended Reconstructed Sea Surface Temperature (ERSST.v5) dataset which is a global, monthly SST analysis derived from the International Comprehensive Ocean-Atmosphere Dataset (ICOADS). The ERSST.v5 dataset includes information from modern buoy observation, Argos-profiling CTD floats, global drift buoys like ICOADS R3.0 (from R2.5), and

Hadley Centre Ice-SST version 2 (HadISST2) sea ice concentration (Huang et al. 2014, Liu et al. 2014, Huang et al. 2015, Huang et al. 2017).

Statistical Analysis

Statistical evaluations were done on the Peruvian fur seal population, which included both males and females, a gender differential evaluation of the PFS, PFS mom-pup pairing evaluation, and a species differential evaluation between male Peruvian fur seal and male South American sea lion. Descriptive statistics for vibrissae data, including range, mean and standard deviation for stable isotope values, were calculated using Microsoft Excel (v. 14.7.2; Microsoft Corporation). Using the statistical package R, both covariance and correlation were calculated between $\delta^{13}C$ and $\delta^{15}N$, $\delta^{13}C$ and SSTA for 1+2 region, and $\delta^{15}N$ and SSTA for 1+2 region for both species and gender. Pearson's correlations were used when the parametric assumptions were met; however, some non-parametric correlations, for sample sizes greater than 30, (Kendall's tau correlation) were used when datasets were unable to be transformed to meet the parametric assumptions. Covariances were assessed to detect how changes in SSTA were associated with changes in vibrissae $\delta^{13}C$ and $\delta^{15}N$. Correlations tested the strength of relationships between the stable isotope ratio of the vibrissae and ENSO conditions, SSTA. An independent two-sample t-test tested the overall difference in stable isotope signatures between adult male and female PFS. A paired two-sample t-test compared the dam-pup pairings' $\delta^{13}C$ and $\delta^{15}N$. In JMP (v. 12.1.0; SAS Institute Inc.) An analysis of variance (ANOVA) for each stable isotope assessed species and gender effect while a multivariate analysis of variance (MANOVA) was used to assess the effect of SSTA on the $\delta^{13}C$ and $\delta^{15}N$ in vibrissae for both species and genders. PRIMER (v. 7.0.13; PRIMER-e, Quest Research Limited) software was used to conduct all additional analyses including a non-parametric one-way analysis of similarity (ANOSIM) test was used to evaluate the differences between both stable isotope values (2004-2016) with varying SSTA using Euclidean dissimilarity. The significance level for all tests was established at $\alpha = 0.05$.

RESULTS

ENSO Conditions

The Niño 1+2 region is the smallest and eastern-most of the Niño regions (0-10°S, 90°W–80°W), developed to understand the effects of ENSO on the coast of Peru (Figure 1). The 1+2 index shows the largest variance of all the Niño indices. Figure 3 chronicles the ENSO cycle for the 1+2 Nino Index from 2000-2017. Sea surface temperature anomalies (SSTA) are the departure from average SST conditions from the top 0.01 mm of ocean surface. SSTA readings between -0.5 to 0.5° C are a classified ENSO Norm, average SST conditions. SSTA readings classified beyond ENSO Norm are as follows: ±0.5-1°C (weak), ±1-1.5°C (moderate), ±1.5-2°C (strong), ±2-2.5°C (very strong), ± >2.5°C (extreme). Positive anomaly readings reflect the warm phase El Niño periods while the negative anomalies reflect the cool phase La Niña periods. These oscillations reveal frequent, variable ENSO conditions over the past 17 years, with more pronounced cool phase conditions from 2000 until 2014 and warm phase conditions dominated through 2017 (Figure 3). The overall trend of SSTA has increased over 1°C from 2000 through 2017 in correspondence to more frequent and increasingly stronger ENSO events.

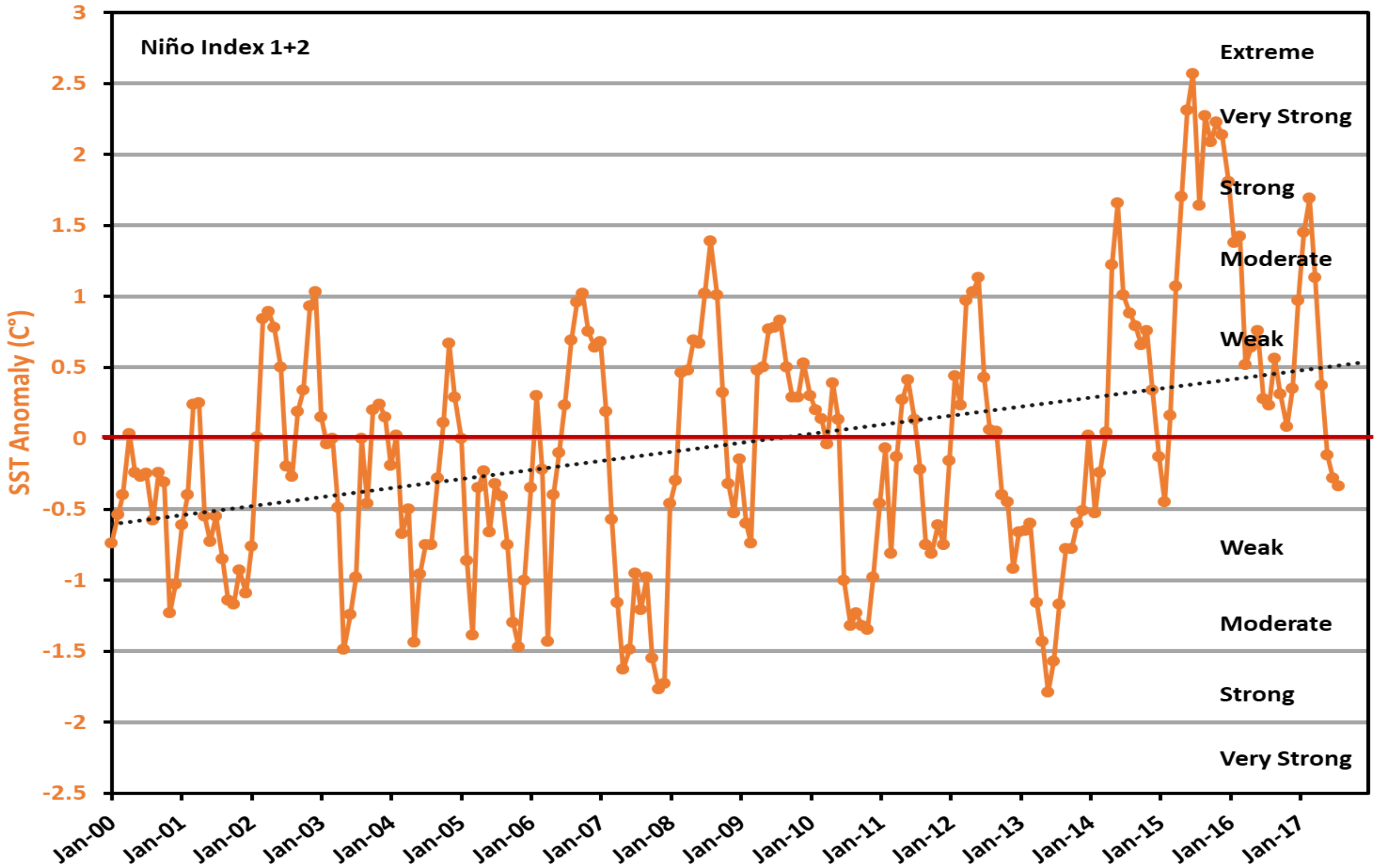

Figure 3. Sea surface temperature anomaly (SSTA) time series for Nino index 1+2 from 2000-2017 (NOAA_ERSST_V5 data provided by the NOAA/OAR/ESRL PSD). Positive anomalies represent warm periods (El Niño) and negative anomalies represent cold periods (La Niña).

Vibrissae

Seventy-six individual pinniped vibrissae were sampled, 70 Peruvian fur seals *Arctocephalus australis* unnamed ssp. and 6 South American sea lions *Otaria byronia*. Adult female fur seals had the highest number of collected individuals (N=47), followed by adult male PFS (N=17), PFS pups (N=6), and subadult SASL (N=6). The sample years included 2010 (N=29), 2011 (N=18), 2012 (N=11), 2015 (N=12), and 2016 (N=6) (Table 1).

Hobson et al. (1997), Hirons (2001), Kurle and Worthy (2001), and Hückstädt et al. (2007) have all demonstrated that otariid tissues can reflect trophic dynamics and production in their respective waters utilizing $\delta^{13}C$ and $\delta^{15}N$. Stable nitrogen isotope ratios ($\delta^{15}N$) detect shifts in trophic levels while stable carbon isotope ratios ($\delta^{13}C$) indicate low or high production due to carbon source in foraging location (Fry & Sherr 1984, Hobson & Welch 1992, Hirons 2001). Since $\delta^{13}C$ and $\delta^{15}N$ represent specific time periods related to vibrissae growth, these values and their meaning can be related to inter-annual SSTA in the ecosystem.

The most recent vibrissa growth is located at the base of the whisker, and an individual whisker can represent several years' growth (Hirons 2001, Hirons et al. 2001, Ginter et al. 2012). The vibrissae growth rate used for both pinniped species in this study was based on Kelleher's (2016) northern fur seal growth rate of 0.09 mm/day. Each 2.5 mm segment in an analyzed vibrissa represented approximately 28 days. With an average of 12.31 ± 3.28 cm in length for adult PFS whiskers, individual whiskers represented 45.6 ± 12 months (3.8 ± 1 years) on average. By analyzing monthly means of individual seals' isotopic signatures, a mean for both $\delta^{13}C$ and $\delta^{15}N$ can be acquired on a monthly scale for the overall population. Across all the sampled vibrissae, a total of 12 years' stable isotope data were recorded.

Vibrissae are metabolically inert tissues that preserve dietary information from the moment they develop. Segmented vibrissae can, therefore, provide a series of isotopic signatures that can be correlated to time of growth. This allows for the evaluation of changes in assimilated prey nutrients over time (Darimont et al. 2002, Bearhop et al. 2004, Hall-Aspland et al. 2005, Rosas-Hernandez 2018). The period represented by the vibrissa from base (the most recent growth) to tip (the oldest growth) was then nested with monthly sea surface temperature anomaly averages. The nesting of SSTA monthly averages with associated dates along a vibrissa allowed for the evaluation of abiotic conditions with vibrissae stable isotope values.

Peruvian Fur Seal Population

Of the 70 Peruvian fur seals sampled, 67% were reproductively mature, adult females, 24% were adult males, and 9% were pups with unidentified genders. The vibrissae stable isotope data from individuals are summarized in Table 4 and individual vibrissa figures are located in Appendix B. All fur seal vibrissae had $\delta^{13}C$ values that ranged from -18.13 to -13.17 ‰ with a mean of -14.31 ± 0.31‰ and $\delta^{15}N$ that ranged from 15.83 to 22.31‰ with a mean of 19.08 ± 0.83‰.

Similar oscillating patterns were observed in both isotope ratios across all vibrissae lengths; however, male fur seals had consistently more enriched $\delta^{13}C$ and $\delta^{15}N$ than females. The $\delta^{13}C$ and $\delta^{15}N$ monthly means from 47 adult female and 17 adult male PFS vibrissae, representing 2004-2016, showed covarying oscillations until 2015 (Figure 4). Both $\delta^{13}C$ and $\delta^{15}N$ exhibited an average decline (0.6‰ and 2.2‰, respectively) from 2004-2009 but in the course of one year (mid-2010 to mid-2011), $\delta^{15}N$ returned to the enriched values of ca. 2006 while $\delta^{13}C$ continued to become 0.3‰ more depleted until late spring of 2011. PFS signatures from 2011 to late 2014 showed a nearly identical, $\delta^{15}N$ decline to those values exhibited by seals from 2004-2009. However, from 2015 through 2016, an inverse stable isotope pattern arose throughout the portion of the population sampled. In the span of 11 months (mid-2015 to mid-2016), $\delta^{13}C$ increased 0.9‰ and then declined 0.7‰ while $\delta^{15}N$ declined 1.3‰ and then increased 2.1‰. Both male and female fur seal vibrissae exhibited nearly identical mean stable isotope patterns, but male fur seals exhibited more enriched values than females in both stable isotopes by up to 0.5‰ ($\delta^{13}C$) and 1.5‰ ($\delta^{15}N$) (Figure 5). Both periods (2010-2011, 2015-2016) corresponded to a moderately strong, persistent La Niña phases (ca. 3+ years) followed by an abnormally extended warm period, each approximately 3-4 years in duration (Figure 3).

Peruvian fur seal $\delta^{13}C$ (Figure 4) exhibited minor fluctuations from 2004 to 2009 (-14.08 to -13.59‰ (Δ 0.49‰)); however, $\delta^{13}C$ was highly variable from 2010 through 2016 (-15.09 to -13.80‰) (Δ 1.29‰). Additionally, from late 2015 through 2016, $\delta^{13}C$

resembled those previously recorded in 2004-2009, where δ^{13}C ranged -14.46 to -13.80‰ (Δ 0.66‰). The δ^{13}C values from 2010-2014 were the most depleted (-14.42 ‰) and had the largest range, -15.09 to -13.91‰ (Δ 1.18‰) across all years of the study.

In contrast to the PFS δ^{13}C, δ^{15}N had much larger fluctuations (Figure 4). From late 2004, the earliest stable isotope data recorded, through 2009, δ^{15}N decreased 2.41‰. The δ^{15}N ranged from 18.40 to 20.81‰. Following this nearly six-year gradual depletion in δ^{15}N, a rapid, approximately 2‰ enrichment, occurred between 2010 and 2011, after which the δ^{15}N returned to levels recorded in previous years (ca. 2004/2005). Figure 4 shows a gradual decline of 4.35‰ in δ^{15}N starting from 20.84‰ and decreasing to 16.49‰ which took place from the beginning of 2012 until 2016. Data from the remainder of 2016 showed a steep enrichment from 17.00 to 18.56‰ (Δ 1.56‰).

A Kendall's tau correlation assessed the relationship between ever-changing SSTA and PFS stable isotope signatures across all 12 years from November 2004 through 2016. PFS mean δ^{13}C did not correlate with SSTA over the 12-year period (p=0.301). However, δ^{13}C signatures did significantly correlate with SSTA over a shorter period of 7-years, 2009 through 2016 (p=0.040). A one-way ANOVA revealed that population δ^{13}C did not significantly change with fluctuating SSTA (p=0.140). An ANOVA also showed no relationship between population δ^{13}C and δ^{15}N (r= 0.266 and p=0.301). A significant inverse correlation existed between the mean δ^{15}N and SSTA (r= -0.254 and p<0.001). Warmer temperature anomalies correlated to more depleted δ^{15}N signatures. PFS whisker δ^{13}C and δ^{15}N did not correlate over the entire 12-year period (p=0.081). Pearson's correlation coefficient showed δ^{13}C and δ^{15}N were significantly inversely correlated during the 2014-2016 ENSO event (p=0.002).

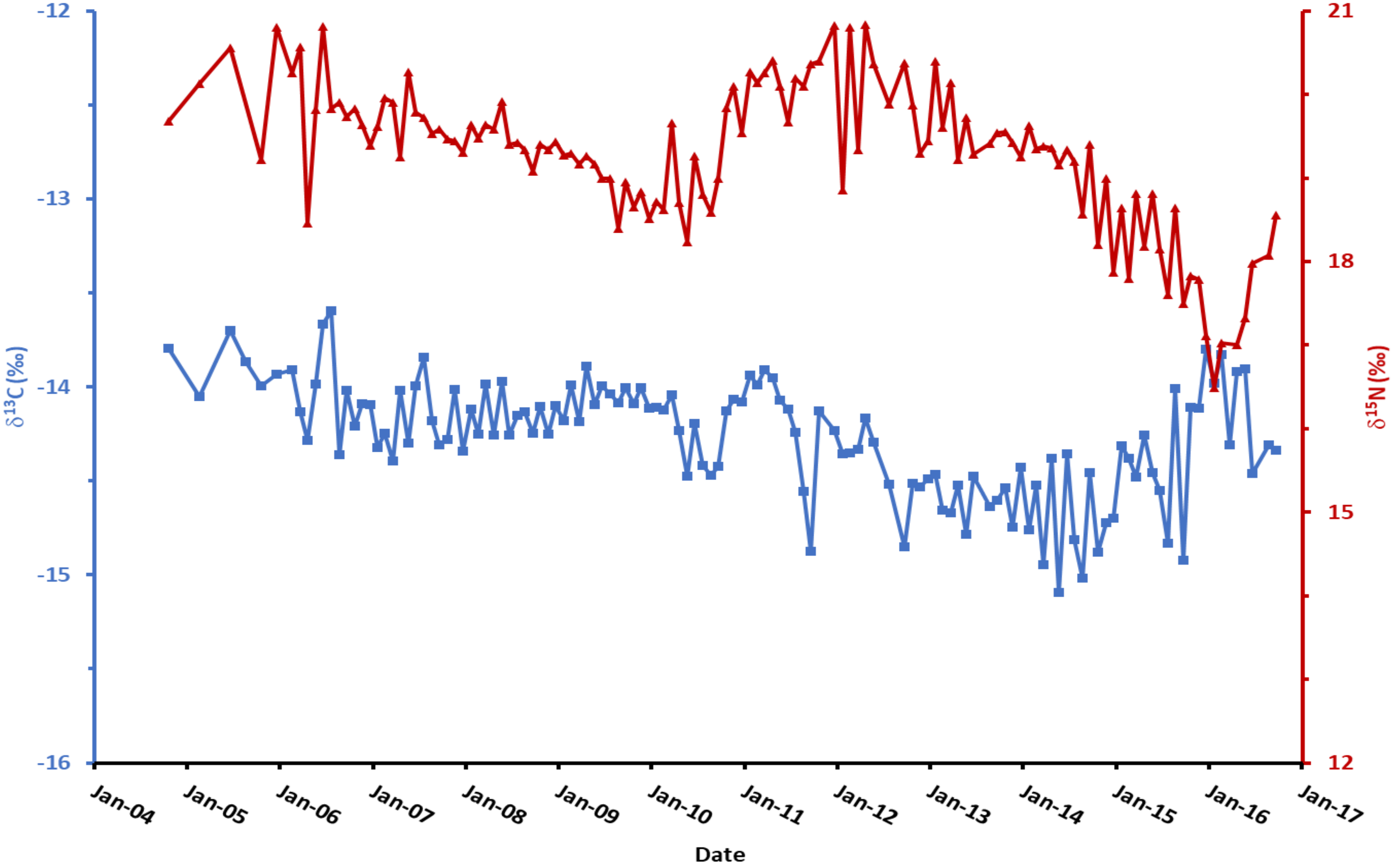

Figure 4. Peruvian fur seal population δ^{13}C (blue) and δ^{15}N (red) in parts per thousand (‰), 2004-2016.

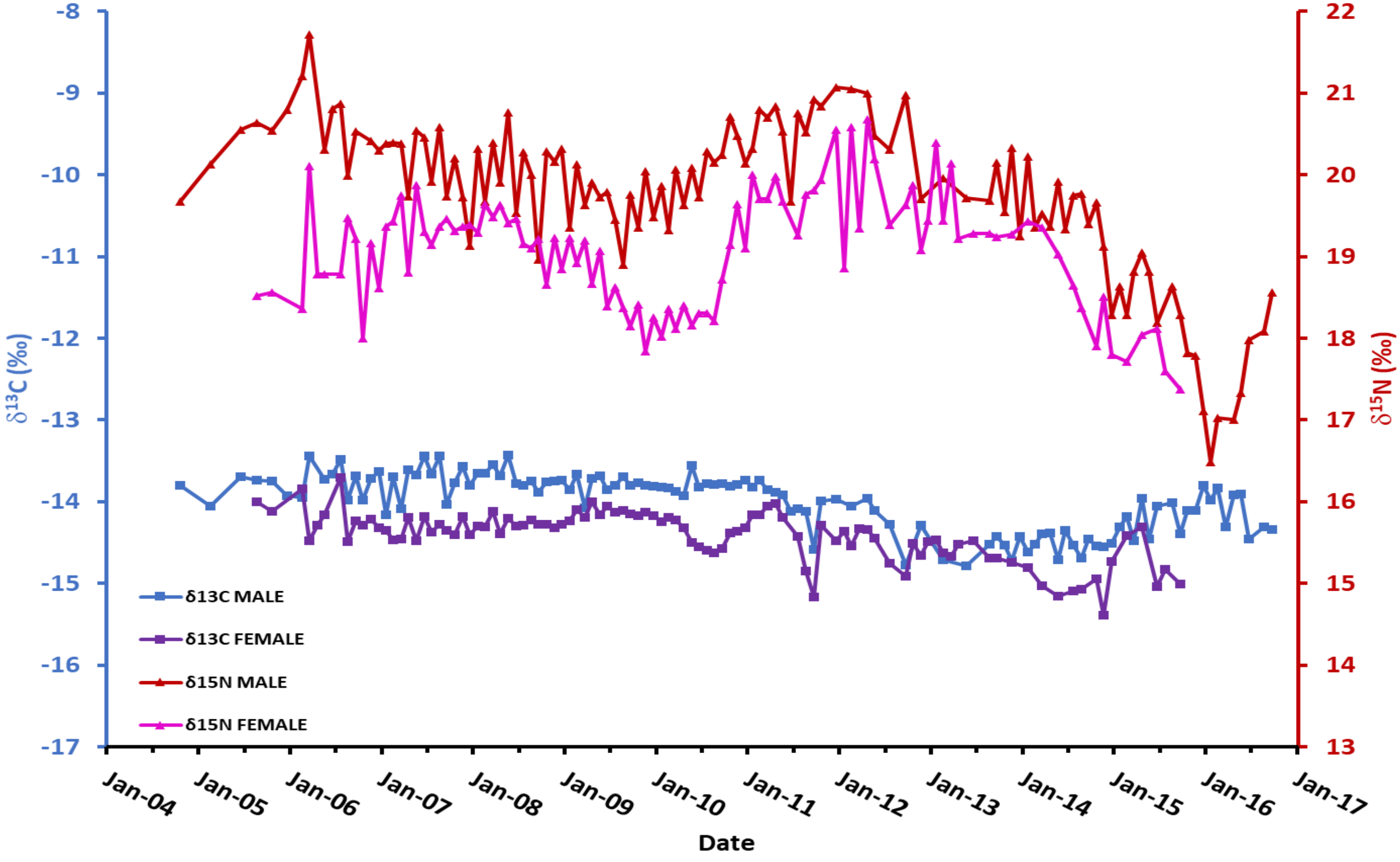

Figure 5. Peruvian fur seal male δ^{13}C (blue), δ^{15}N (red) and female δ^{13}C (purple), δ^{15}N (pink) in parts per thousand (‰), 2004-2016.

Principal component analysis (PCA) of PFS male and female (population) $\delta^{13}C$ and $\delta^{15}N$ and SSTA factored by year revealed a grouping of years 2014, 2015 and 2016 (Strong to Extreme ENSO condition years) compared to all other years evaluated (Figure 6). According to the angle of the vectors, $\delta^{13}C$ and $\delta^{15}N$, as well as $\delta^{13}C$ and SSTA are not strongly correlated variables (~90°); however, $\delta^{15}N$ and SSTA are negatively correlated variables (>180°). The circle is used for the vector lengths demonstrating whether variables were represented enough in the data in order for properly infer relationships between variables; all variables in this PCA were equally represented. The vectors of this PCA indicated a strong correlation between stable isotope signatures with increasing SSTA during 2015 and 2016.

Analysis of variance (ANOVA) revealed a significant correlation between increasing SSTA and depleted $\delta^{15}N$ ($P<0.001$). A one-way ANOVA revealed a significant correlation ($p<0.001$) between $\delta^{15}N$ and ENSO phase (i.e. cold, norm, warm SST); greater variation in SSTA and most depleted $\delta^{15}N$ occurred during warm phases while cold phases had consistently enriched $\delta^{15}N$. Increasing magnitude of ENSO conditions (i.e. weak, moderate, strong, very strong, extreme) revealed significant correlation to depleted $\delta^{15}N$, where strong, very strong and extreme magnitude conditions were all below PFS population mean $\delta^{15}N$ of 19‰, whereas norm, weak and moderate magnitudes of ENSO conditions all varied at or slightly above the mean PFS population $\delta^{15}N$ ($p=0.009$).

A one-way analysis of similarity (ANOSIM), testing differences in mean vibrissae $\delta^{13}C$ and $\delta^{15}N$ with SSTA factored by year revealed a significant difference between years ($p=0.001$; $r=0.467$), indicating stable isotopes did vary with SSTA among years. A year-to-year comparison revealed that 2015 and 2016 were significantly distinct from 2005 through 2014 ($p=0.001$ to 0.006, $r=0.566$ to 0.981).

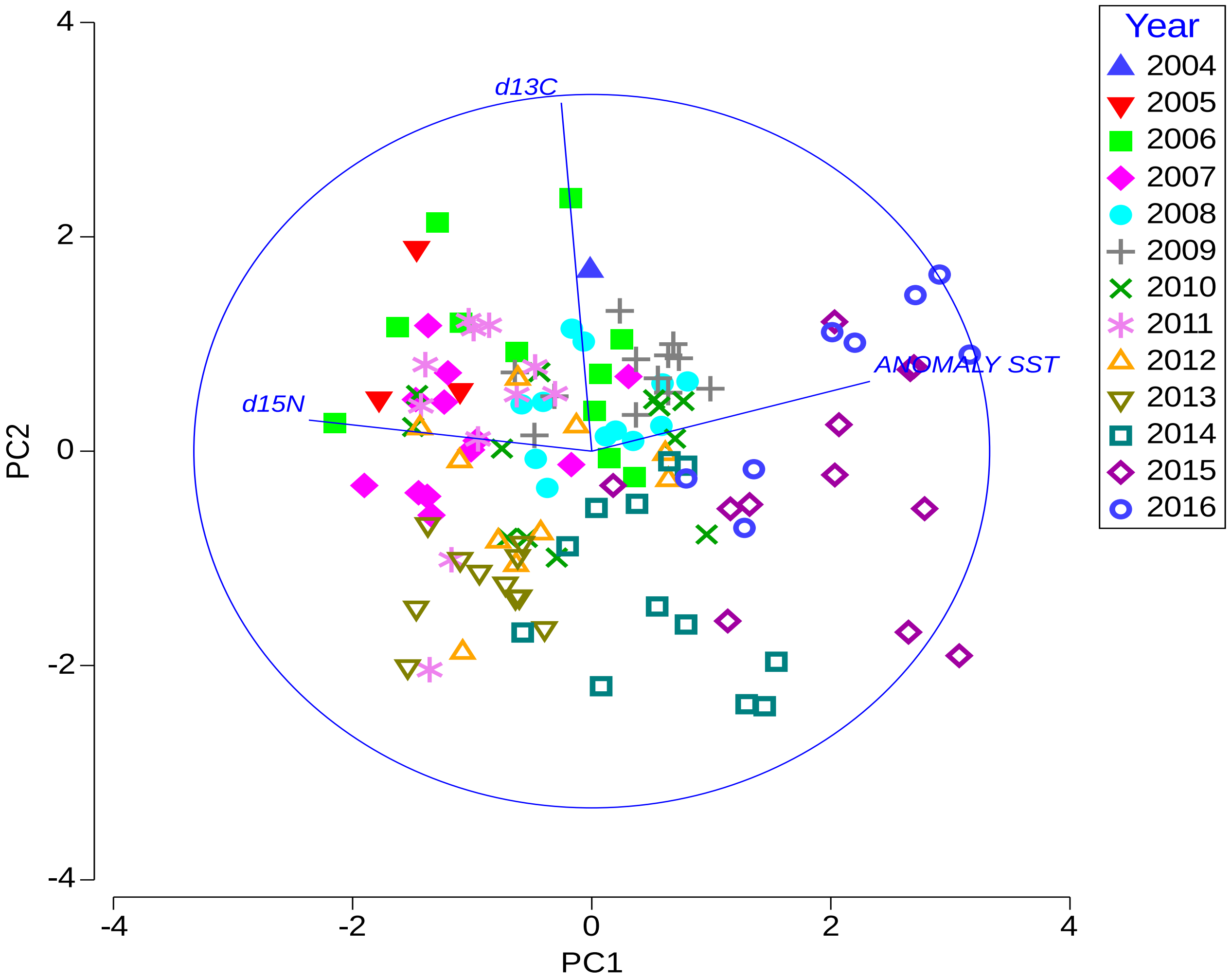

Figure 6. Principal component analysis of mean Peruvian fur seal population vibrissae $\delta^{13}C$, $\delta^{15}N$ and sea surface temperature anomaly factored by year (2004-2016).

Peruvian Fur Seal Males

Vibrissae stable isotopes from adult male fur seals spanned a total of 12-years (2004-2016); vibrissae were collected in 2011, 2012, and 2016. A Kendall's tau correlation revealed that male $\delta^{15}N$ were significantly inversely correlated to SSTA ($r= -0.292$ and $p<0.001$), while $\delta^{13}C$ was not ($r= -0.107$ and $p=0.084$). However, a Kendall's tau correlation between $\delta^{13}C$ and $\delta^{15}N$ revealed a significant correlation between the two stable isotopes ($r=0.227$ and $p=0.002$); as $\delta^{13}C$ became enriched, $\delta^{15}N$ became more enriched. Male $\delta^{13}C$ ranged (Figure 7) between -14.16 and -13.44‰ from November 2004 until mid-2011; at that time a single $\delta^{13}C$ decrease of 0.67‰ occurred during a 4-month period. Proceeding this unusual drop, $\delta^{13}C$ rebounded back to -14.00‰ in one month followed by a depletion of 0.84‰ over a 20-month period. Vibrissae $\delta^{13}C$ from mid-2013 until early 2016 showed a steady enrichment of 1‰, until the latter part of 2016; $\delta^{13}C$ had not rebounded to values seen in earlier years (ca. 2004-2011), indicating that the environment was more depleted in $\delta^{13}C$ than seen in previous years.

Adult male $\delta^{13}C$ ranged ~2‰ from -15.16 to -13.17‰ with a mean -14.01 ± 0.26‰. Male $\delta^{15}N$ ranged ~6‰ from 16.18 to 22.31‰ with a mean 19.66 ± 0.89‰. Male PFS $\delta^{15}N$ were their most enriched in mid- 2006 (21.72‰) and most depleted in early 2016 (16.49‰), a total decline of 5.23‰ over ten years. Patterns of ~2‰ enrichment followed by a ~2‰ depletion seemed to be the natural trend of $\delta^{15}N$ for eight years (Figure 8). From late 2004 to mid-2006, a 2.04‰ enrichment occurred followed by a depletion of 2.82‰, which lasted until mid-2009; followed by an enrichment of 2.17‰ until early 2012. Following these oscillations, a steady decline of 4.58‰ occurred until early 2016 when a drastic increase of 2.07‰ in $\delta^{15}N$ occurred through 2016. However, even after this drastic enrichment, $\delta^{15}N$ was still 1.56‰ below the mean male vibrissae of 20.12‰.

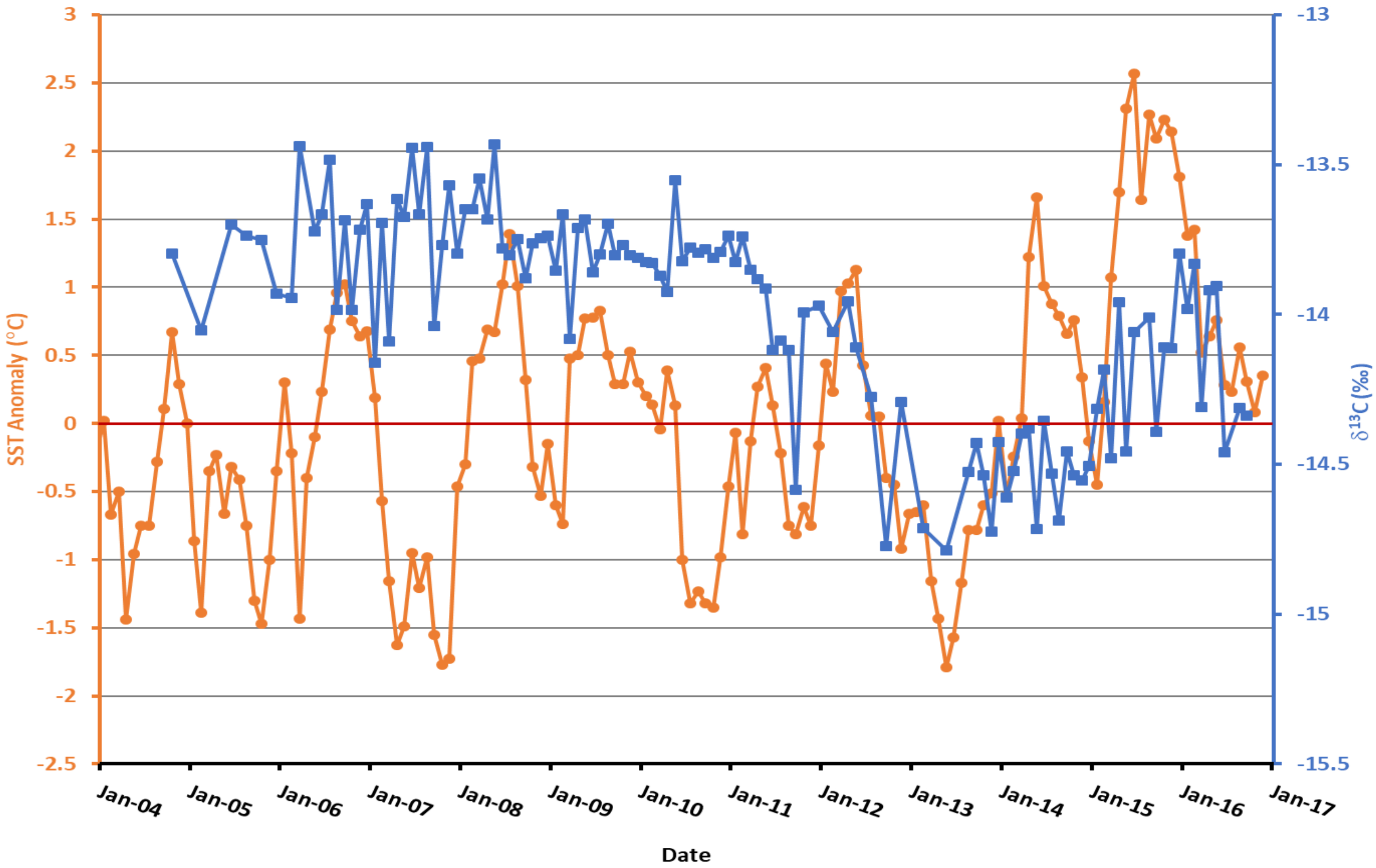

Figure 7. Male Peruvian fur seal $\delta^{13}C$ (blue) in comparison to sea surface temperature anomaly (orange), 2004-2016.

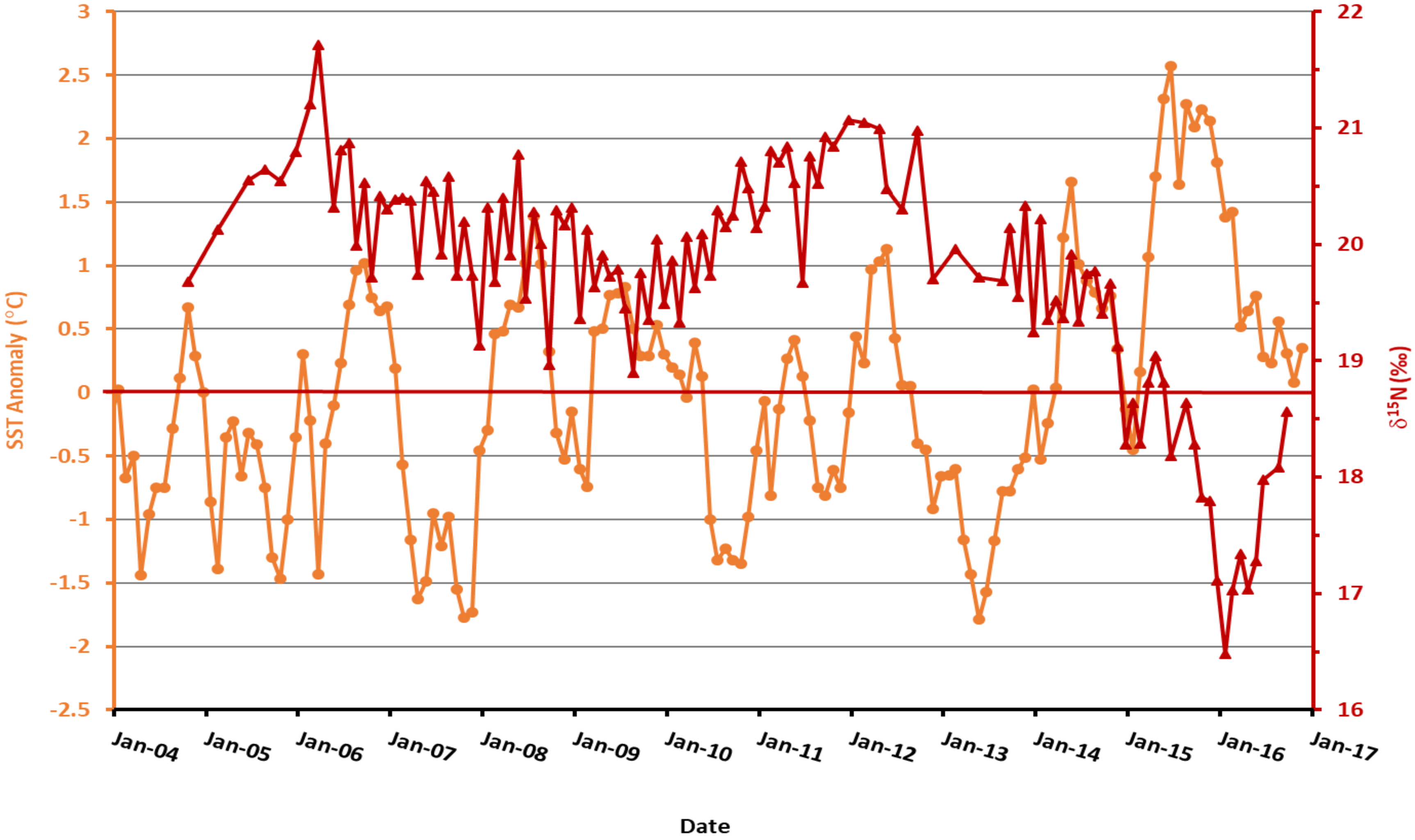

Figure 8. Male Peruvian fur seal δ^{15}N (red) in comparison to sea surface temperature anomaly (orange), 2004-2016.

Principal component analysis of PFS male mean $\delta^{13}C$ and $\delta^{15}N$ and SSTA factored by year (2004-2016) showed 2015 and 2016 were distinct from all other years (Figure 9). Similarly to the population PCA analysis, the angle of the vectors, $\delta^{13}C$ and $\delta^{15}N$, as well as $\delta^{13}C$ and SSTA are not strongly correlated variables (~90°); however, $\delta^{15}N$ and SSTA are negatively correlated variables (>180°), and all variables were equally represented. The vectors of this PCA indicated distinct depletion in $\delta^{15}N$ with increasing SSTA and little variation in $\delta^{13}C$, with exception to the years 2015 and 2016.

An ANOVA showed a significant correlation between increasing SSTA and decreasing $\delta^{15}N$, and $\delta^{15}N$ enrichment with negative SSTA conditions ($p<0.001$). A one-way ANOVA of $\delta^{15}N$ by ENSO phase (i.e. cold, norm, warm) revealed a significant correlation ($p<0.013$). During warm phases, $\delta^{15}N$ was more depleted while $\delta^{15}N$ was consistently enriched during cold phases. The magnitude of ENSO event (SSTA) did not correlate to either $\delta^{13}C$ or $\delta^{15}N$ ($p=0.573$). Although $\delta^{13}C$ did not show a significant change with fluctuating SSTA, $\delta^{13}C$ and $\delta^{15}N$ were significantly correlated; as $\delta^{13}C$ became more enriched, $\delta^{15}N$ also became more enriched ($p=0.008$). An ANOSIM revealed a significant difference in $\delta^{13}C$ and $\delta^{15}N$ to relative to SSTA between years ($p=0.001$; $r=0.507$). Additionally, the years 2013, 2014, 2015 and 2016 were different from 2004 through 2012 ($p=0.001$ to 0.006, $r=0.566$ to 0.981). Furthermore, 2013 and 2014 were significant different from 2015 and 2016 ($p=0.001$ to 0.003; $r=0.595$ to 0.953). No significant difference occurred between 2015 and 2016 ($p=0.297$).

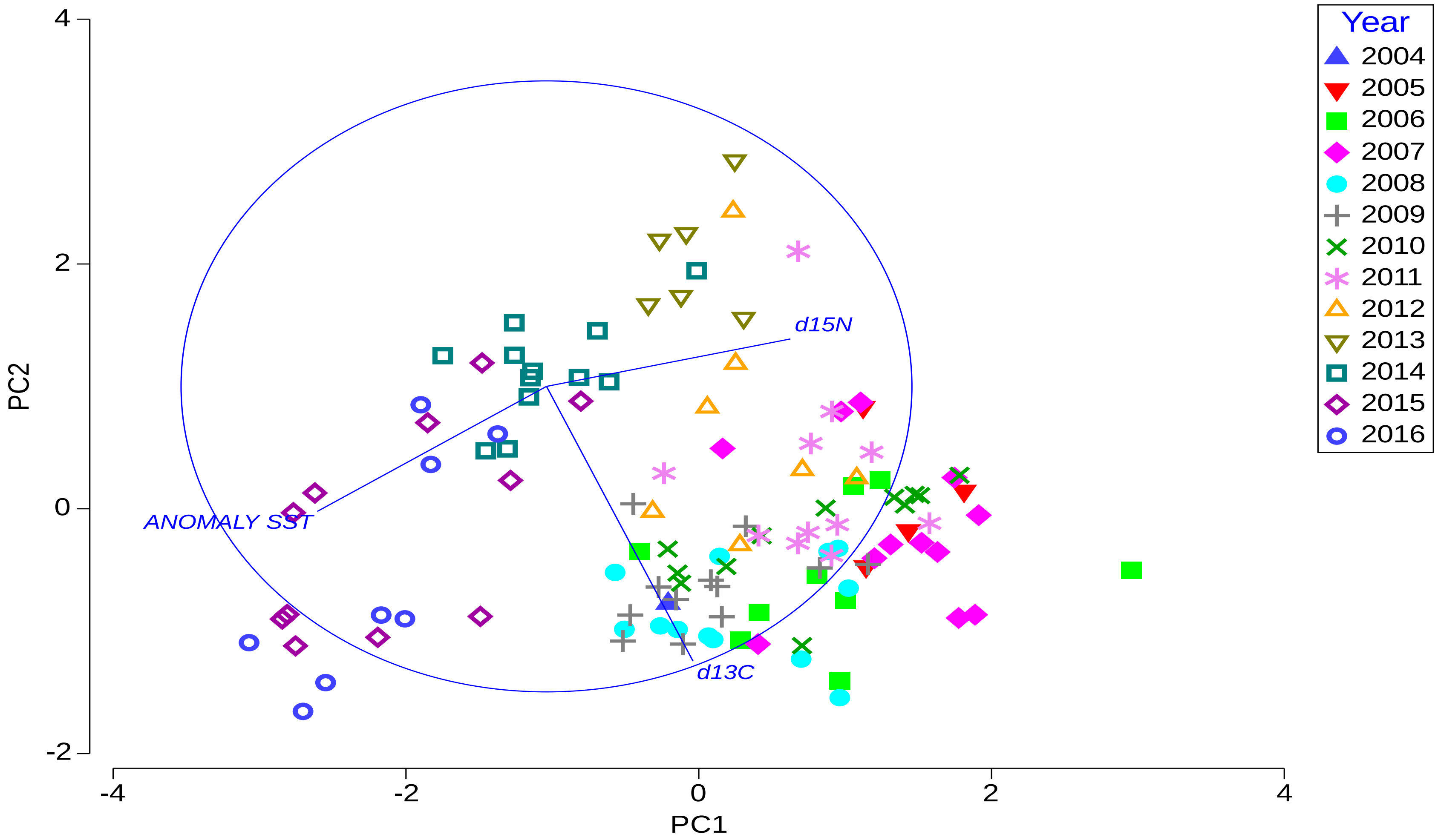

Figure 9. Principal component analysis of mean subadult and bull male Peruvian fur seal δ^{13}C, δ^{15}N and sea surface temperature anomaly factored by year (2004-2016).

Peruvian Fur Seal Females

Approximately 11 years (2005-2015) of $\delta^{13}C$ and $\delta^{15}N$ data were collected from 47 adult female vibrissae. Adult female $\delta^{13}C$ ranged from -18.13 to -13.19 ‰ with a mean -14.35 ± 0.33 ‰ while the $\delta^{15}N$ ranged from 15.83 to 21.55 ‰ with a mean 18.93 ± 0.85 ‰. A Kendall's tau correlation revealed a significant inverse correlation between $\delta^{15}N$ and SSTA readings (p=0.007 and r= -0.183), while $\delta^{13}C$ was not correlated to SSTA (p=0.272 and r=0.074). Unlike the male fur seals, adult females' stable carbon and nitrogen isotope values were not significantly correlated over the 11-year period (p=0.206 and r= -0.086).

Female $\delta^{13}C$ was most enriched in mid-2006 (-13.70‰) and the most depleted in late 2014 (-15.39‰), a change of 1.69‰ (Figure 10). During the span of one year, mid-2005 to mid-2006, $\delta^{13}C$ ranged 0.78‰. Smaller oscillations, less than 0.5‰, occurred from mid-2006 until mid-2010.A decline of 1.39‰ in mean $\delta^{13}C$ occurred from 2010 through 2014 followed by a nearly 1‰ enrichment (mid-2015) and was depleted by 0.70‰ the following month. Overall, female $\delta^{13}C$ decreased more than 1‰ between 2005 and 2015.

Female mean $\delta^{15}N$ values (Figure 11) revealed a five-year pattern that entailed a period of enrichment, followed by a period of depletion. This pattern repeated twice in all PFS vibrissae from 2005 to 2015. The most enriched mean $\delta^{15}N$ values occurred in May 2012 (20.68‰) followed by a gradual depletion to the most depleted values in October 2015 (17.37‰). The 5-year pattern was more pronounced from 2010 until 2015, $\delta^{15}N$ increasing 2.48‰ over two years and decreasing 3.31‰ in 3 years. This suggests that PFS females foraged within two or more trophic levels over several years.

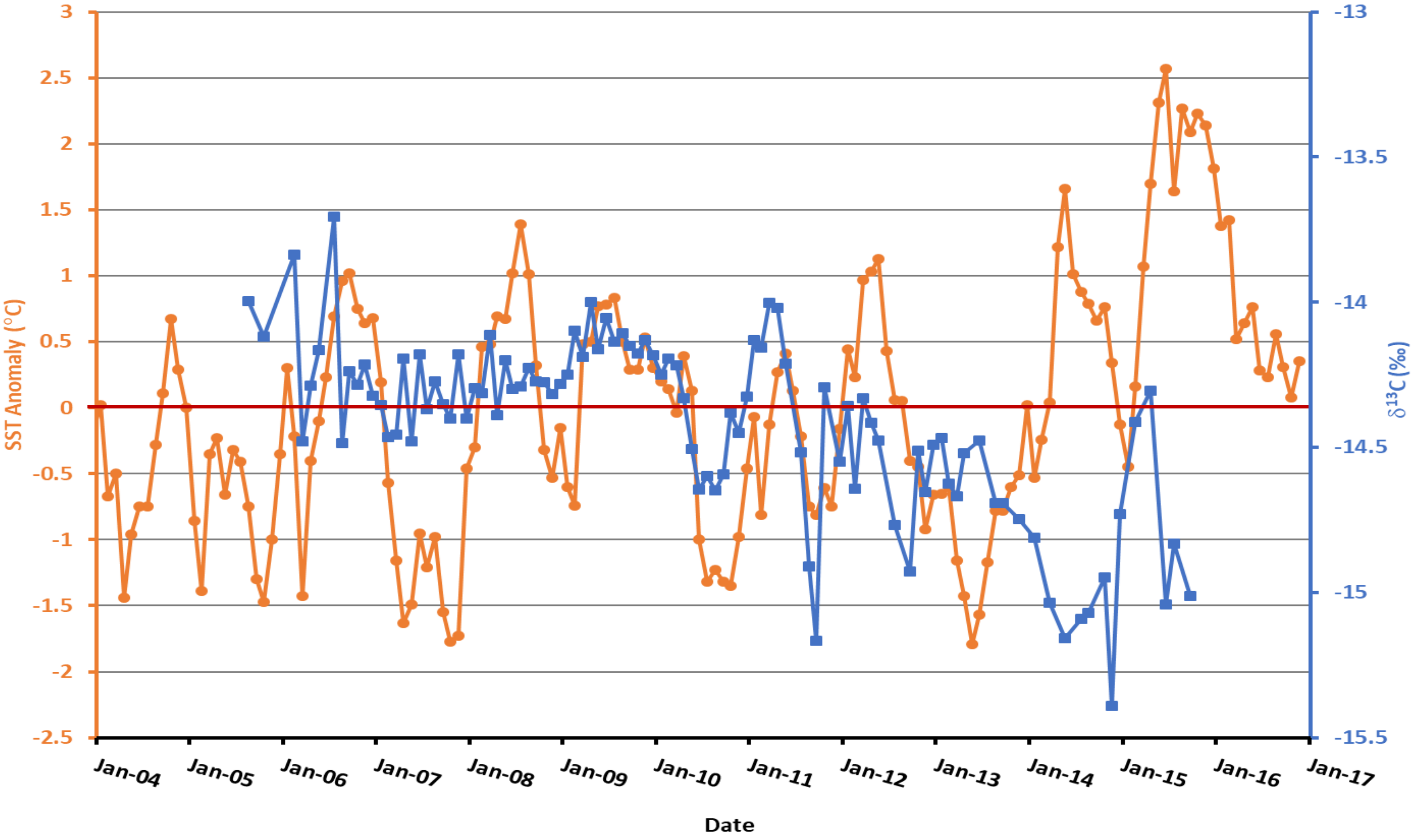

Figure 10. Mean female Peruvian fur seal (n=47) $\delta^{13}C$ (blue) in comparison to sea surface temperature anomaly (orange) (°C), 2005-2015.

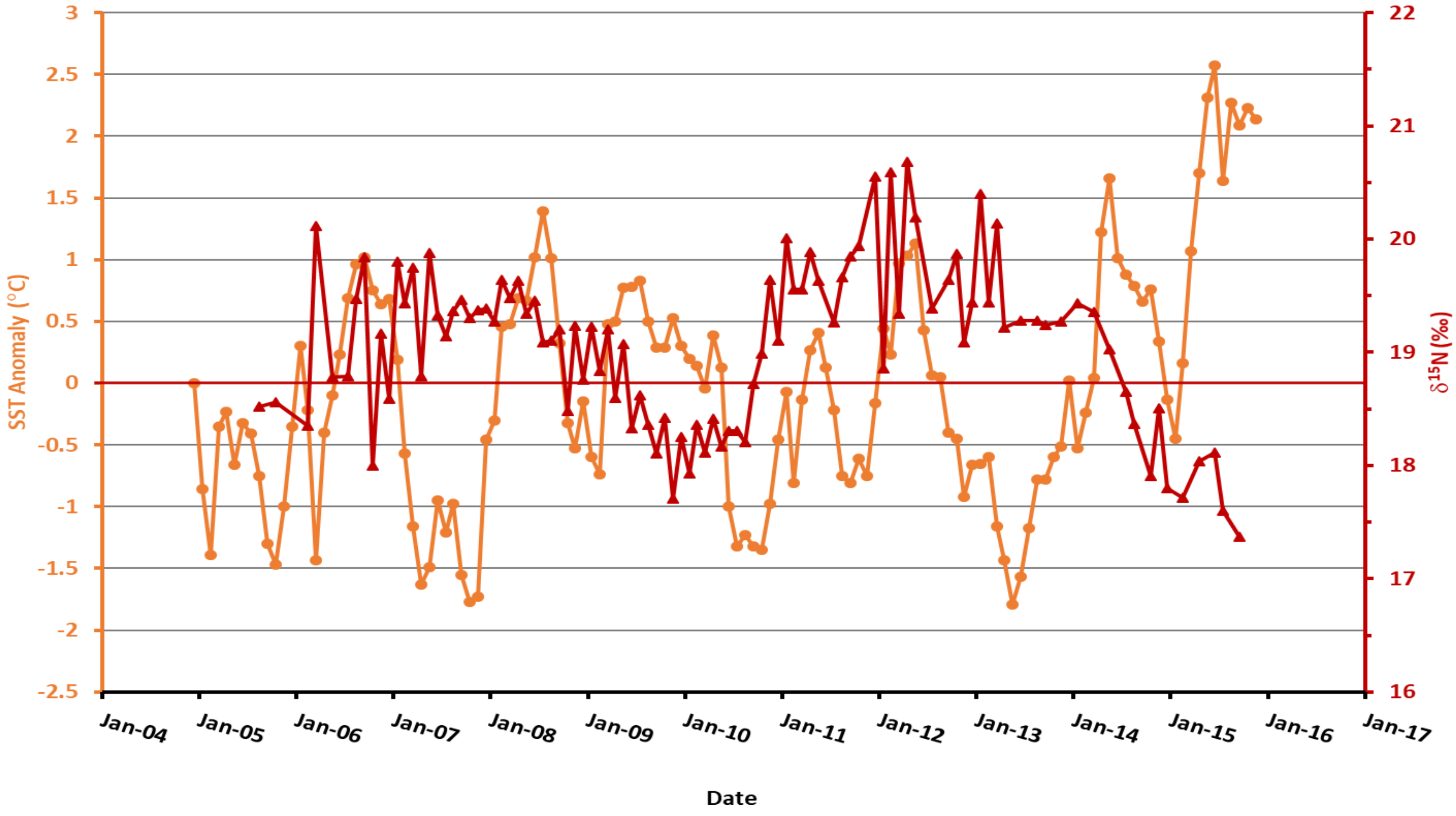

Figure 11. Mean female Peruvian fur seal (n=47) δ^{15}N (red) in comparison to sea surface temperature anomaly (orange) (°C), 2005-2015.

Principal component analysis of PFS female mean $\delta^{13}C$ and $\delta^{15}N$ and SSTA factored by year (2004-2016) revealed data from 2015 were different from the remaining years (Figure 12). Similarly to the population PCA analysis, the angle of the vectors, $\delta^{13}C$ and $\delta^{15}N$, as well as $\delta^{13}C$ and SSTA are not strongly correlated variables (~90°); however, $\delta^{15}N$ and SSTA are negatively correlated variables (>180°), and all variables were well represented. The vectors of this PCA indicated distinct depletion in $\delta^{15}N$ with increasing SSTA, especially in the years 2014 and 2014, with little variation in $\delta^{13}C$.

An ANOVA revealed a significant correlation between increasing SSTA and declining $\delta^{15}N$, and $\delta^{15}N$ enrichment with below average SSTA conditions (P=0.003). The magnitude of ENSO events did not correlate significantly to PFS adult female stable isotope values (p=0.056); an ANOVA detected no significance between $\delta^{13}C$ and SSTA (p=0.512); additionally, $\delta^{13}C$ and $\delta^{15}N$ were not significantly in correlation (p=0.802). An ANOSIM testing for differences between years in recorded female whisker $\delta^{13}C$ and $\delta^{15}N$ in relation to SSTA, revealed a significant difference (p=0.001; r=0.431). A pairwise comparison of $\delta^{13}C$ and $\delta^{15}N$ showed 2015 differed significantly from all other years (2004-2014) (p=0.001 to 0.036, r=0.484 to 0.947).

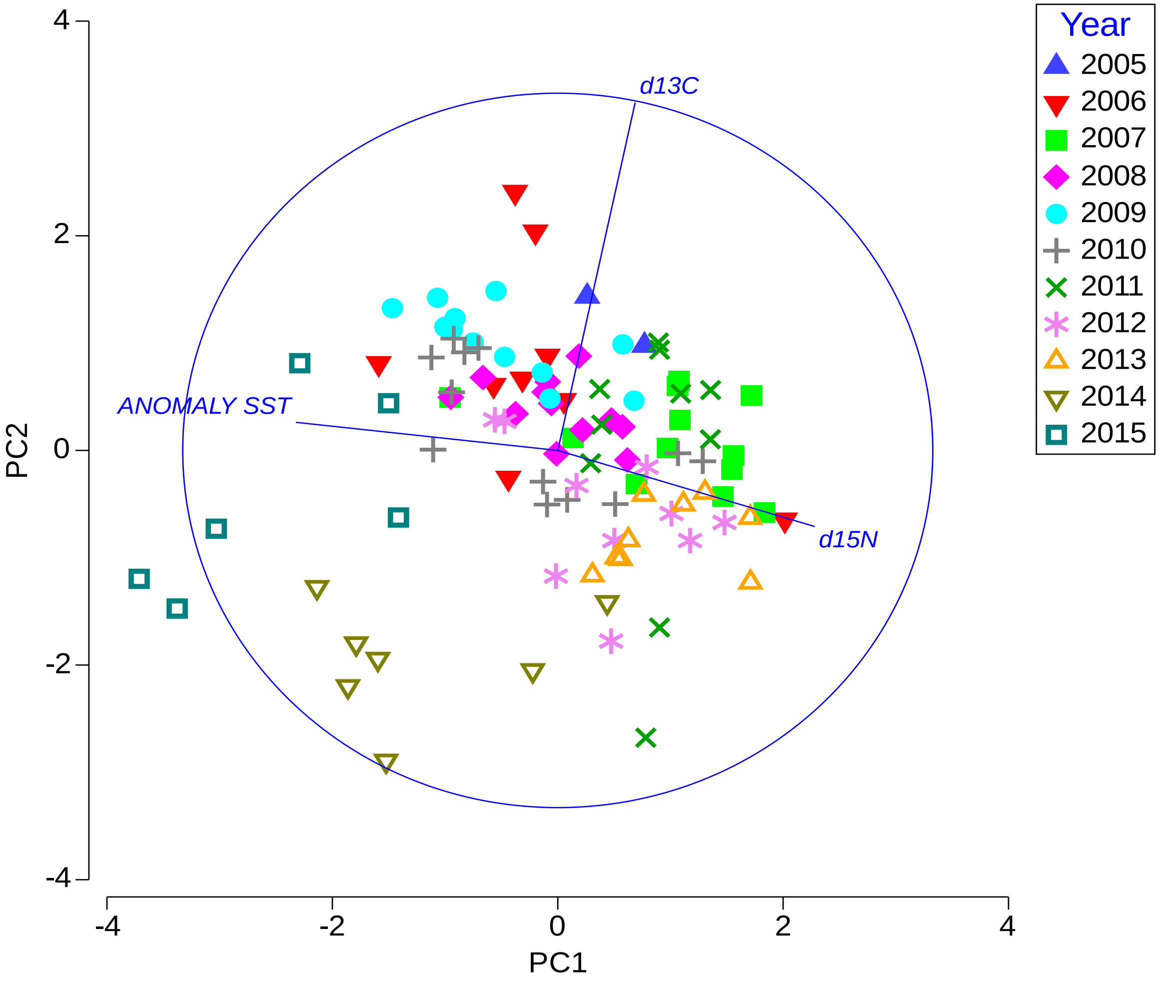

Figure 12. Principal component analysis of mean female Peruvian fur seal vibrissae δ^{13}C, δ^{15}N and sea surface temperature anomaly factored by year (2005-2015).

Peruvian Fur Seal Male/Female

Principal component analysis between male and female PFS detected a separation between female and male isotope signatures (Figure 15). According to the angle of the vectors, $\delta^{13}C$ and $\delta^{15}N$, as well as $\delta^{13}C$ and SSTA were positively correlated variables (<90°); however, $\delta^{15}N$ and SSTA are negatively correlated variables (>180°); all variables were equally represented. Males and females subjected to increasing SSTA, revealed more depleted $\delta^{15}N$ and more enriched $\delta^{13}C$. Additionally, males revealed the most enriched signatures in comparison to females.

An independent two-sample t-test detected a significant difference in $\delta^{13}C$ and $\delta^{15}N$ values of subadult male and adult female fur seal vibrissae for 2011 and 2012 ($p<0.001$ for both). Female fur seal $\delta^{13}C$ and $\delta^{15}N$ were significantly more depleted than male fur seals in both years ($p<0.001$ for both). A MANOVA for the combined effect of $\delta^{13}C$ and $\delta^{15}N$ revealed a significant difference between genders ($p=0.001$, $r=0.114$); the mean male vibrissae $\delta^{13}C$ was -13.83‰ while the mean female vibrissae was -14.34‰ (Figure 13). The mean male vibrissae $\delta^{15}N$ (20.22‰) was 1.36‰ more enriched than the mean female vibrissae (18.86‰) (Figure 14).

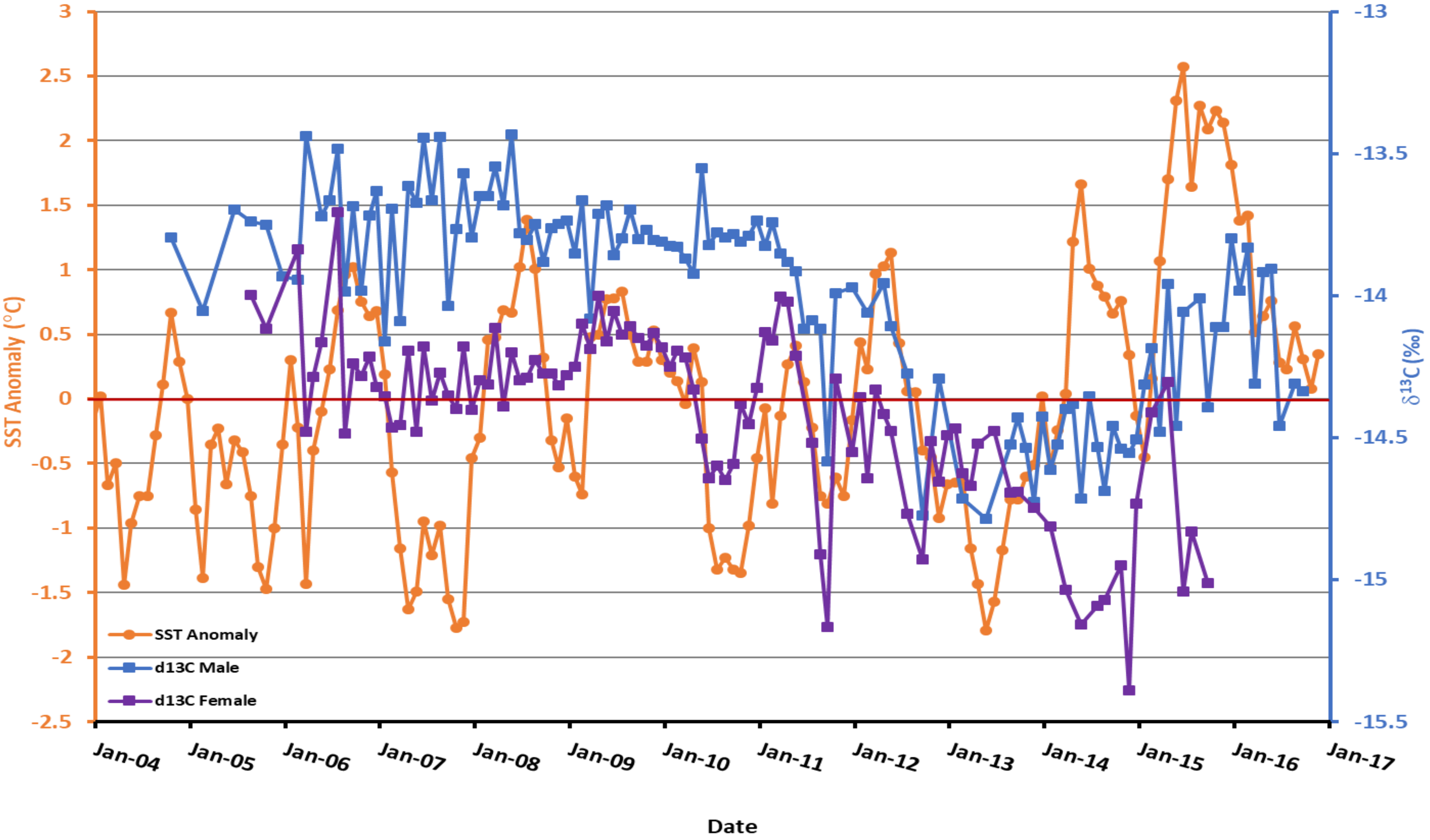

Figure 13. Mean $\delta^{13}C$ for 17 male (blue) and 47 female (purple) Peruvian fur seal vibrissae and sea surface temperature anomaly (°C), 2004-2016.

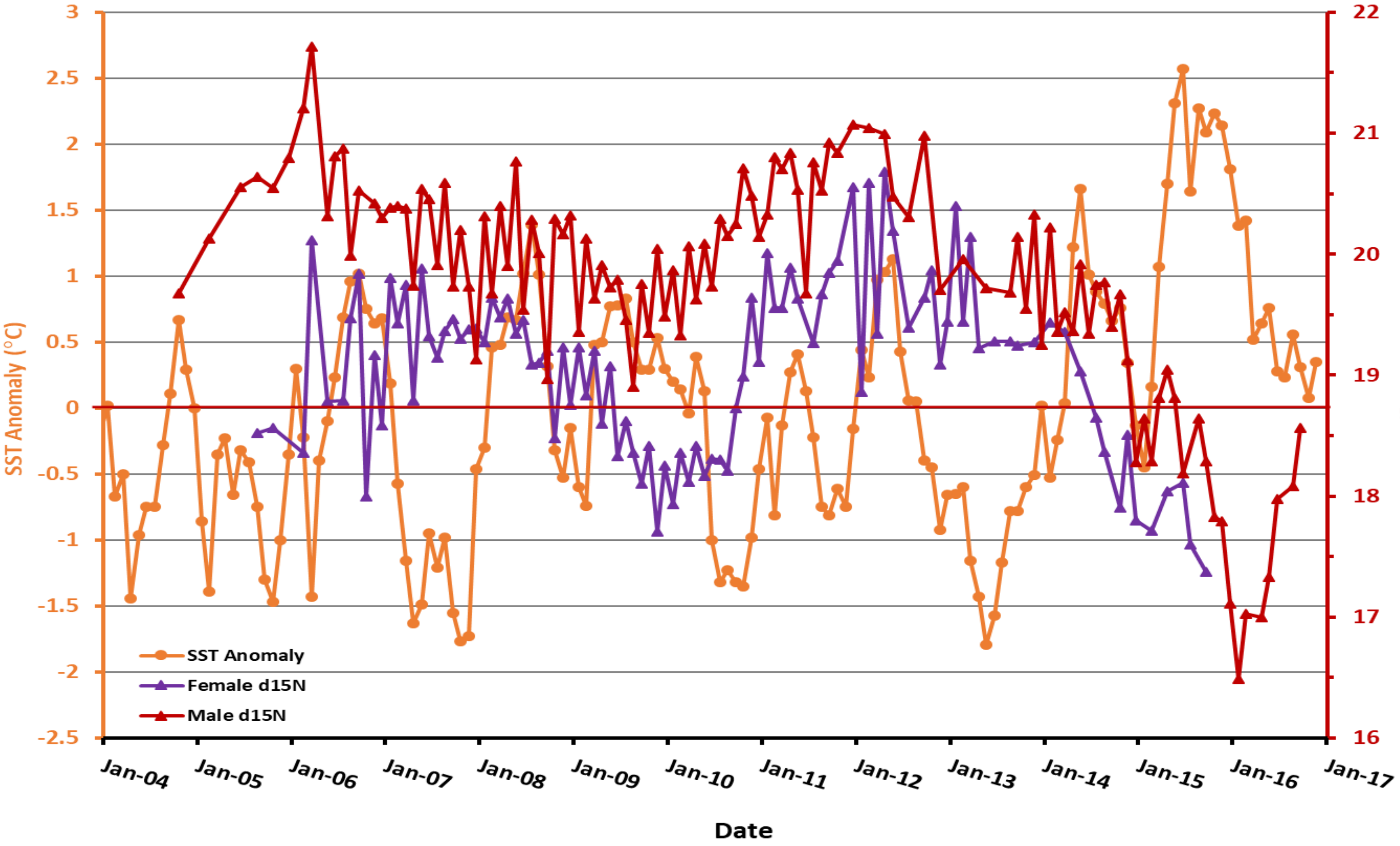

Figure 14. Male versus female Peruvian fur seal mean δ^{15}N 17 male (red), 47 female (purple) and sea surface temperature anomaly (°C), 2004-2016.

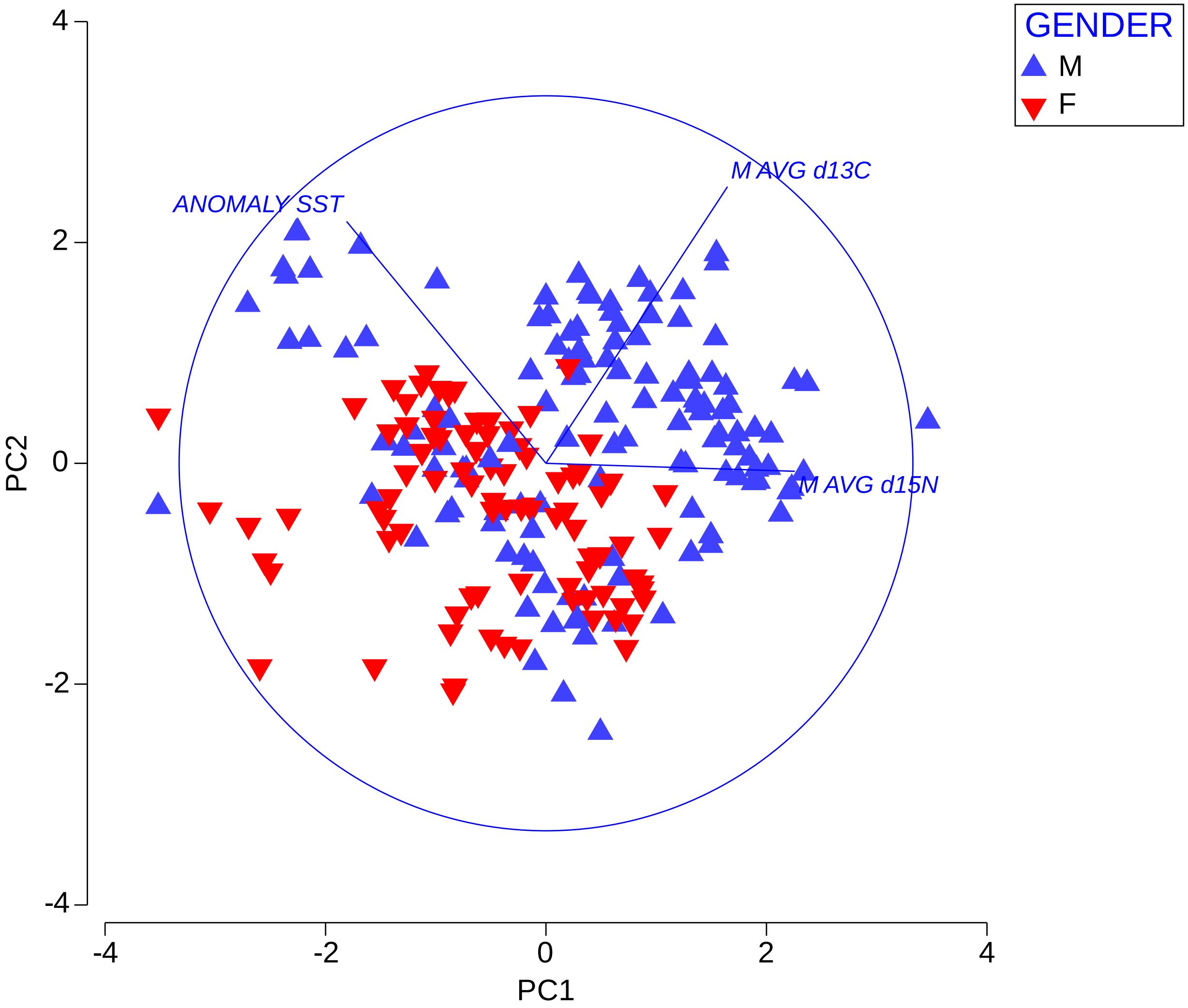

Figure 15. Principal component analysis of male (blue=M) and female (red=F) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N from 2011 and 2012 vibrissae samples, representing 2004-2011.

Peruvian Fur Seal Dam-Pup Pairs

A vibrissa from each individual of six dam-pup pairs in 2015 were analyzed for $\delta^{13}C$ and $\delta^{15}N$. The mean length of dam whiskers was 10.29 ± 2.2 cm and one-week-old pup whisker mean length was 6.13 ± 1.1 cm. A paired two-sample t-test revealed no significant difference between the 6 dam-pup pairings' $\delta^{13}C$ and $\delta^{15}N$ ($p=0.490$, $p=0.573$, respectively), indicating pup whiskers represented growth in utero and reflected the maternal stable isotope values. An estimated one-week old PFS pup had a calculated whisker growth rate of 0.29 ± 0.05 mm/day. This growth rate was calculated by taking the length of each newborn whisker and dividing it by the active gestation period in which vibrissae are growing (~7 months). Gestation periods in PFS last 11 months (Hewer et al. 1968); PFS experience a 2-3 month diapause, followed by active gestation K. Colegrove & M. Adkesson, personal communication, 2018. Fetus whiskers begin to develop 2 months after early embryo gestation, followed by 6-7 months of active whisker growth in utero (Lerner et al. 2018, K. Colegrove & M. Adkesson, personal communication, 2018). The stable isotope data for the 7-month period matched for each dam-pup pair. The dam-pup pair's whiskers averaged -14.79 ± 0.28‰ and -14.82 ± 0.29‰, respectively, for $\delta^{13}C$, and 18.69 ± 0.17‰ and 18.59 ± 0.11‰ for $\delta^{15}N$, respectively.

South American Sea Lion Male

Male SASL vibrissae had $\delta^{13}C$ values ranging from -14.38 to -13.43‰ with a mean of -13.43 ± 0.16‰ and $\delta^{15}N$ ranging from 15.95 to 22.82‰ with a mean of 20.06 ± 0.48‰. A principal component analysis of mean $\delta^{13}C$, $\delta^{15}N$ and SSTA factored by year (2004-2011) showed no distinction among years analyzed (Figure 16). Similar to that of the PFS, the angle of the vectors, $\delta^{13}C$ and $\delta^{15}N$, as well as $\delta^{13}C$ and SSTA are not strongly correlated variables (~90°); however, $\delta^{15}N$ and SSTA are negatively correlated variables (>180°). This PCA indicated depleted $\delta^{13}C$ and a range of $\delta^{15}N$ over the same year, with no differences among years, besides one outlier in 2011with enriched $\delta^{13}C$.

An ANOVA evaluating the effect of $\delta^{15}N$ with changing SSTA revealed a significant correlation between increasing SSTA and depletion of $\delta^{15}N$, and enrichment with below average SSTA conditions ($p=0.002$). A one-way ANOVA analysis evaluating $\delta^{15}N$ by ENSO phase (i.e. cold, norm, warm) revealed a significant correlation ($p=0.003$).

Whisker plots indicate depleted $\delta^{15}N$ with warmer phases and more enriched with colder phases. Magnitude of ENSO event did not correlate significantly to SASL male signatures (p=0.401). SASL $\delta^{13}C$ signatures did not reveal a significant change with fluctuating SSTA. A one-way ANOVA showed no correlation between $\delta^{13}C$ and $\delta^{15}N$. A one-way ANOSIM testing differences between years revealed $\delta^{13}C$ and $\delta^{15}N$ varied relative to SSTA (p=0.001; r=0.304). The year 2009 was consistently the most diverse from all other years analyzed (2004 through 2011) (p<0.001; r=0.516 to 0.757.

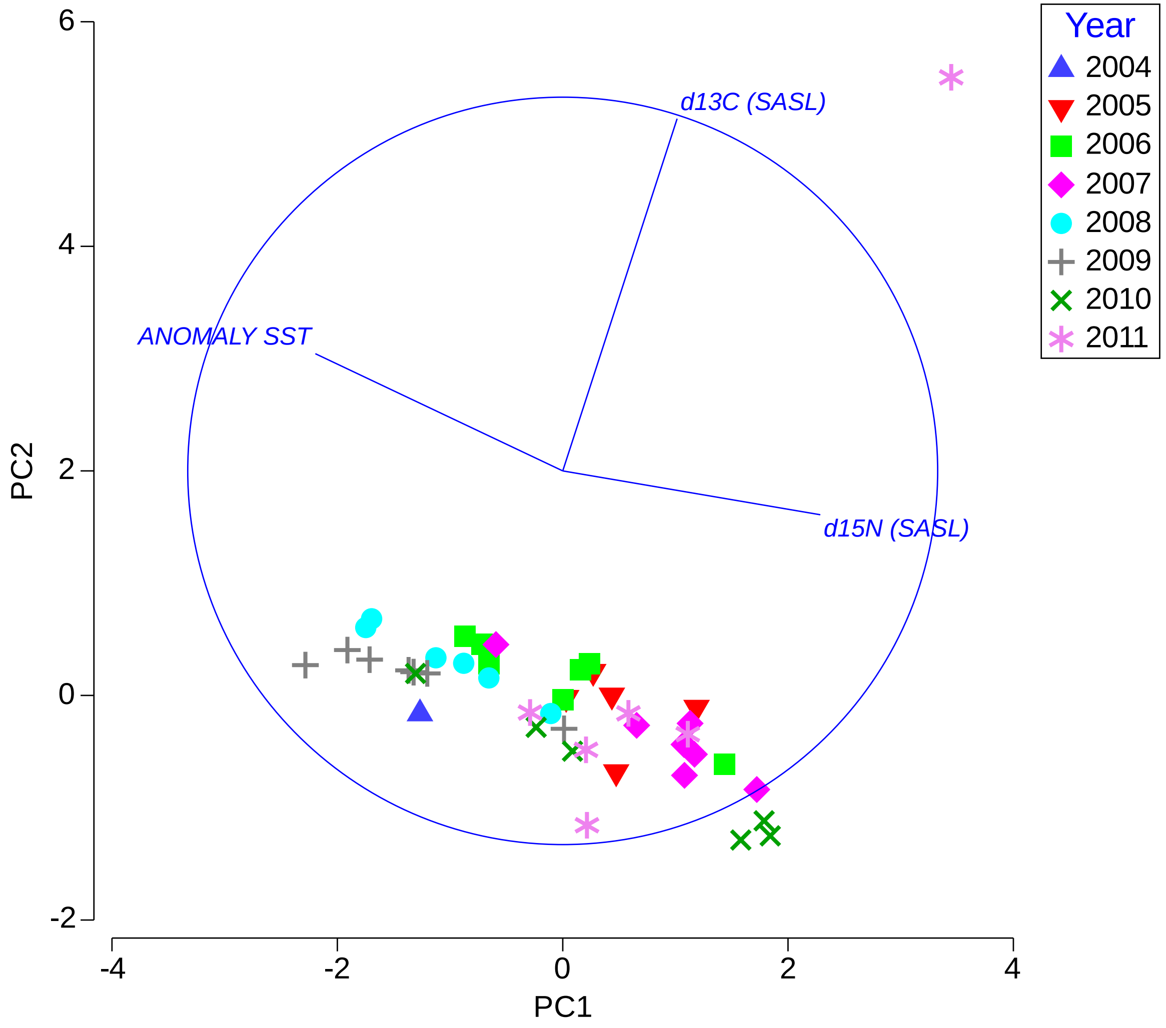

Figure 16. Principal component analysis of South American sea lion male vibrissae mean δ^{13}C, δ^{15}N and sea surface temperature anomaly (°C) factored by year (2004-2011).

Sympatric Species

A PCA of SASL and PFS sub-adult males both sampled in 2011 evaluating mean $\delta^{13}C$, $\delta^{15}N$ factored by year revealed differences between years 2005 to 2011 (Figure 17). According to the angle of the vectors, $\delta^{13}C$ and $\delta^{15}N$ were not strongly correlated variables (~90°); both variables were equally represented. This PCA revealed a trajectory of years from 2005 until 2011 in PFS (red) and SASL (blue), which went in different directions over the same years indicating slight variation between these species isotope signatures by year.

No significant difference was found between SASL and PFS male $\delta^{13}C$ and SSTA ($p=0.889$). A MANOVA of $\delta^{15}N$ for PFS and SASL versus SSTA revealed that SASL $\delta^{15}N$ signatures were more correlated to ENSO phase ($p=0.013$) than in PFS ($p=0.003$). Warm phase ENSO conditions had the most depleted $\delta^{15}N$, and cold phases had the most enriched $\delta^{15}N$ in both species. ENSO condition magnitude; however, did not significantly correlate with SASL and PFS male signatures ($p=0.401$ and $p=0.542$; respectively).

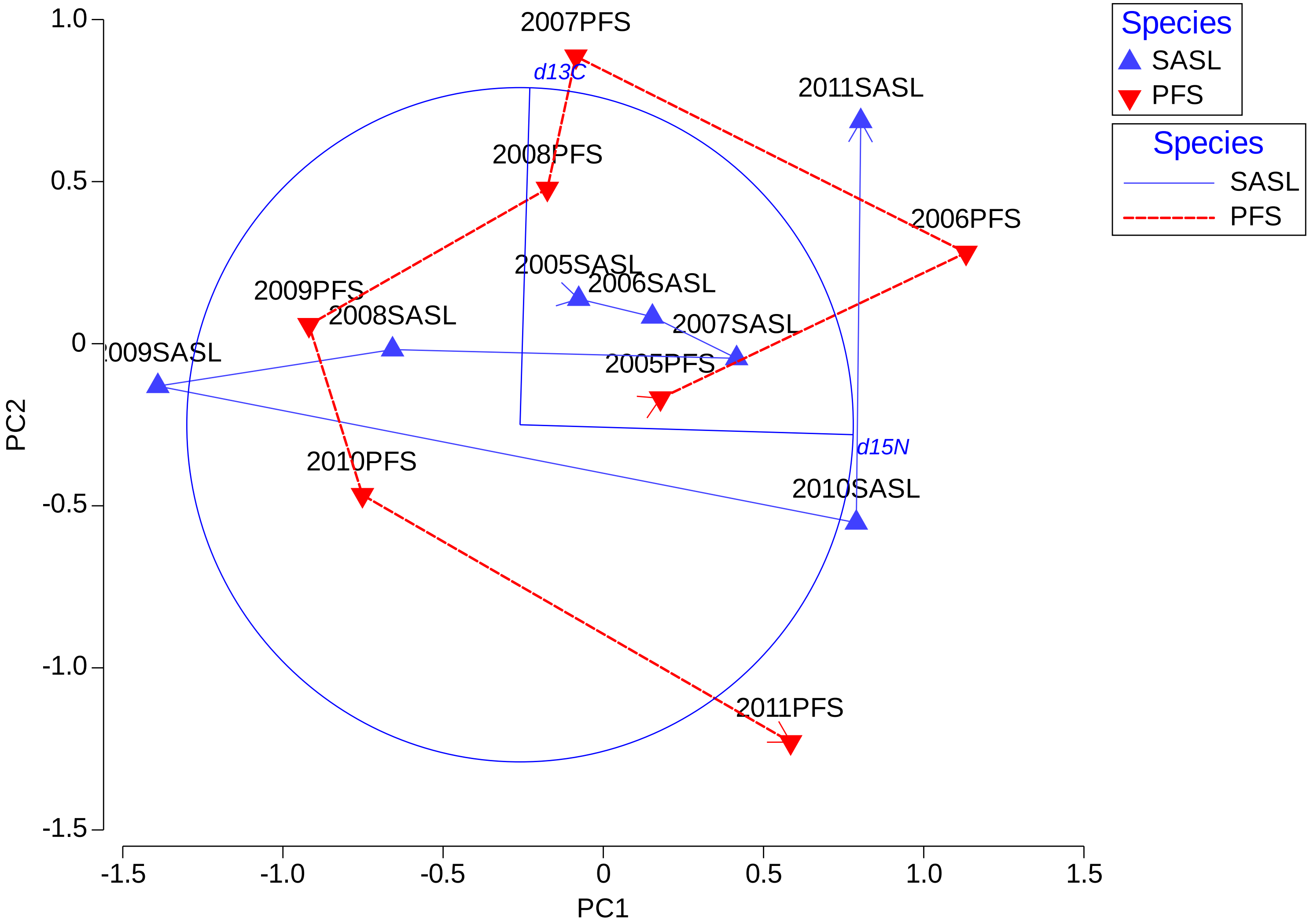

Figure 17. Principal component analysis with trajectory of mean male δ^{13}C, δ^{15}N and sea surface temperature anomaly factored by year (2005-2011) from Peruvian fur seal and South American sea lion vibrissae.

Table 2. Vibrissae mean, standard deviation, and range δ^{13}C and δ^{15}N) sampled from 2010 to 2016. Aa= *Arctocephalus australis* unnamed ssp., Ob=*Otaria byronia*

Species	**Age Class**	**Gender**	**N**	**δ^{15}N Vibrissae Data**		**δ^{13}C Vibrissae Data**	
				$\bar{X}$± SD (‰)	**Range (‰)**	**$\bar{X}$± SD (‰)**	**Range (‰)**
Aa	Pup	Unknown	6	18.59 ± 0.47	17.74 to 19.44	-14.11 ± 0.24	-15.72 to -14.11
	Adult	Male	17	19.66 ± 0.89	16.18 to 22.31	-14.01 ± 0.26	-15.16 to -13.17
		Female	47	18.93 ± 0.85	15.83 to 21.55	-14.35 ± 0.33	-18.13 to -13.19
Ob	Subadult	Male	6	20.06 ± 0.48	15.95 to 22.82	-13.43 ± 0.16	-14.38 to -13.43

DISCUSSION

South American pinnipeds, resident apex predators of coastal Peru, occupy food webs by predating on economically important fishes. These marine mammals, which are known to forage within the upwelling ecosystem, serve as sentinel species, indicating the ecological health of their environments throughout fluctuating ENSO conditions (Fossi & Panti 2017). The Peruvian coastline, home to various marine macro-fauna such as the vulnerable Peruvian fur seal, is modulated by ENSO conditions and associated physical oceanographic properties that alter the biological oceanic conditions in these habitats. Well known for its continual upwelling-driven ecosystems, Peruvian coastal habitats are extremely dynamic where conditions can be either favorable for marine mammals and associated prey, or potentially catastrophic with risk of total population collapses and mass mortality events. The effect of ENSO conditions on the feeding ecology, trophic interactions, and movements of Peruvian pinnipeds are of significant interest because of their ecological importance in coastal ecosystems. This is the first study of its kind to capture potential ecosystem changes recorded by apex predators and related to ENSO conditions.

Sea Surface Temperature Anomaly

The proxy for ENSO conditions, monthly SSTA readings, in this study were collected from the closest Niño index, Niño 1+2, which is located more than 800 km from the Punta San Juan rookeries. Although this is a substantial distance, previously documented ENSO years have shown to have impacts on the coastal Peruvian ecosystem, including the 1997/98 anchoveta fishery collapse and PFS mass mortality event (Arias-Shreiber & Rivas 1998, Cardenas-Alayza 2012). An analysis of stable carbon and nitrogen isotope ratios (δ^{13}C and δ^{15}N) from whiskers of these two pinniped species provided a timeline of trophic and production changes in this dynamic system, one where ENSO conditions fluctuate and organisms must adapt in order to survive potentially stressful conditions. According to the SSTA from the Niño 1+2 region (Figure 3), ENSO cold phase conditions persisted during the years 2004, 2005, 2007, 2010, 2011, 2013 and ENSO warm phase conditions occurred in 2006, 2008, 2009, 2012, 2014-2016 (Table 3); though duration and magnitude differed among years. The strongest ENSO on record occurred during this study, 2014 to 2016 (Figure 3); the biotic results of the events were captured in 2015 and 2016 whiskers.

Peruvian Fur Seal ($\delta^{13}C$)

Mean vibrissae δ^{13}C signatures represented the carbon source in the seals diet, carbon undergoes a small fractionation off less than 1‰ during assimilation and can therefore trace primary production changes within the seals environment (DeNiro & Epstein 1978, Lajtha & Michener 1994, France 1995, Gannes et al. 1998). The comparison of consumer tissue δ^{13}C values over time provides information regarding ocean productivity in foraging grounds throughout fluctuating ENSO conditions (France & Peters 1997, Hirons 2001, Kurle & Worthy 2001). Among recorded patterns, the PSJ population δ^{13}C signatures from 2004-2009 varied within 0.49‰ and 2015-2016 within 0.66‰, which revealed foraging within approximately one to two trophic levels; however, from 2010-2014, δ^{13}C revealed a change of 1.18‰, indicating foraging in two or more trophic levels over this time period. Additionally, observations from 2010 to 2016 represented the largest variance of δ^{13}C (Δ 1.29‰). This could indicate that the population was foraging in an environment with fluctuating primary production due to fluxing ENSO conditions or geographical variability in their foraging as an adaptation to foraging stressors in correspondence to ENSO conditions.

Both male and female fur seals exhibited nearly identical δ^{13}C patterns though males were more enriched by no more than 0.5‰ (Figure 5). This could be indicating a potential dissimilarity in foraging location between male and female PFS. Male whisker δ^{13}C signatures had depleted from 2010 until 2013, where it began a steady enrichment; however, δ^{13}C did not return to values seen in earlier years (ca. 2004-2011) for the remainder of studied data. Carbon source absorbed within the PFS diet exposes a change between the later years (ca. 2004-2011) and present-day isotope recordings. Throughout the overall time series the whiskers covered (2004-2016), both male and female δ^{13}C did not reveal a significant change with fluctuating SSTA; however, males revealed a significant correlation between δ^{13}C and δ^{15}N (p=0.0076), while females did not in 2011

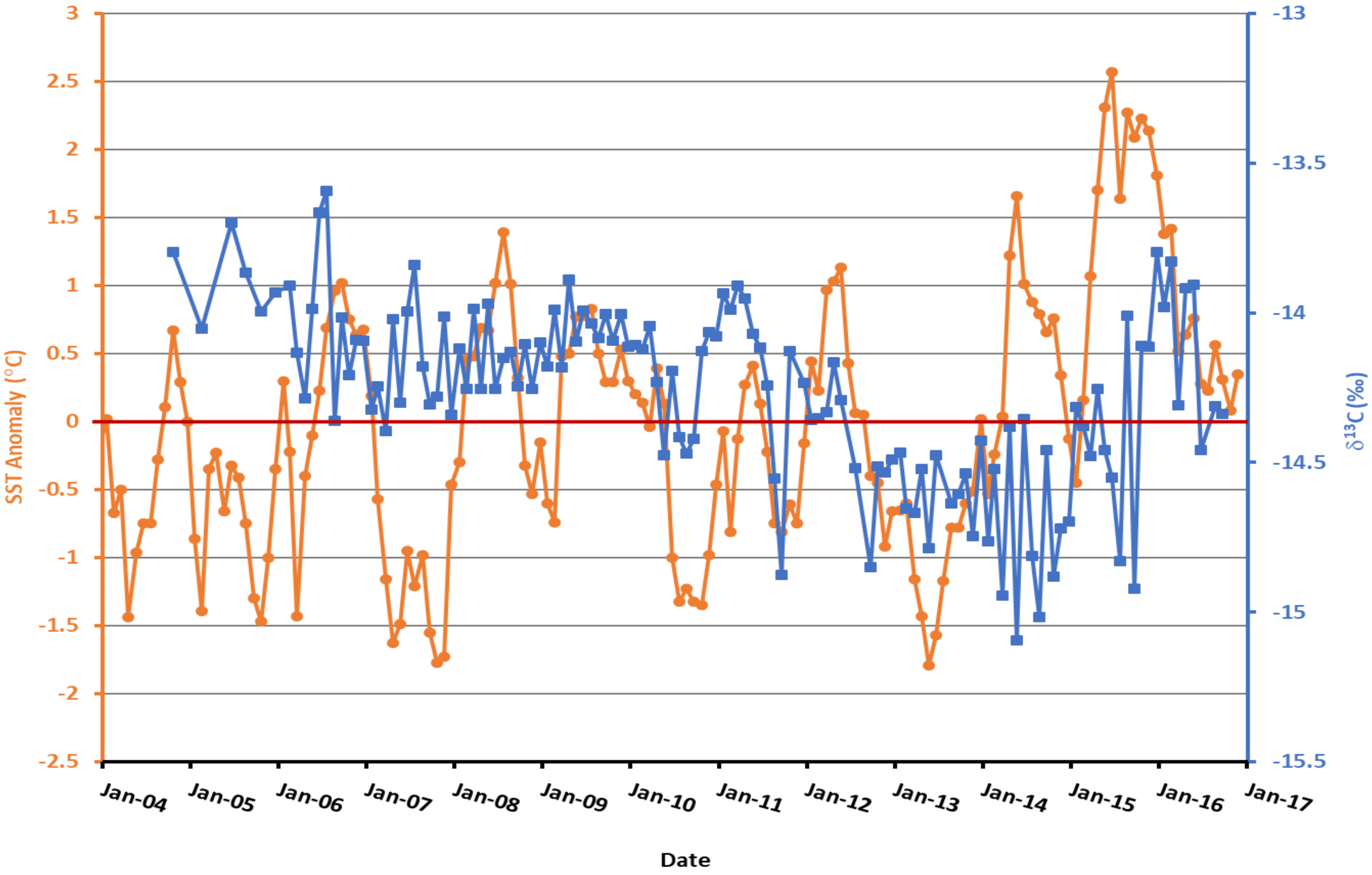

Figure 18. Peruvian fur seal mean $\delta^{13}C$ (blue) relative to sea surface temperature anomaly (°C), 2004-2016.

and 2012 whisker samples. Inclusive of the population over a shorter timeframe of 7 years (e.g. 2009-2016), $\delta^{13}C$ signatures significantly correlated with SSTA. Additionally, $\delta^{15}N$ and $\delta^{13}C$ signatures were significantly inversely correlated during the extreme El Nino event in 2014-2016 ($p=0.001663$).

Related studies with sampling efforts in the Humboldt Current, such as Espinoza-Morriberón et al. (2017), revealed findings of more depleted $\delta^{13}C$ values farther offshore (Sydeman et al. 1997, Hill et al. 2006, Miller et al. 2008). Sampling distance from shore corresponded to more depleted $\delta^{13}C$ in animals, which is common in upwelling ecosystems (Sydeman et al. 1997, Miller et al. 2008, Espinoza-Morriberón et al. 2017). Carbon isotope signatures ($\delta^{13}C$) decrease sequentially between coastal, neritic, and oceanic species due to decreasing productivity offshore (France and Peters 1997, Hill et al. 2006, Espinoza-Morriberón et al. 2017). ENSO conditions could also contribute fluctuating patterns in primary production during warm and cold phases, which fluctuates resource availability within an environment.

Peruvian Fur Seal ($\delta^{15}N$)

Nitrogen enrichment per trophic level is 3-5‰ relative to the diet it is consuming, initiated through the bioaccumulation of the nitrogen isotopes necessary to build proteins (Deniro & Epstein 1981). The comparison of consumer tissues' $\delta^{15}N$ without their prey source provides baseline information regarding potential food web linkages, such as how many trophic levels these organisms are feeding within and if it varies over a time series (France & Peters 1997, Hirons 2001, Kurle & Worthy 2001). According to the PSJ population's $\delta^{15}N$ recordings, a large-scale pattern occurred in PFS foraging where a long-term gradual depletion followed by a quick enrichment cycled. Whether this pattern corresponds to ENSO conditions is uncertain; however, as ENSO conditions strengthened and lasted longer, increased depletion occurred. An oscillation occurred with a depletion from 2004-2009 (Δ -2.41‰) until 2010-2011, which had a period of enrichment of (Δ +2.17‰). Following these conditions, the similar pattern that persisted from 2012 through the end of 2016 revealed an oscillation of a five-year depletion (Δ -4.35‰) followed by a nine-month (Δ +1.56‰) enrichment; however, this may have persisted but was beyond our recordings.

Above normal sea surface temperatures correlated to more depleted $\delta^{15}N$ signatures in PFS whiskers ($p<0.001$). When evaluating ENSO conditions by phases (i.e. cold, norm, warm), a significant correlation between warmer phases and more depleted $\delta^{15}N$ as well as colder phases and more enriched $\delta^{15}N$ were identified ($p<0.001$). During warmer phases, more widespread variation and the most depleted $\delta^{15}N$ is seen, whereas the most narrowly spread and consistently enriched $\delta^{15}N$ signatures was seen during cold phases. Increasing magnitude of ENSO conditions revealed significant correlation to depleted $\delta^{15}N$, where strong, very strong, and extreme were all below average $\delta^{15}N$ signatures, whereas norm, weak, and moderate magnitudes all varied at or slightly above the mean PFS population $\delta^{15}N$ ($p=0.009$).

Males that experienced above average SSTA were strongly correlated to depletion in $\delta^{15}N$ ($p<0.001$), with a significant correlation to warm phase conditions ($p=0.013$). Warm phase ENSO conditions revealed a widely variable $\delta^{15}N$ and also the most depleted. Females that experienced above average SSTA, like males, were significantly correlated with depleted $\delta^{15}N$ ($p=0.003$). ENSO phase correlated significantly to $\delta^{15}N$ signatures ($p=0.013$), where warm phases were wide spread and more depleted and cold phases were narrow spread and enriched in $\delta^{15}N$. However, the magnitude of these ENSO events did not seem to have a significant effect on male and female $\delta^{15}N$ signatures.

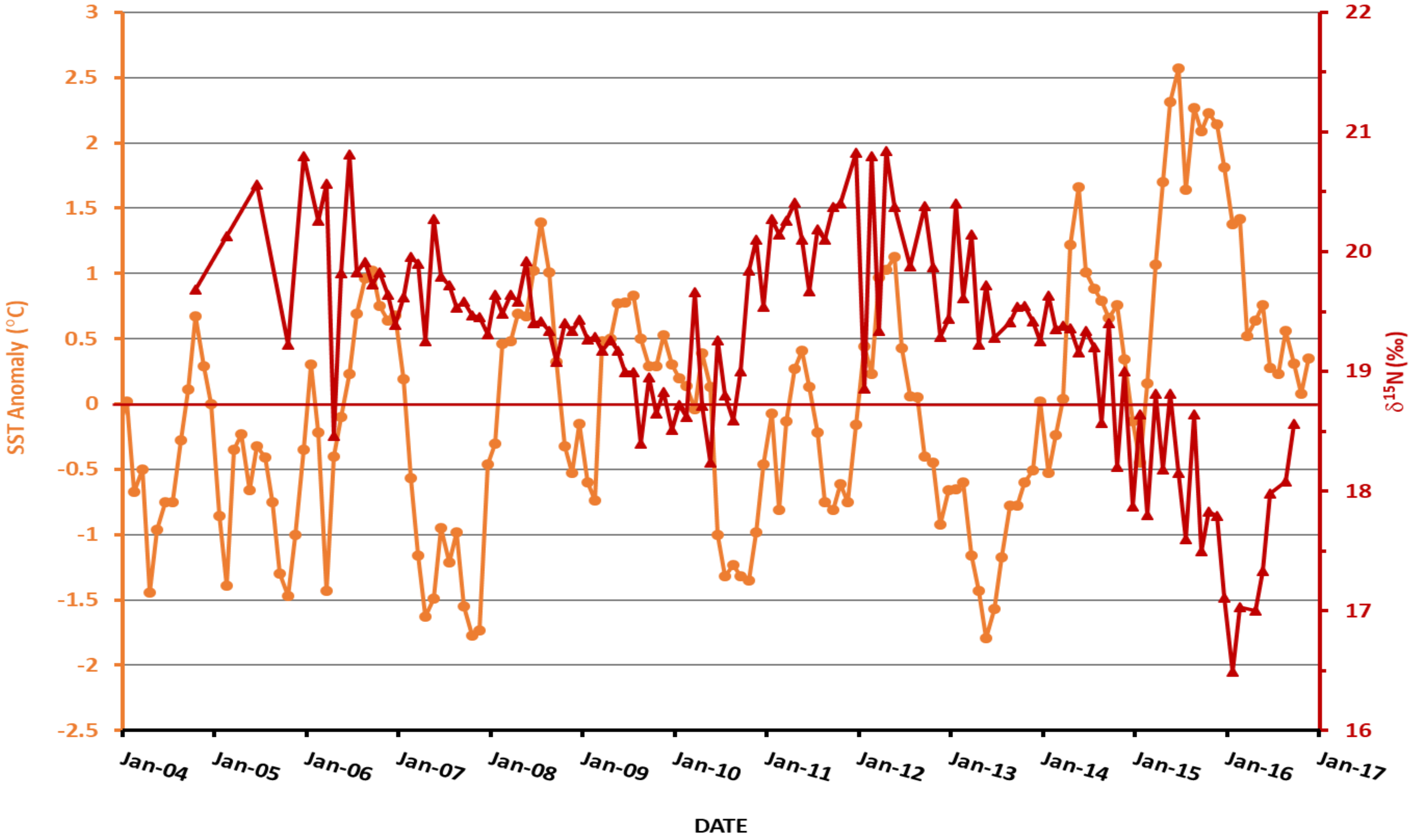

Figure 19. Peruvian fur seal mean δ^{15}N (red) relative to sea surface temperature anomaly (°C), 2004-2016.

Peruvian Fur Seal Dam-Pup Pairs

Evaluation of the 2015 PFS dam-pup pairings concluded that pups $\delta^{13}C$ and $\delta^{15}N$ whisker readings were indicative of the dam, making pup whiskers a proxy for maternal diet during the gestation period. While this method has yet to be done before in Peruvian fur seals, pup tissues have been used to examine adult female diets in other phocid and otariid seal species using stable isotope analyses such as Steller sea lions, Bearded seals, and Gray seals (Hewer et al. 1968, Newsome et al. 2010, Hindell et al. 2012, Scherer et al. 2015, Lerner et al. 2018). Post birth, pups reflect a trophic level higher than dam due to feeding from her milk (Cherel et al. 2015). A paired two-sampled t-test confirmed that pup whiskers represented growth in-utero and were indicative of the dam ($\delta^{13}C$ p=0.490, $\delta^{15}N$ p=0.573,).

Adult female PFS at Punta San Juan have been observed nursing a newborn, pup, and yearling simultaneously; the more stressful the environments, the more likely young still need to be nursing on adult female milk to meet metabolic needs for survival. With the increasing occurrence of ENSO conditions noted in Figure 3, dam's may experience a higher metabolic demand resulting in extended time at sea foraging, which subsequently may leave to pup starvation. Isotope signatures from milk would aid in understanding the dam-pup nutritional relationship that followed the gestation period resembled from pup whiskers. This information would provide further insight on potential malnutrition occurring during ENSO years when birth rates are lower (CSA-UPCH 2016, Cherel et al. 2015, CSA-UPCH 2017, 2018).

It is possible that this malnutrition has already been exemplified in the Punta San Juan reserve's population during the 2014-2016 ENSO. Population growth in the PSJ rookery had revealed a relatively steady increase from the years 2000 until approximately 2014 when the population plateaued, followed by a drastic decrease from 2015 continuing through 2017 by nearly 50% (CSA-UPCH 2016, 2017, 2018). In addition to this observed population decrease, data from the main breeding beach of PSJ revealed poor breeding seasons in 2012, 2014, 2015, and 2017, with 2014 and 2017 among the lowest fecundity observed (>300 individuals) (CSA-UPCH 2017, 2018).

Peruvian Fur Seal Males and Females

In both male and female Peruvian fur seals sampled from 2011 and 2012, $\delta^{15}N$ and $\delta^{13}C$ values were significantly different ((2011) p<0.001, (2012) p<0.001), foraging differences between adult males and females can be inferred. Females $\delta^{15}N$ and $\delta^{13}C$ were significantly more depleted than males (p<0.001, p<0.001, respectively) and no difference existed between the years analyzed (sample years 2011 and 2012). The male's average $\delta^{13}C$ was 0.51‰ higher than the females and the $\delta^{15}N$ was slightly enriched (1.36‰) relative to the female seals. These variances between male and female PFS detect potential differences in forging habits such as foraging within different trophic levels. Whether this is due to physical ability, metabolic capability, foraging location or depth, or simply different or larger prey preference cannot be inferred without potential prey source isotope signatures or tracking data.

South American Sea Lions

South American sea lion $\delta^{15}N$ signatures revealed a significant correlation with changing SSTA (p=0.002) and with ENSO phase (p=0.003), where anomalous warm phases corresponded with depleted $\delta^{15}N$ and cold phases corresponded with more enriched $\delta^{15}N$. Although, magnitude of ENSO event did not correlate significantly to SASL male signatures, this could be because these individuals were sampled in 2011. During the stretch of time these whiskers represented (prior to Nov. 2011), ENSO conditions were for the majority neutral (norm) to moderate cold phases with sporadic weak warm phases. Most of these anomalous ENSO conditions were short lived if beyond weak magnitudes. This leaves question to whether longevity of conditions holds more effect to trophic dynamics in these ecosystems rather than magnitude of these conditions. SASL $\delta^{13}C$ signatures did not reveal a significant change with fluctuating SSTA, which again, could be in relation to the longevity of these conditions rather than the magnitude or phase associated to the varying SSTA.

Sympatric Species

These sympatric marine mammal species did not reveal a significant difference in isotope signatures. However, the isotope signatures revealed large changes in PFS between years, while the SASL signatures revealed smaller variation between most years with some large-scale changes between select years (Figure 17); this could be a distinction between species response times to various ENSO conditions. ENSO phase correlated to SASL δ^{15}N more than PFS, while magnitude of ENSO phase effected SASL and PFS equally. SASL and PFS δ^{13}C signatures were similar and did not reveal a significant change with fluctuating SSTA. Although these species revealed similar isotope values, a PCA with trajectory involving δ^{15}N and δ^{13}C in combination revealed that both the PFS and SASL behaved differently throughout the time series. It could be assumed that PFS and SASL adapt differently in order to take advantage of productive conditions or survive resource-limited conditions.

This information could be indicative of different foraging behaviors throughout various ENSO events. Further evaluation of both prey items and biologging data would aid in determining the survival strategy these sympatric species must encounter in order to adapt to this apparent trophic niche overlap.

Conclusions

The Punta San Juan rookery is home to two sympatric species of Otariids, where ENSO conditions fluctuate frequently, producing ecological ramifications. This study provides an understanding of the impact of certain oceanographic influences on these pinnipeds. Vibrissae demonstrated multi-year timelines, which allowed evaluation of long term foraging in apex predators within this dynamic ecosystem. Stable isotope ratios from Peruvian pinnipeds reveal temporal dietary variations; gender- and species-related resource and habitat use were seen by providing a proxy of foraging habitat (δ^{13}C) and trophic level (δ^{15}N) inside and outside anomalous ENSO conditions.

All individual pinnipeds resembled that of others within the population; however, isotope signatures varied between gender and species. Assessment of PFS pup vibrissae grown in-utero in conjunction with dam whiskers, revealed that pup vibrissae are interchangeable with dam vibrissae as a proxy of maternal diet throughout the gestation period, similar to studies done with bearded seals and gray seals (Hindell et al. 2012, Lerner et al. 2018). Pups revealed identical signatures to that of the dam within the gestation period, revealing that signatures evaluated in females resemble dietary conditions pups were also influenced by throughout developmental stages.

Females revealed significantly more depleted δ^{13}C and δ^{15}N than males; males fed within more enriched environments and potentially at a higher trophic level. However, SASL and PFS males did not reveal a significant difference between isotope signatures. It can be presumed that males of both species adapt to ENSO conditions differently than females do, but similarly to that of one another. This is most likely due to demands associated with maternal pup attendance, unlike males who after mating can forage and move as necessary. Males are also not metabolically taxed by feeding young. These sympatric species revealed differences between years that could resemble successful survival adaptations to resource limitation.

Varying SSTA readings were correlated to fluctuations in δ^{15}N isotope signatures revealing evidentiary support that ENSO conditions alter the foraging of these apex predators over time. Anomalous warm phase temperatures had a strong influence on δ^{15}N, which revealed the most depleted signatures, whereas cold phase anomalous conditions revealed the most enriched δ^{15}N signatures. Although δ^{13}C revealed minor fluctuations over the 12-year timeframe, δ^{13}C did reveal trophic significant enrichment and depletion during specific points in time. Additionally, both δ^{13}C and δ^{15}N were inversely correlated from 2014 to 2016 during the strongest El Nino-Southern Oscillation event on record. As δ^{15}N became depleted, δ^{13}C became more enriched; this could indicate that as SSTA became more positive (e.g. ENSO warm phase conditions), prey availability in their foraging grounds changed, possibly forcing pinnipeds to forage farther off shore or scavenging within foraging grounds, potentially spending more time at sea to do so. This observation resembles Majluf’s (1987) observations where females were absent for long periods of time, upwards of 20 days, during El Nino events causing major ramifications on offspring growth and survival (Gentry & Kooyman 1986, Majluf 1987b). The PFS δ^{13}C and δ^{15}N signatures recorded reflect a shift in available prey, as environmental conditions become unfavorable for anchoveta and favorable for sardines, vice versa (Benson and Trites 2002, Alheit and Niquen 2004).

The approximate growth rate of 0.09 mm/day revealed an average of 3.5 years represented in individual PFS whiskers and 5.3 years within individual male SASL whiskers. Although behavioral adaptations could not be evaluated based solely on these pinniped isotope ratios, fluctuations in both stable isotopes across years revealed that the seals were still feeding within these stressful conditions and managed to adapt in order to survive. Considering that the 2014-2016 ENSO event was the strongest on record, it leaves question to whether these adaptations could be executed for such a strong magnitude (e.g., Extreme) and long duration of time (e.g., ~3 years). With the mean trend of SSTA in the 1+2 Nino region continuously increasing over 1°C over the past decade (Figure 3), both increased duration and magnitude threaten these vulnerable species. These anomalous climatic conditions elicit changes in primary production, which may force alternative foraging strategies for the survival of these locally endangered marine mammals.

Future Research

Comparing apex predator $\delta^{13}C$ and $\delta^{15}N$ to those values found in common prey species helps to detect food web changes (DeNiro & Epstein 1981). By comparing vibrissae stable isotope data as done in this baseline study, with those of potential prey, these data would provide information regarding food web linkages and ocean productivity along the coast of Peru and other associated ecosystems (France & Peters 1997, Hirons 2001, Kurle & Worthy 2001). This information would serve fisheries with valuable information on prey available during various ENSO conditions, as PFS are selective foragers by nature and primarily forage on anchovy when available. If PFS do not target this prey during select periods, this could be in relation to fish species abundances and would allow for a better overall understanding of ENSO-induced ecosystem shifts.

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Appendix

Appendix A: Sea Surface Temperature Plots and Tables
Appendix B: Vibrissae Plots (Peruvian Fur Seal)
Appendix C: Vibrissae Plots (South American Sea Lion)
Appendix D: Vibrissae Tables

Appendix A: Sea Surface Temperature Plots and Tables

Table 3. Monthly Sea Surface Temperature Averages from Nino Index 1+2 Region (Years 2000 to 2016). Blue=cold phase ENSO, Red=warm phase ENSO (NOAA_ERSST_V5 data provided by the NOAA/OAR/ESRL PSD).

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC
2000	-0.74	-0.54	-0.40	0.03	-0.24	-0.27	-0.25	-0.58	-0.24	-0.31	-1.23	-1.03
2001	-0.61	-0.40	0.24	0.25	-0.55	-0.73	-0.55	-0.85	-1.14	-1.17	-0.93	-1.09
2002	-0.76	0.01	0.84	0.89	0.78	0.50	-0.20	-0.27	0.19	0.34	0.93	1.03
2003	0.15	-0.04	0.00	-0.49	-1.49	-1.24	-0.98	0.00	-0.46	0.20	0.24	0.15
2004	-0.19	0.02	-0.67	-0.50	-1.44	-0.96	-0.75	-0.75	-0.28	0.11	0.67	0.29
2005	0.00	-0.86	-1.39	-0.35	-0.23	-0.66	-0.32	-0.41	-0.75	-1.30	-1.47	-1.00
2006	-0.35	0.30	-0.22	-1.43	-0.40	-0.10	0.23	0.69	0.96	1.02	0.75	0.64
2007	0.68	0.19	-0.57	-1.16	-1.63	-1.49	-0.95	-1.21	-0.98	-1.55	-1.77	-1.73
2008	-0.46	-0.30	0.46	0.48	0.69	0.67	1.02	1.39	1.01	0.32	-0.32	-0.53
2009	-0.15	-0.60	-0.74	0.48	0.50	0.77	0.78	0.83	0.50	0.29	0.29	0.53
2010	0.30	0.20	0.14	-0.04	0.39	0.13	-1.00	-1.32	-1.23	-1.32	-1.35	-0.98
2011	-0.46	-0.07	-0.81	-0.13	0.27	0.41	0.13	-0.22	-0.75	-0.81	-0.61	-0.75
2012	-0.16	0.44	0.23	0.97	1.03	1.13	0.43	0.06	0.05	-0.40	-0.45	-0.92
2013	-0.66	-0.65	-0.60	-1.16	-1.43	-1.79	-1.57	-1.17	-0.78	-0.78	-0.60	-0.51
2014	0.02	-0.53	-0.24	0.04	1.22	1.66	1.01	0.88	0.79	0.66	0.76	0.34
2015	-0.13	-0.45	0.16	1.07	1.70	2.31	2.57	1.64	2.27	2.09	2.23	2.14
2016	1.81	1.38	1.42	0.52	0.64	0.76	0.28	0.23	0.56	0.31	0.08	0.35

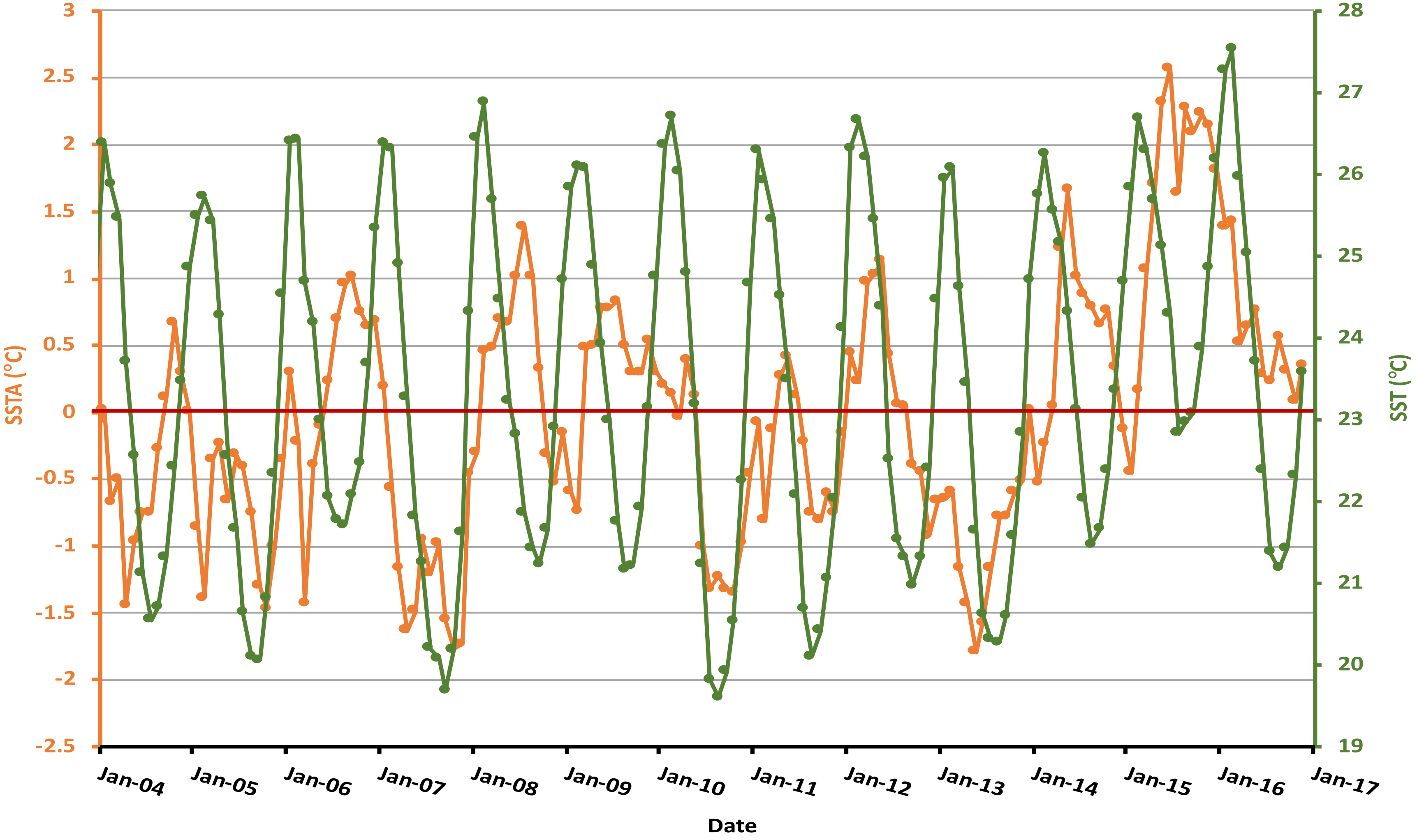

Figure A-1. Sea surface temperature versus sea surface temperature anomaly (°C) from 1+2 Nino index, 2004-2016 (NOAA_ERSST_V5 data provided by the NOAA/OAR/ESRL PSD).

Appendix B: Vibrissae Plots (Peruvian Fur Seal)

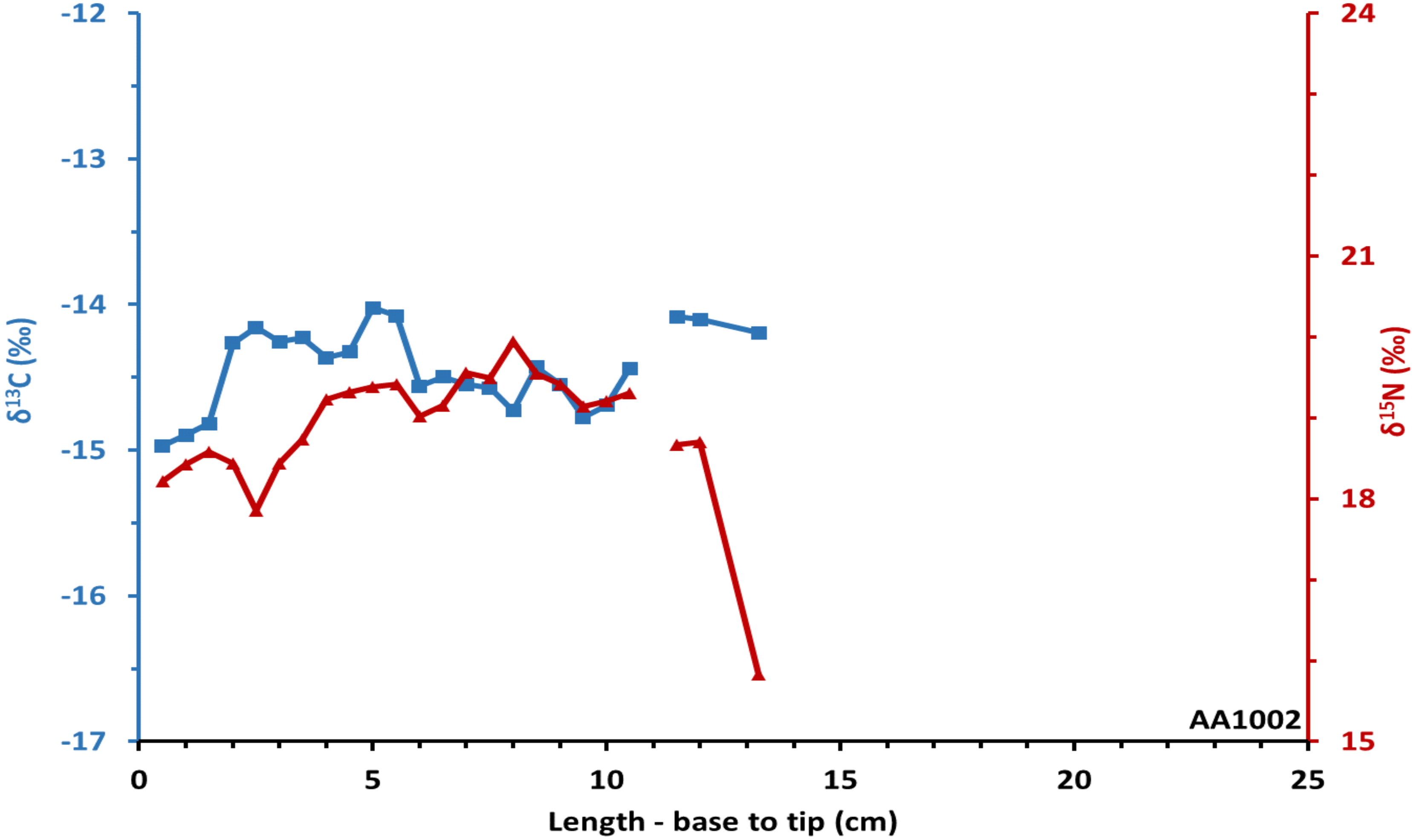

Figure B-1. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1002), 2010.

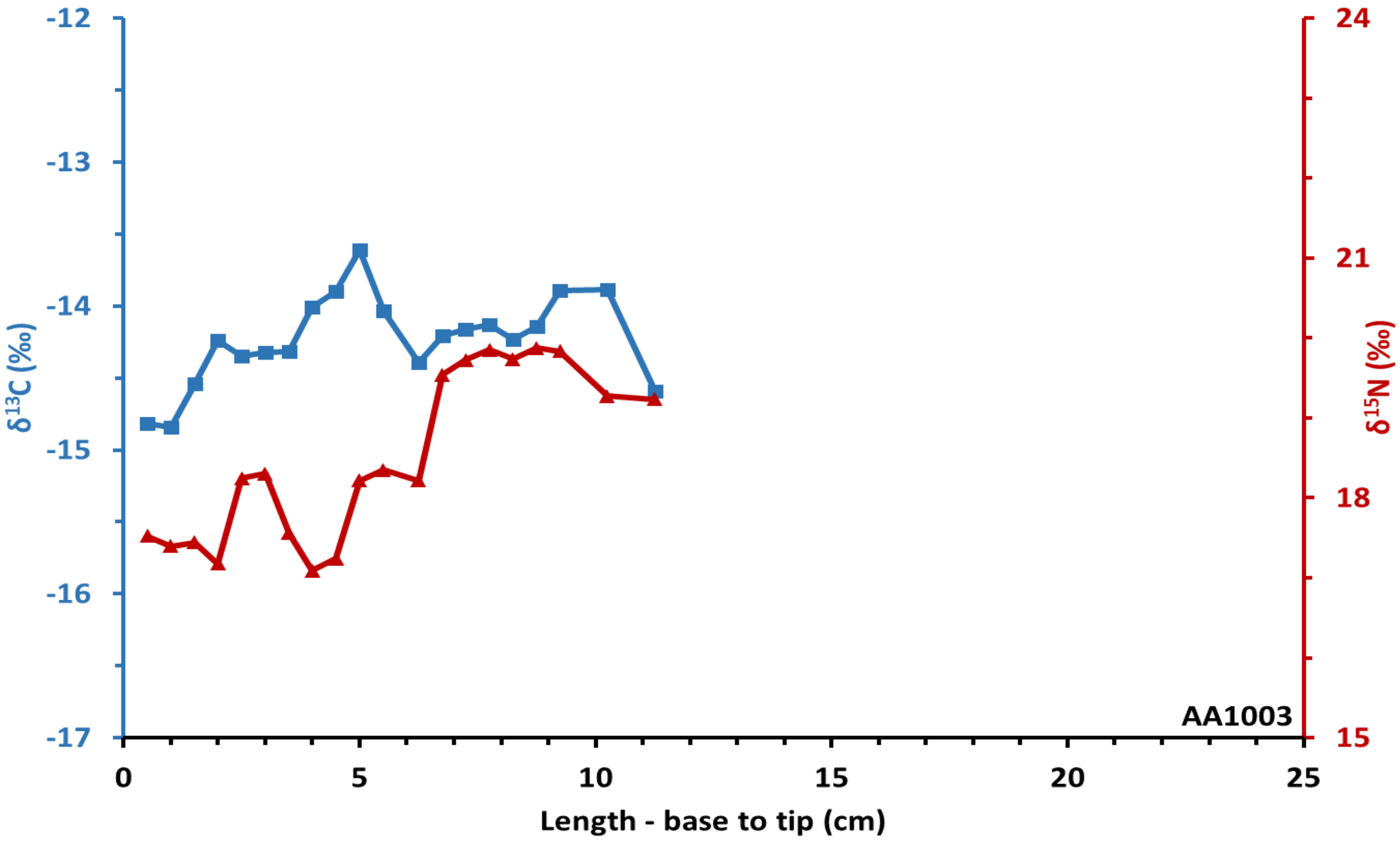

Figure B-2. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1003), 2010.

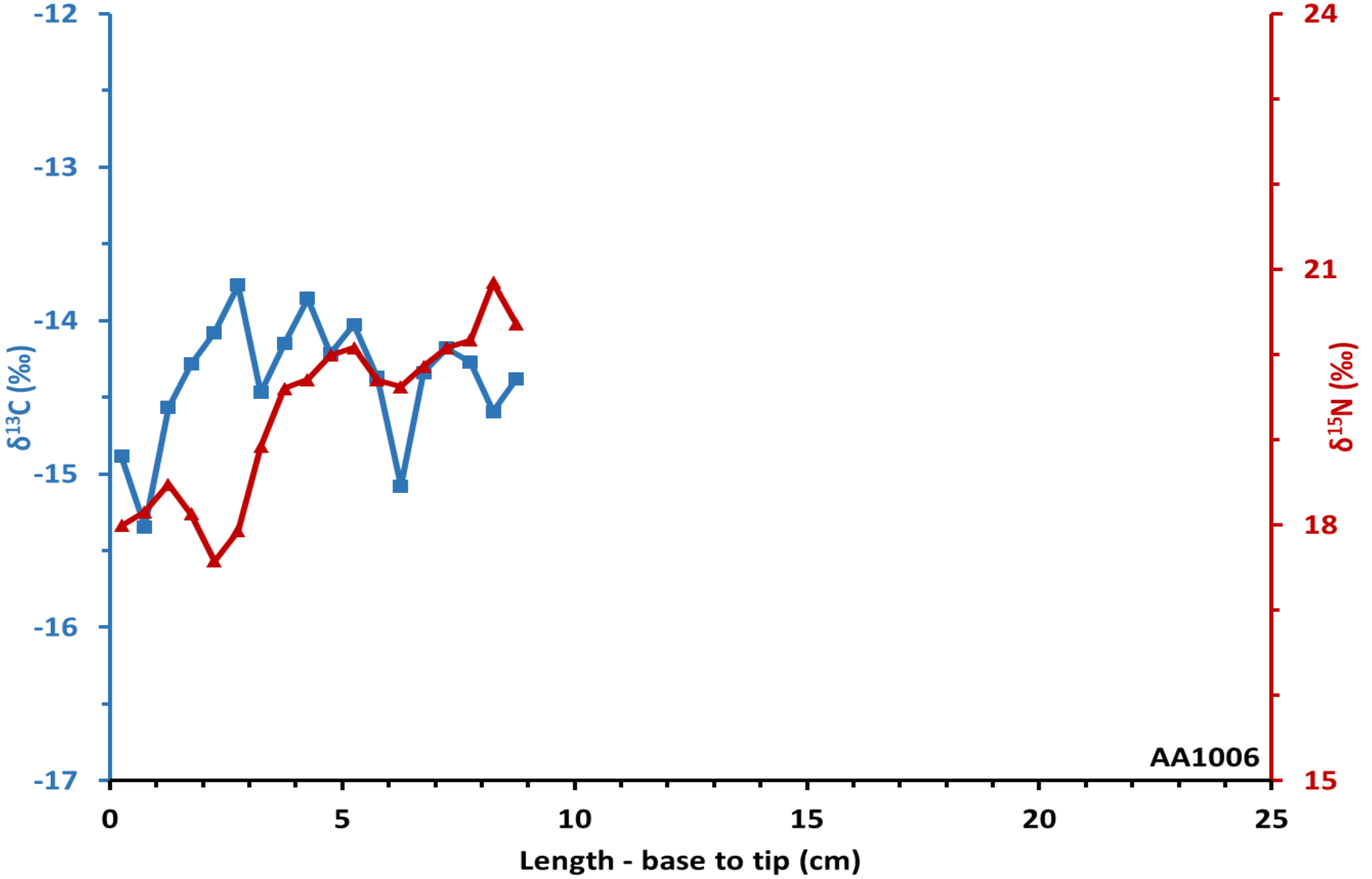

Figure B-3. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1006), 2010.

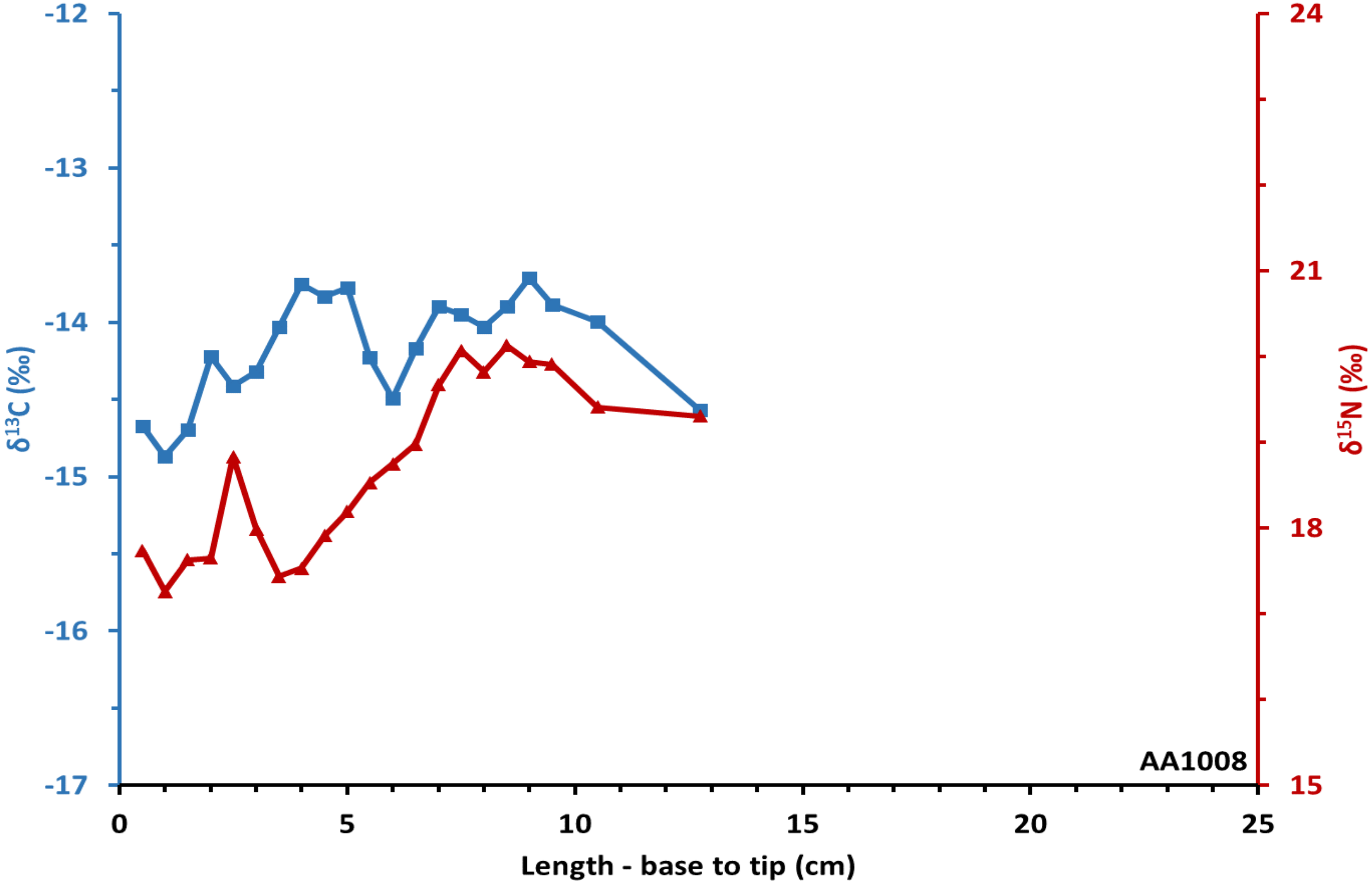

Figure B-4. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1008), 2010.

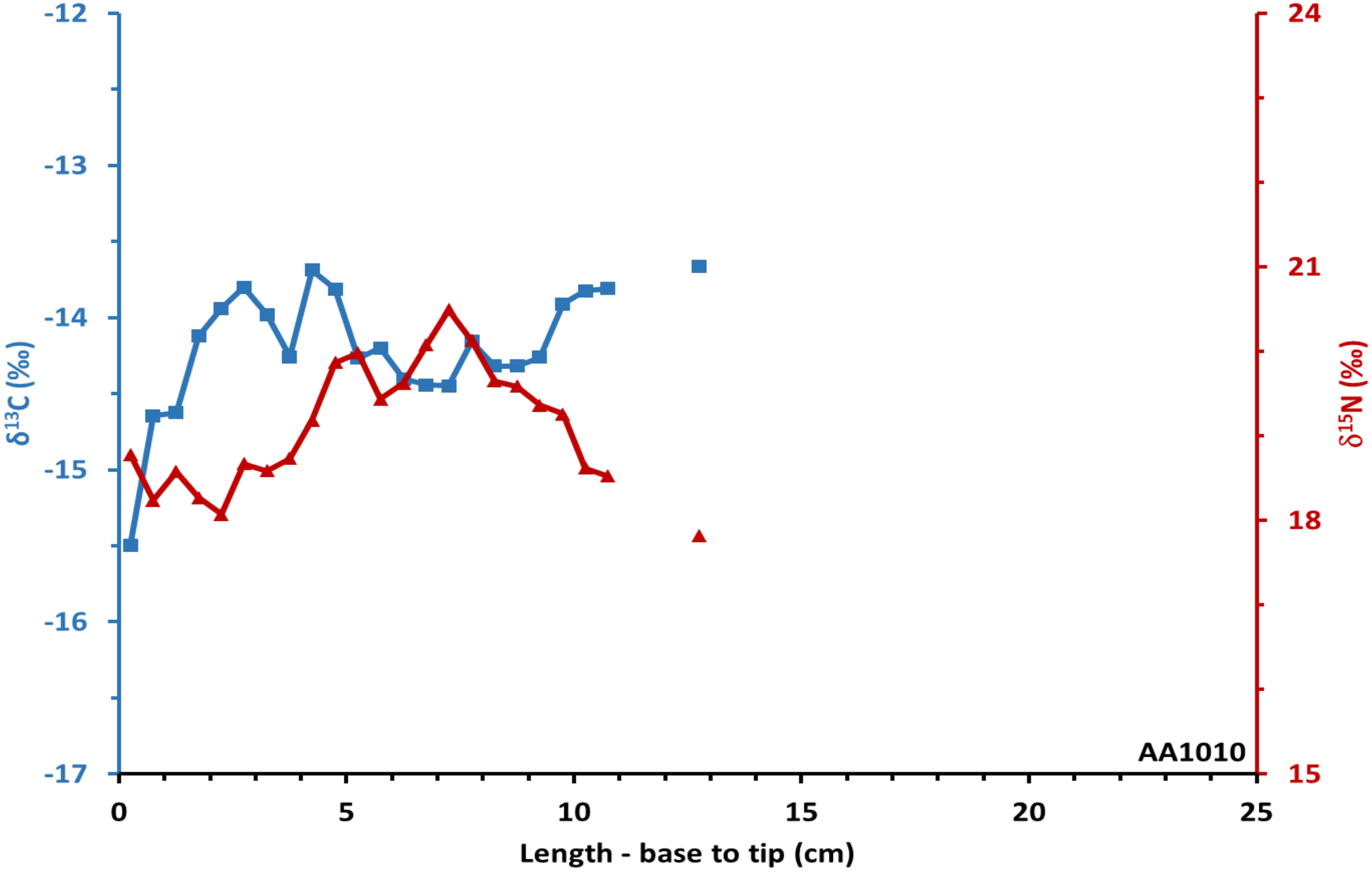

Figure B-5. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1010), 2010.

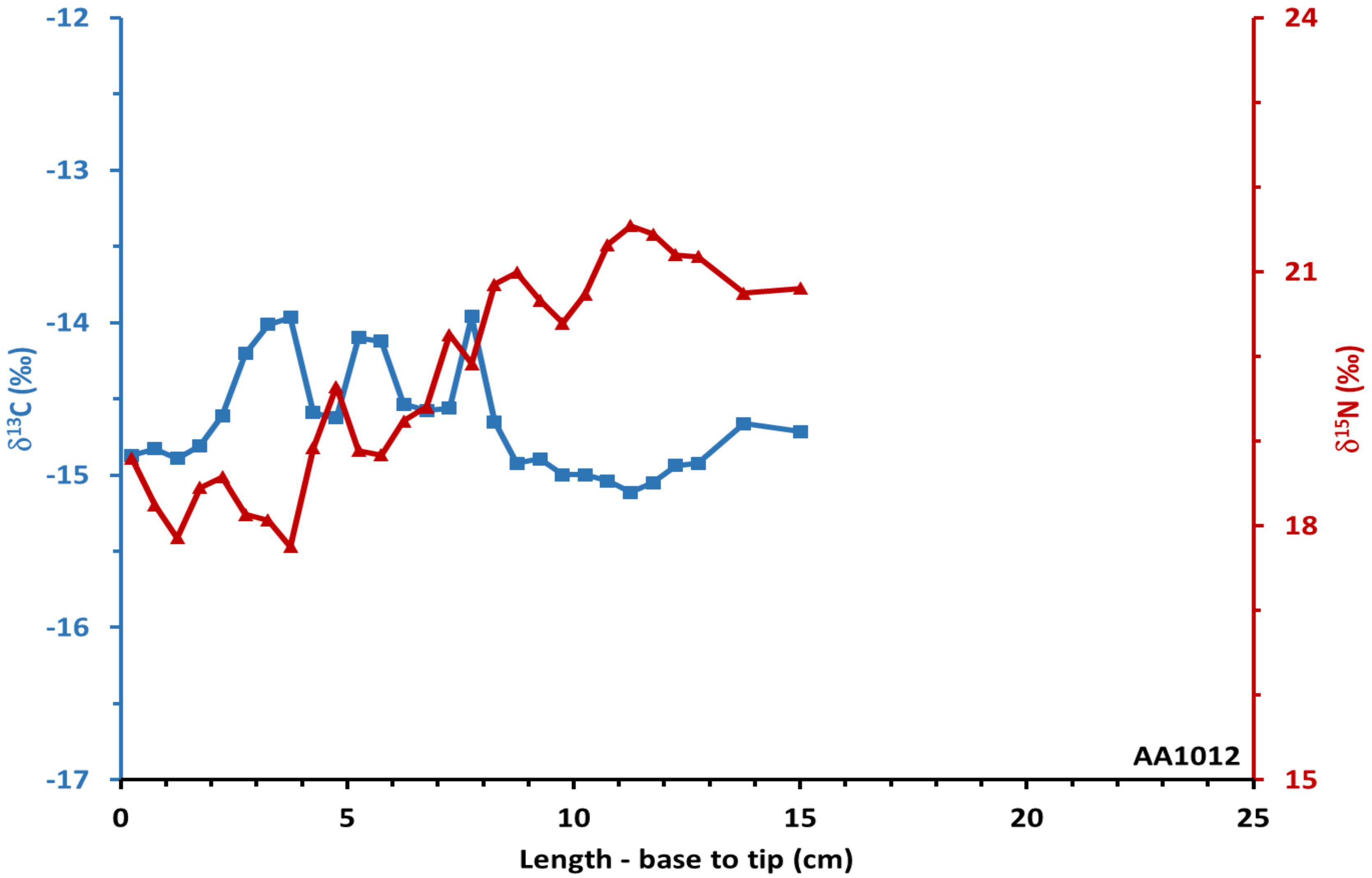

Figure B-6. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1012), 2010.

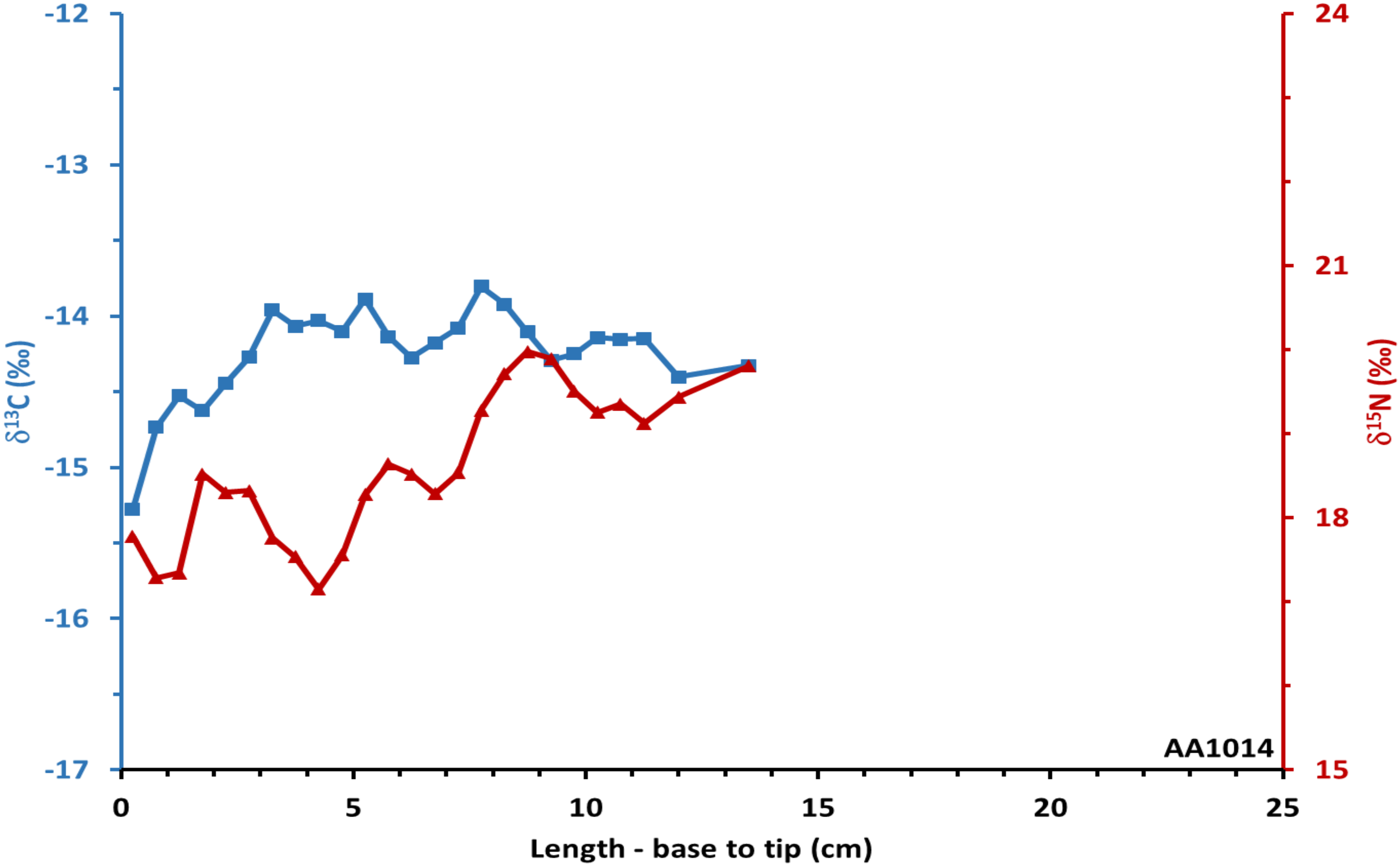

Figure B-7. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1014), 2010

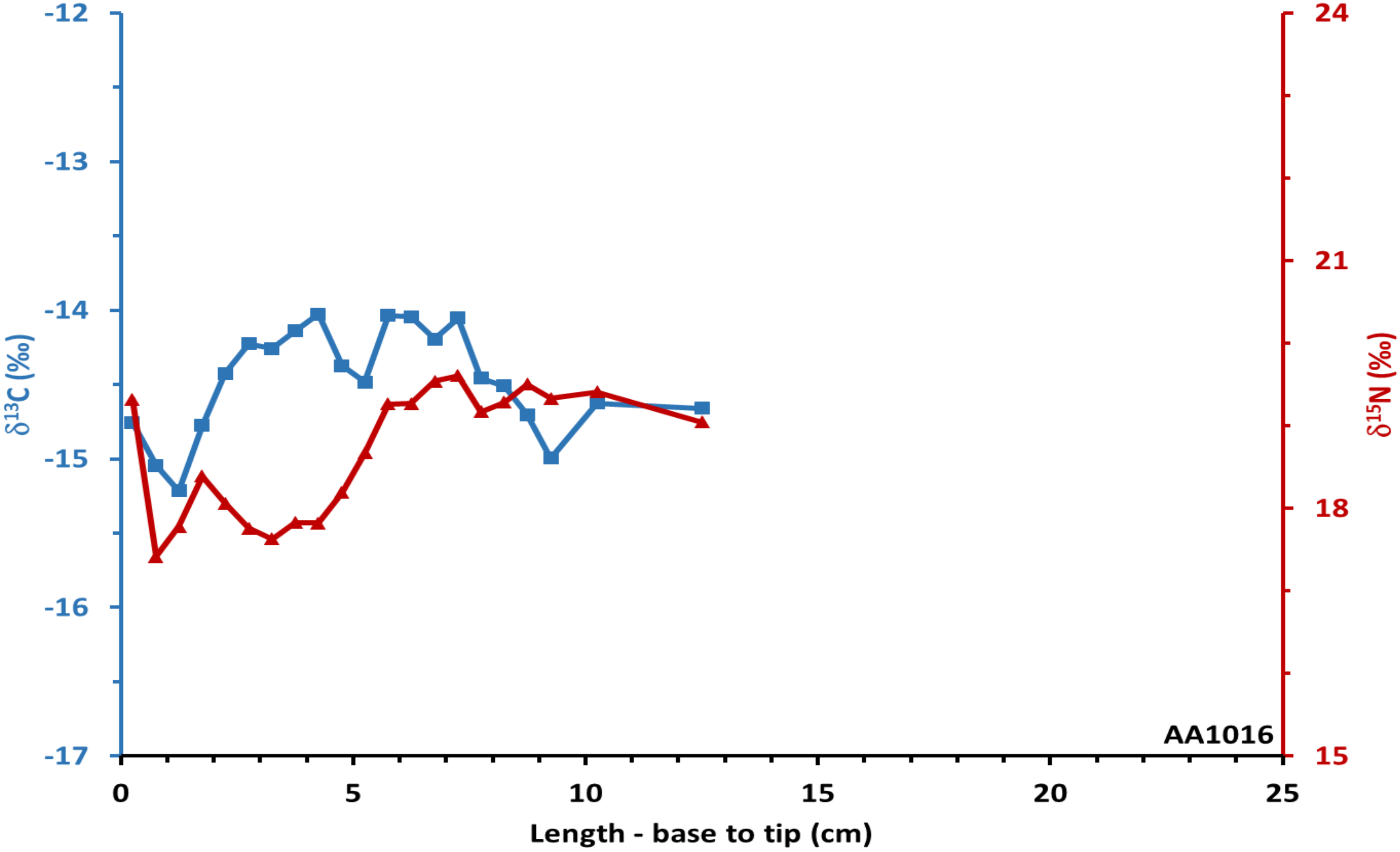

Figure B-8. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1016), 2010.

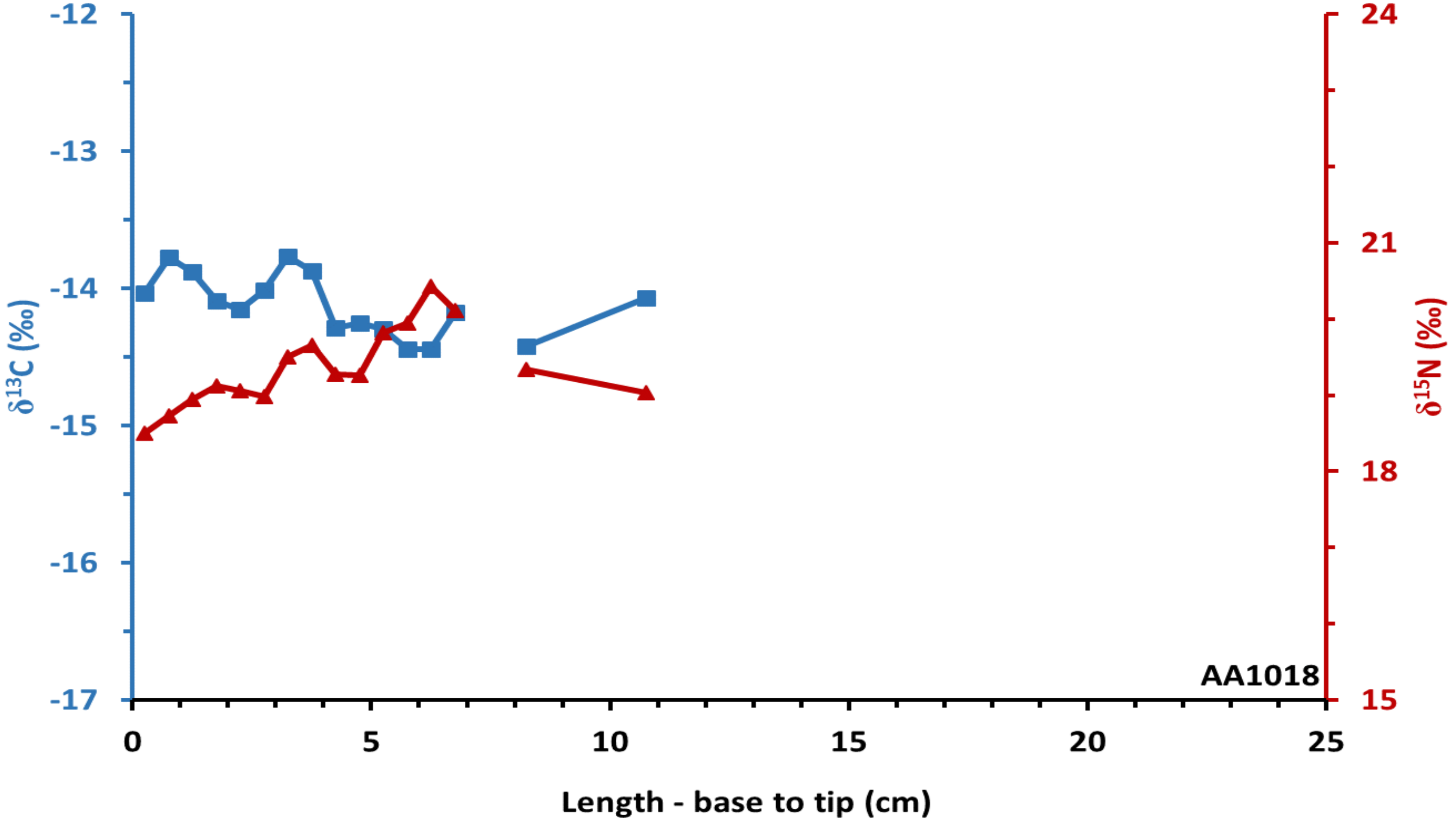

Figure B-9 Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1018), 2010.

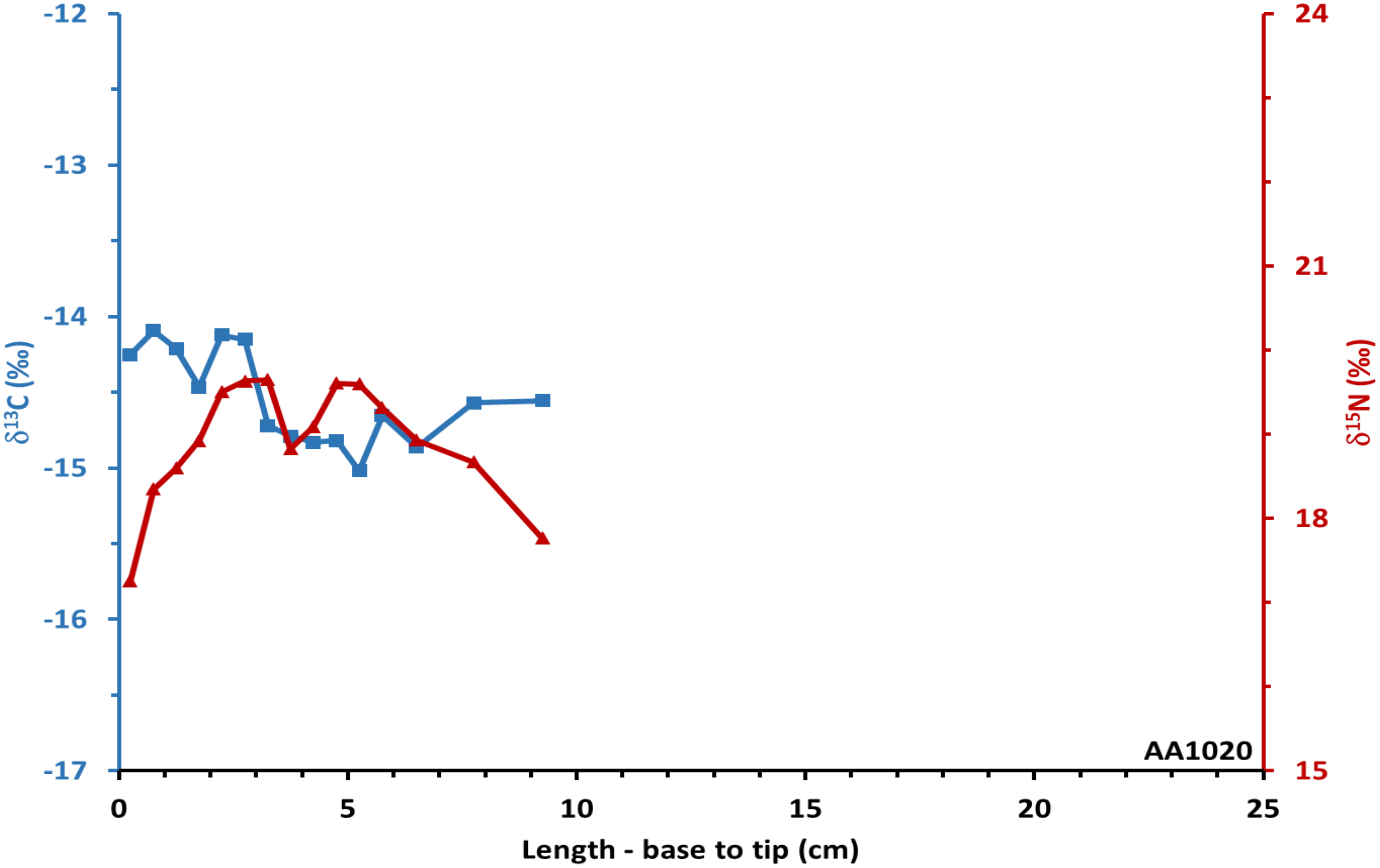

Figure B-10. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1020), 2010.

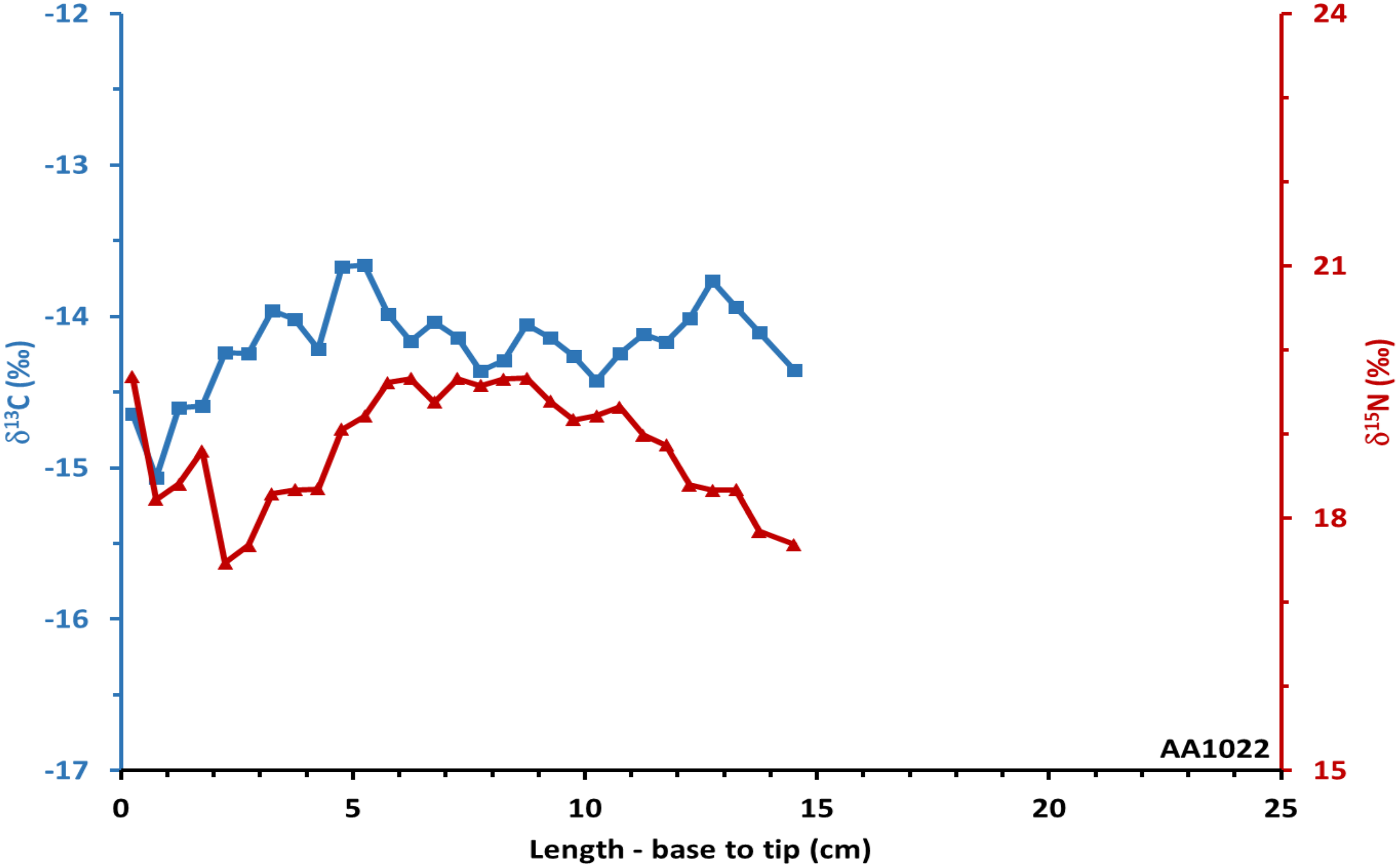

Figure B-11. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1022), 2010.

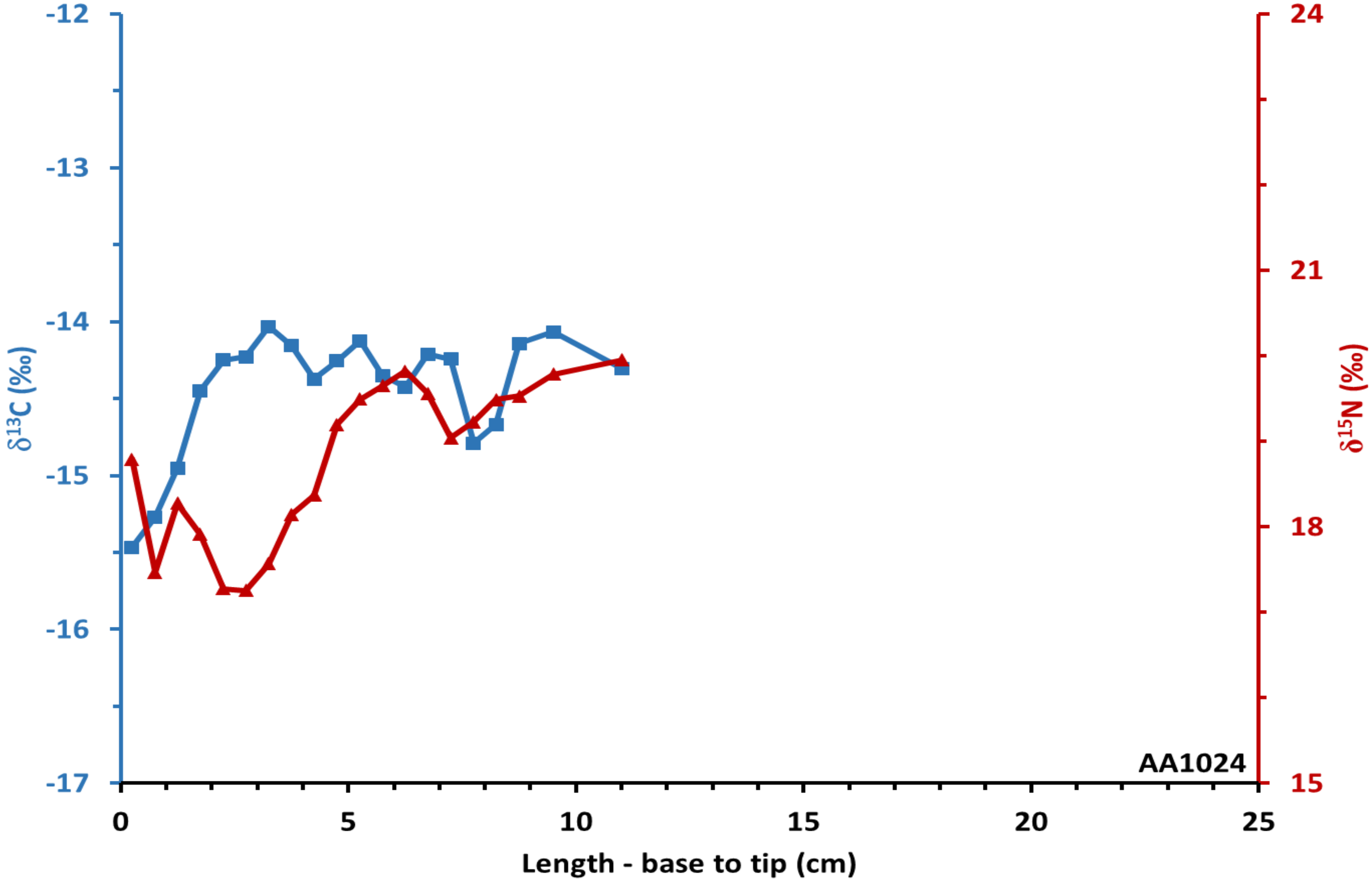

Figure B-12 Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1024), 2010.

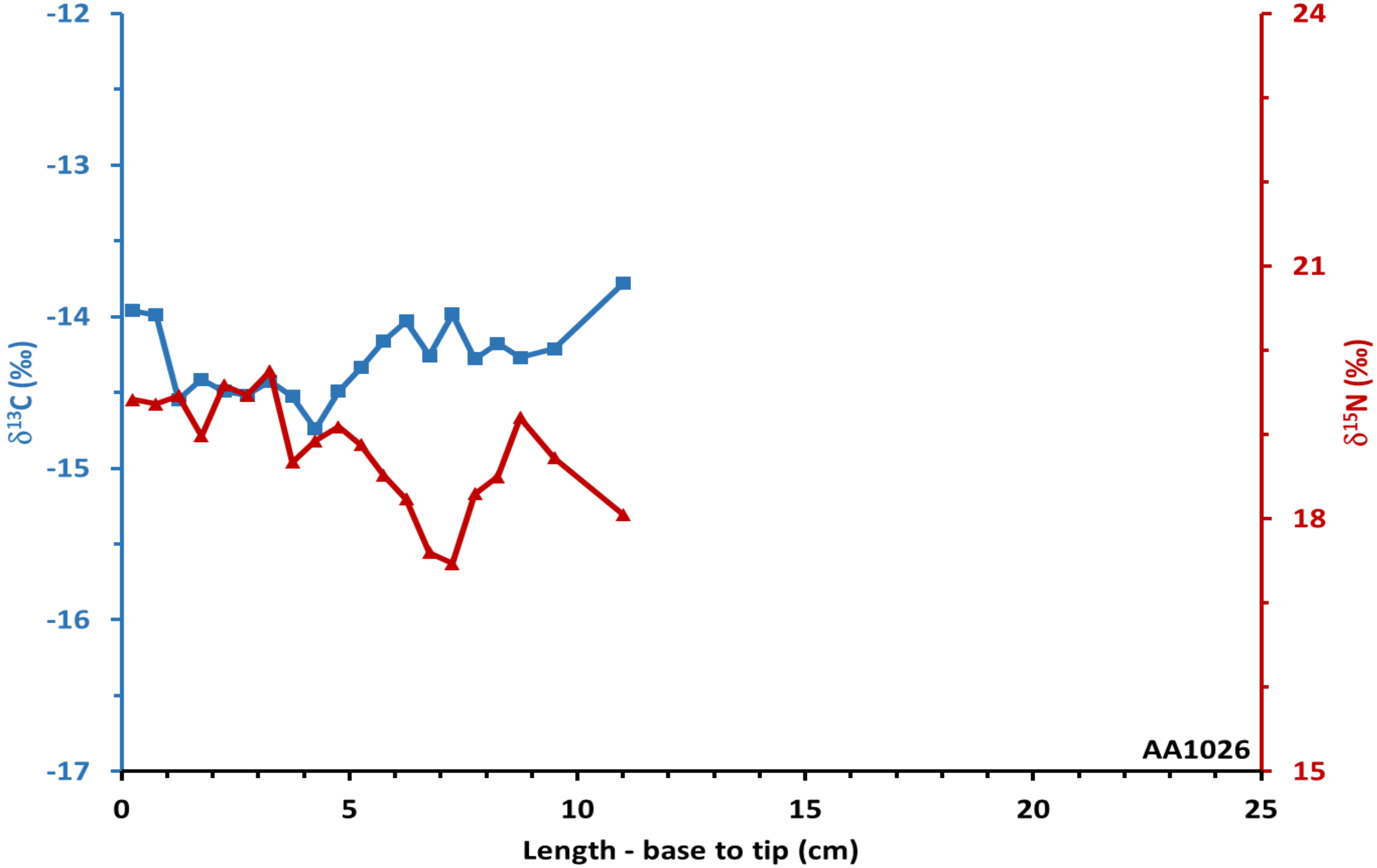

Figure B-13. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1026), 2010.

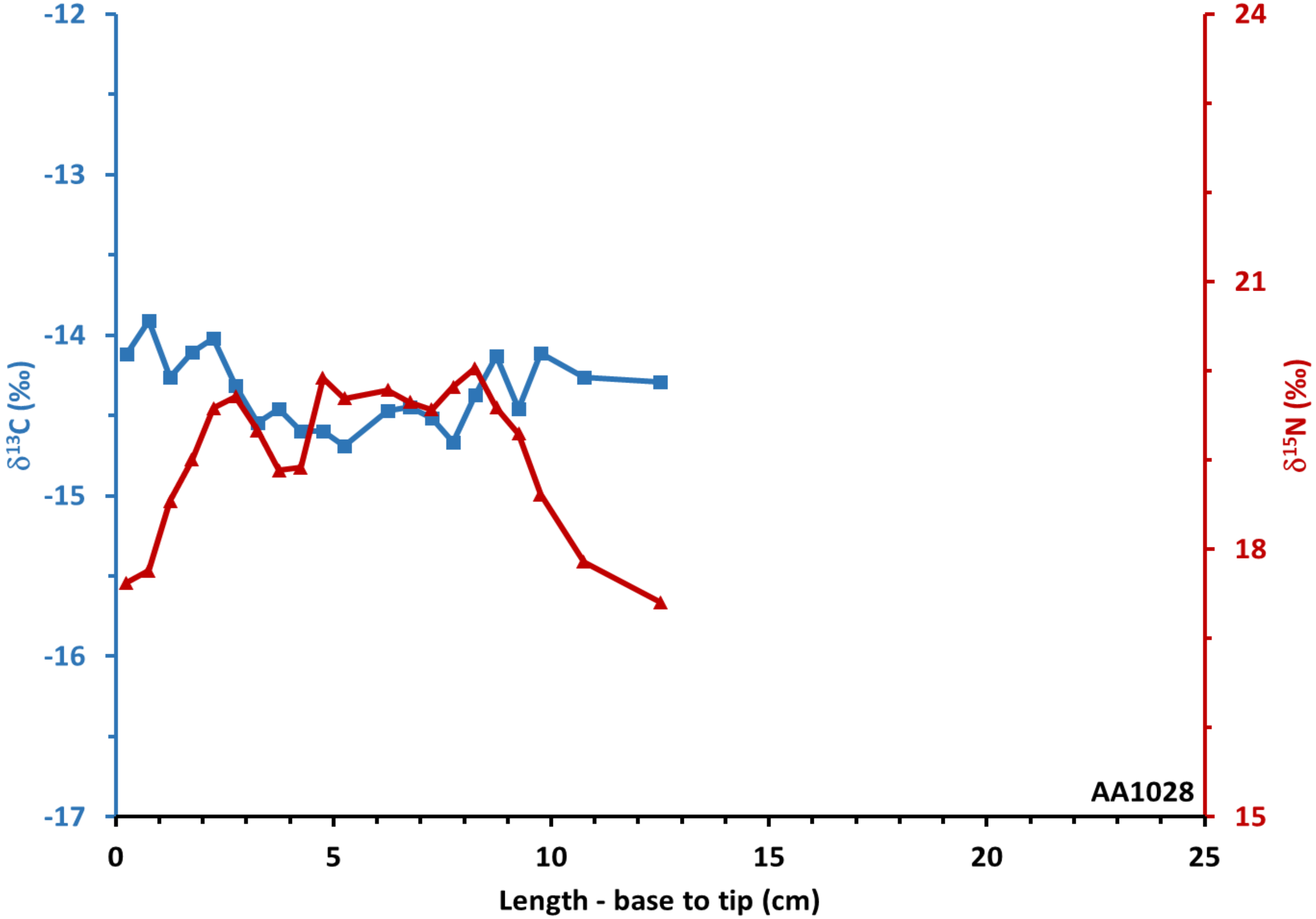

Figure B-14. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1028), 2010.

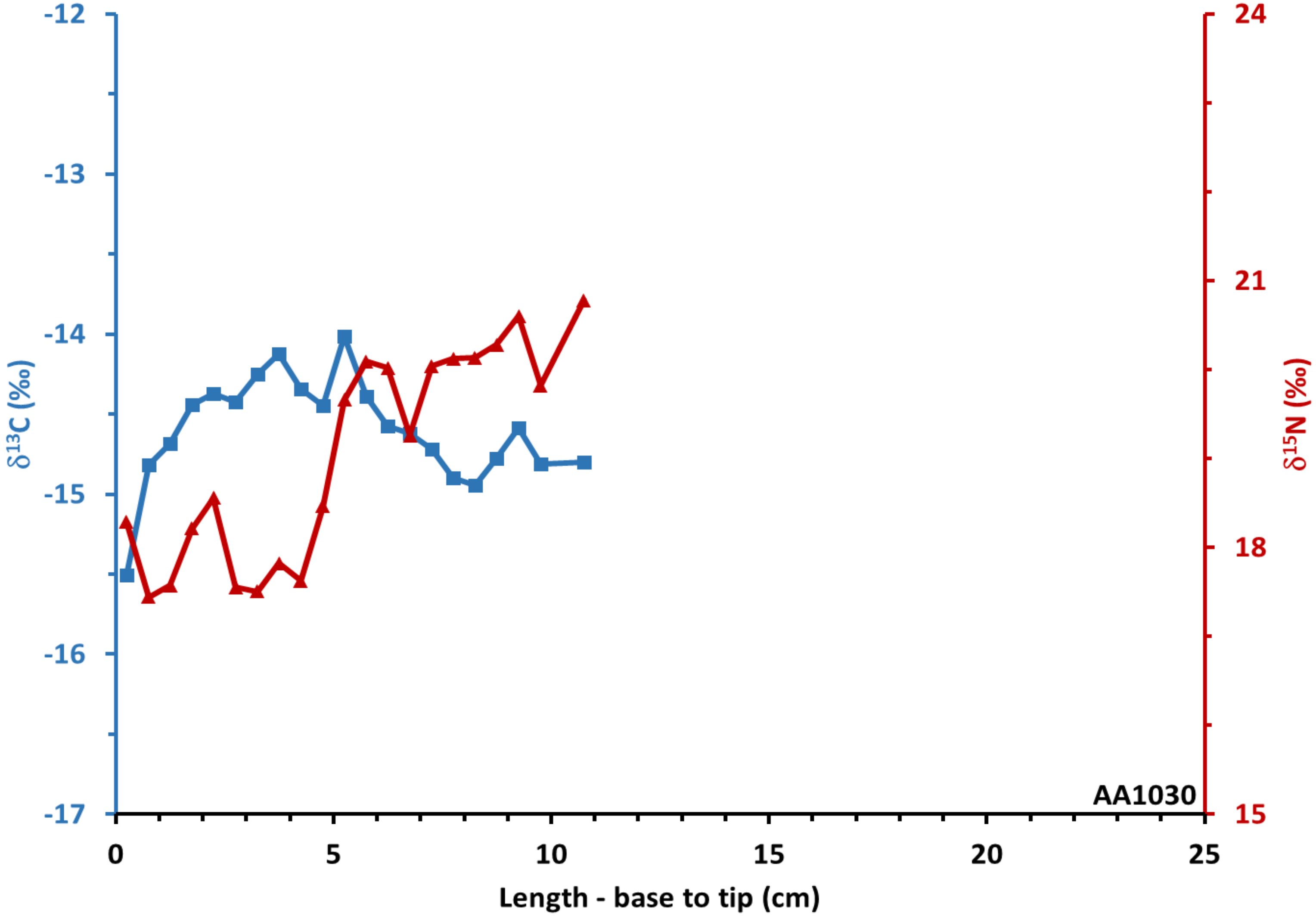

Figure B-15. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1030), 2010.

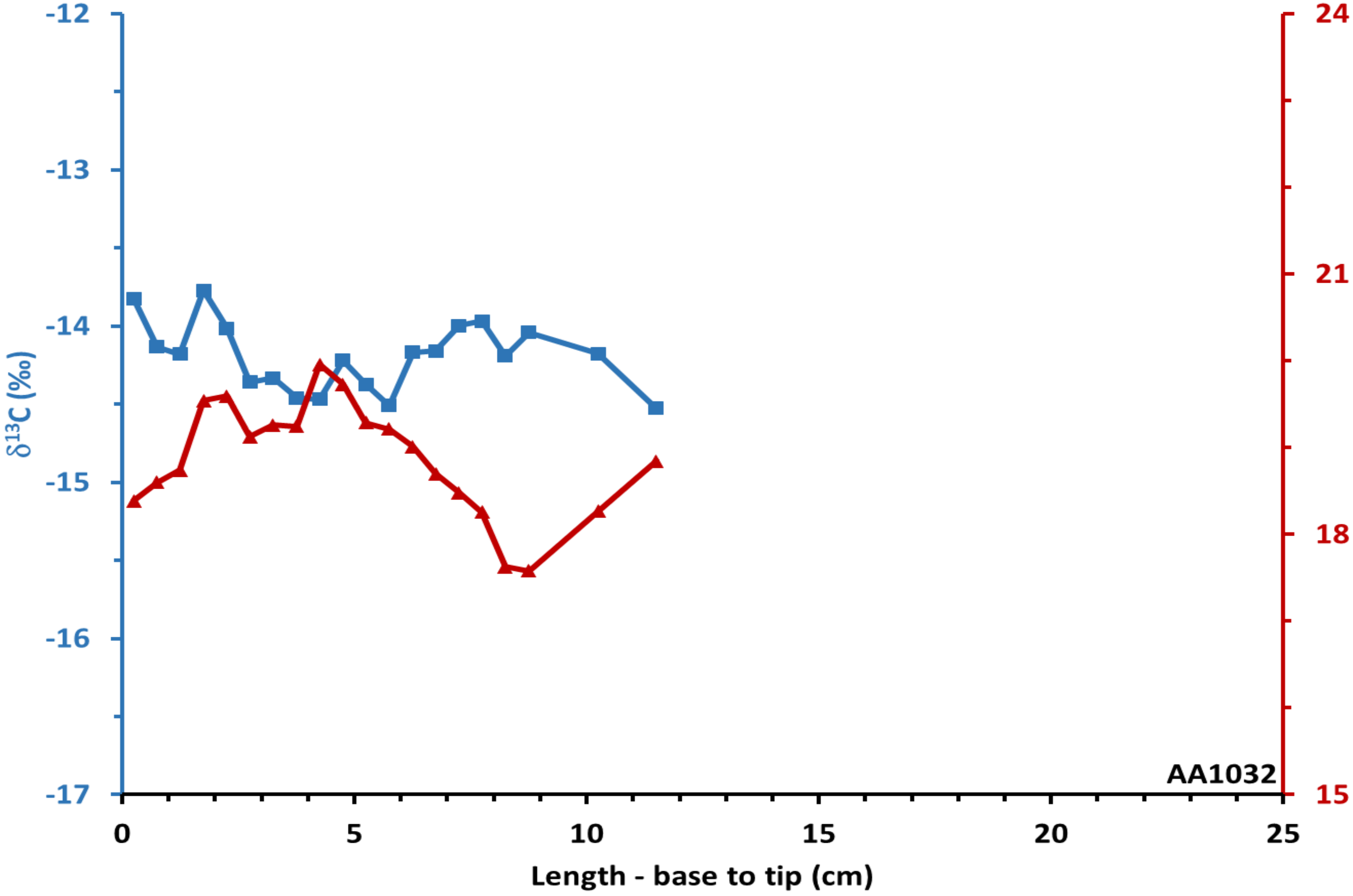

Figure B-16. Adult female Peruvian fur seal vibrissae δ13C and δ15N (AA1032), 2010.

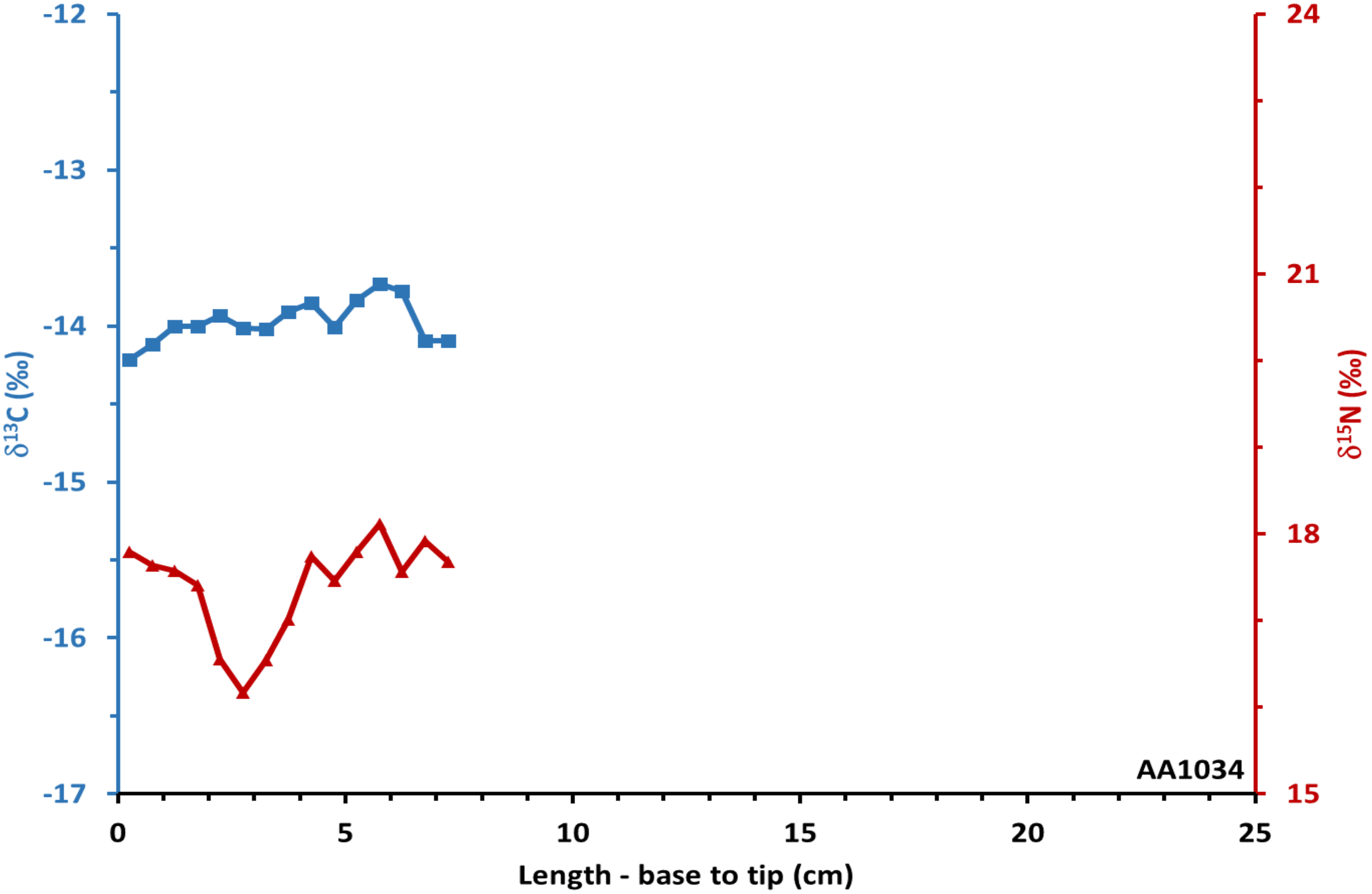

Figure B-17. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1034), 2010.

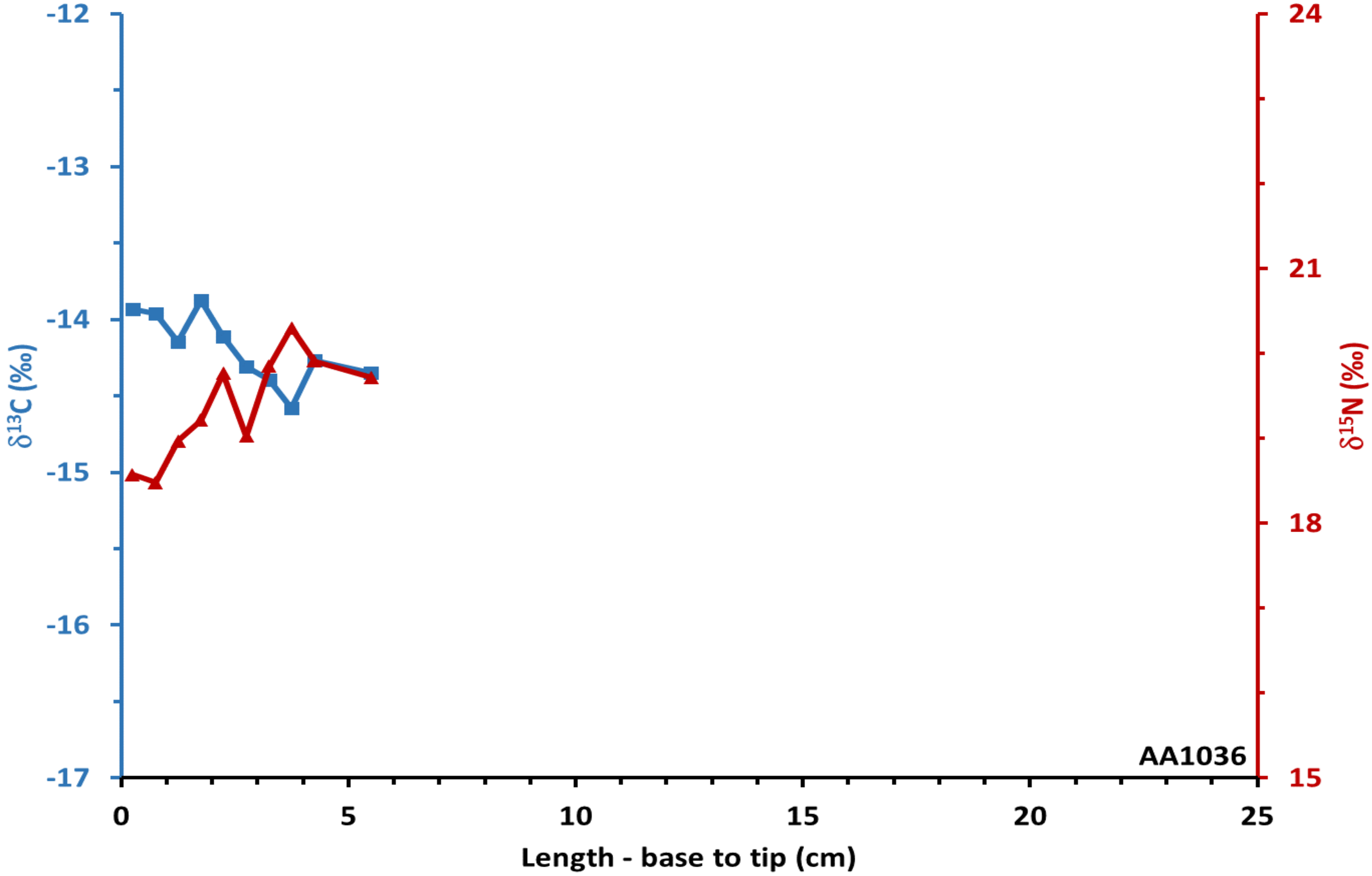

Figure B-18. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1036), 2010.

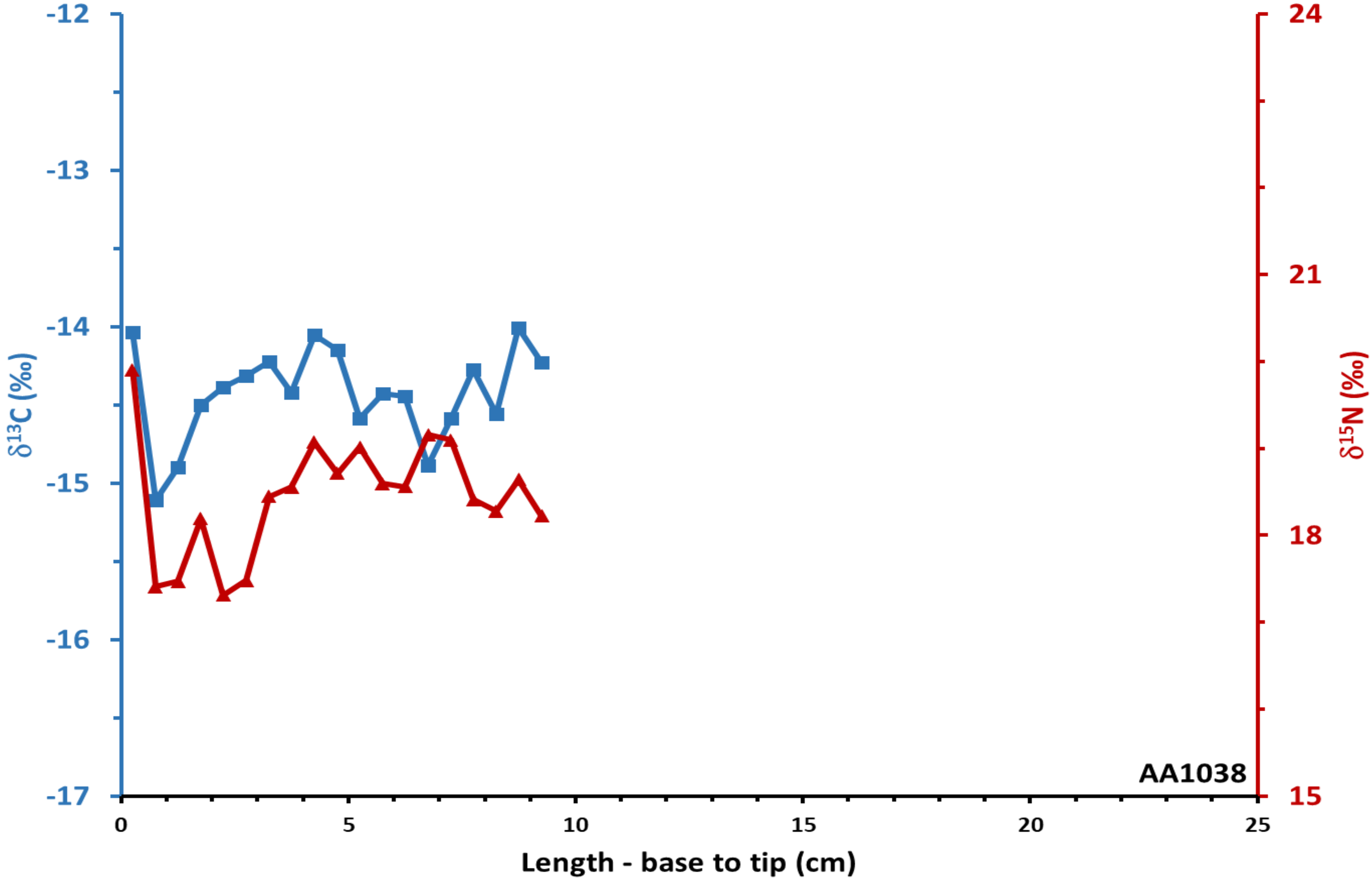

Figure B-19. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1038), 2010.

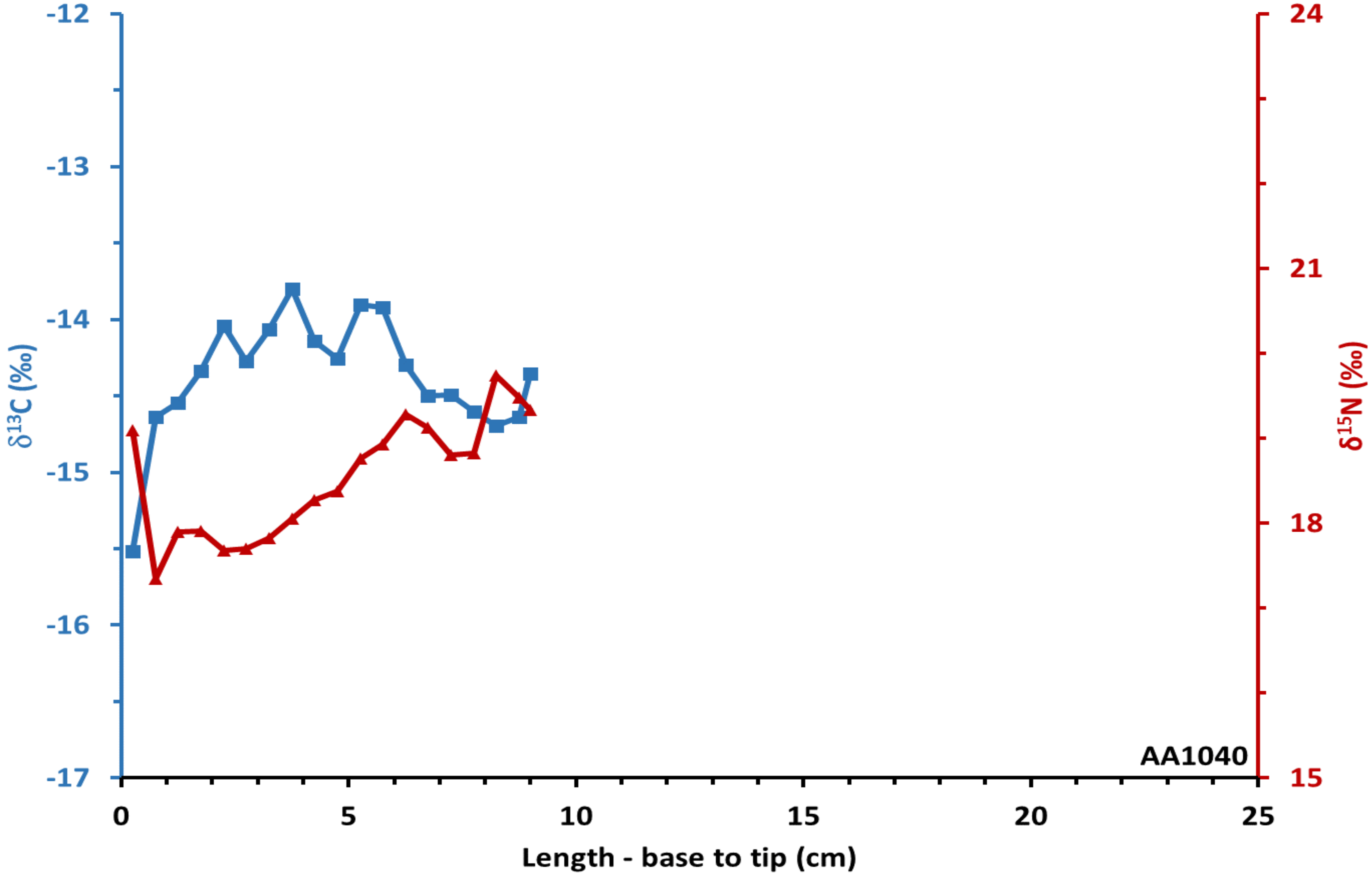

Figure B-20. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1040), 2010.

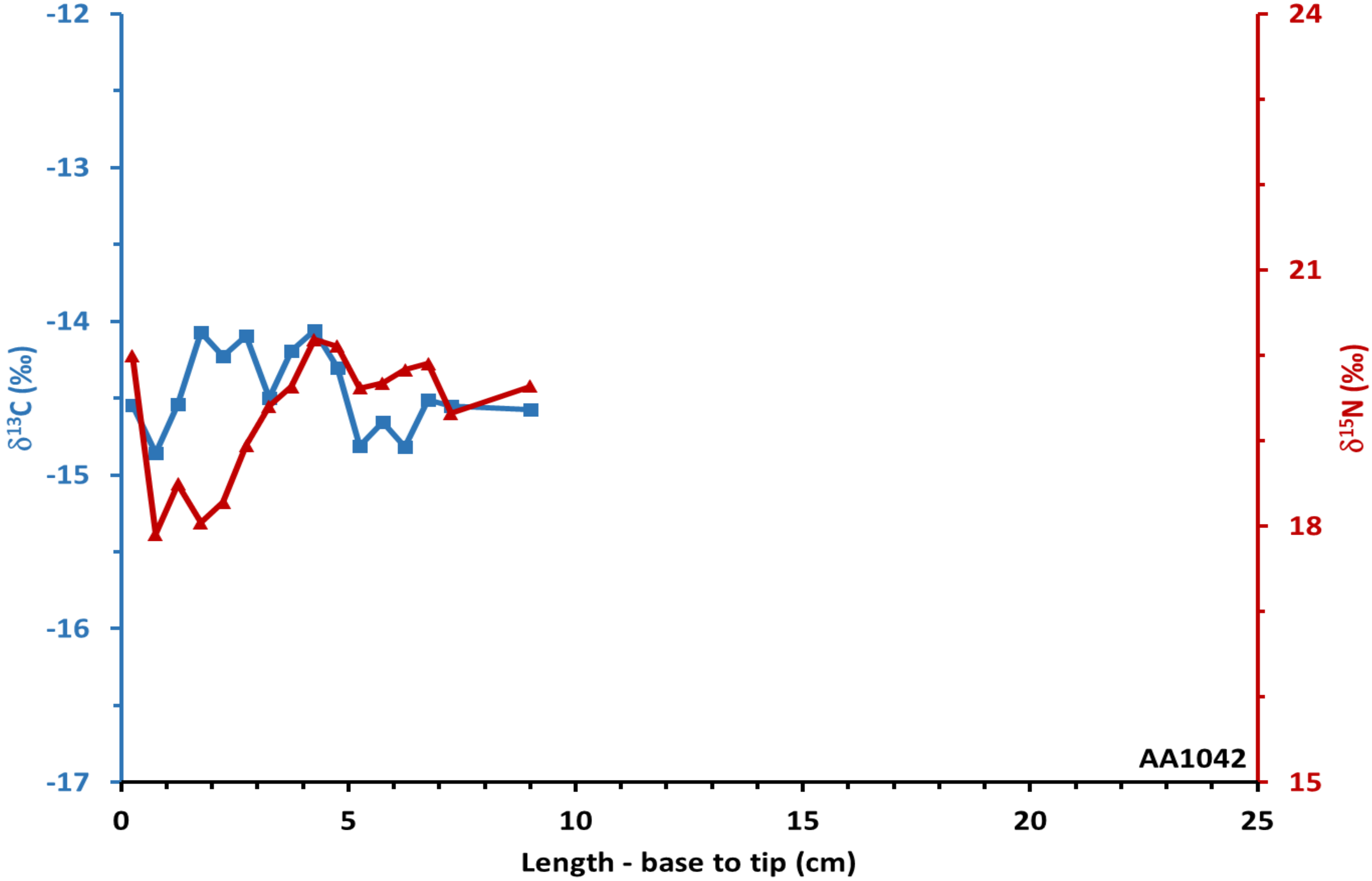

Figure B-21. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1042), 2010.

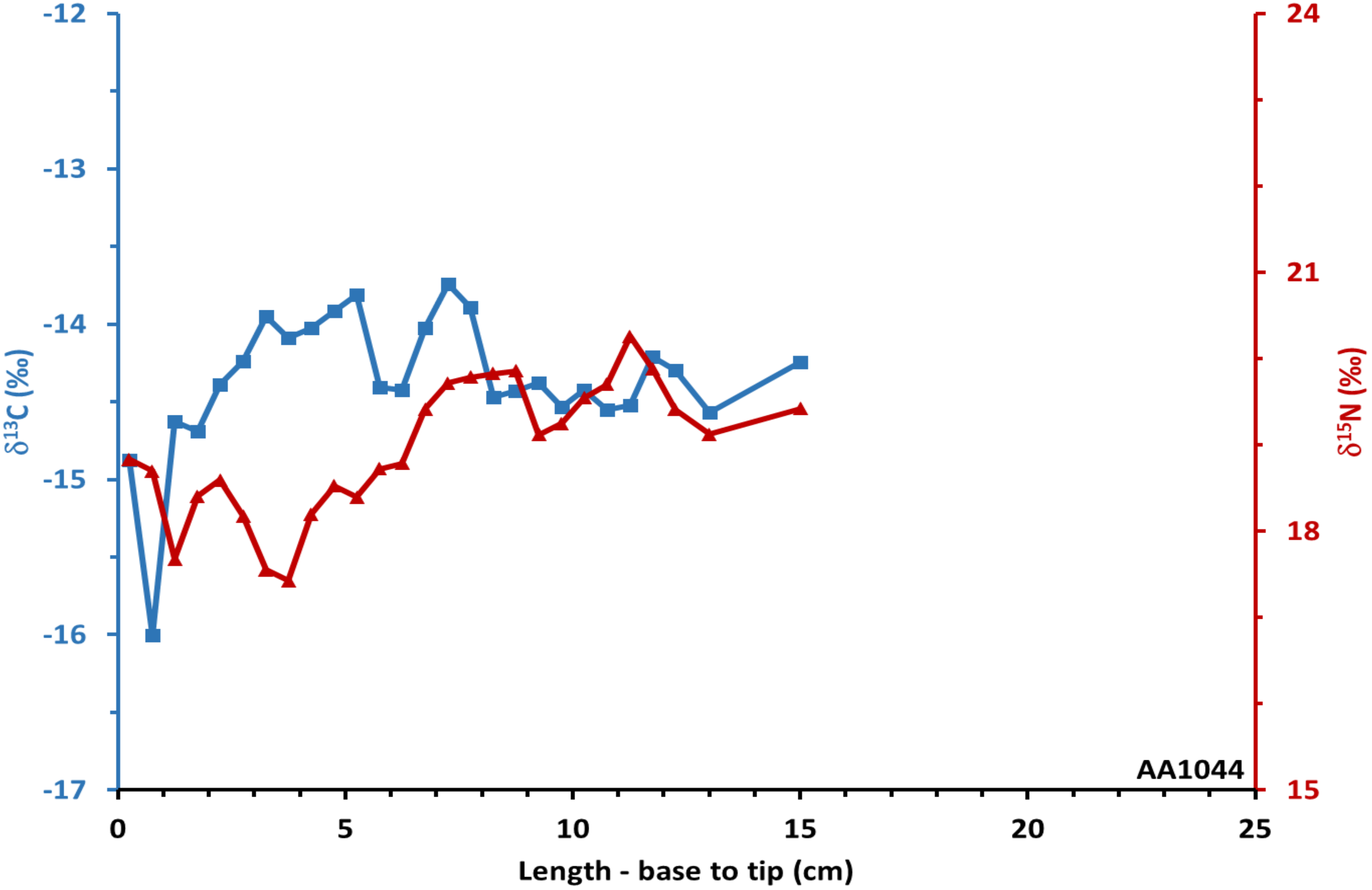

Figure B-22. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1044), 2010.

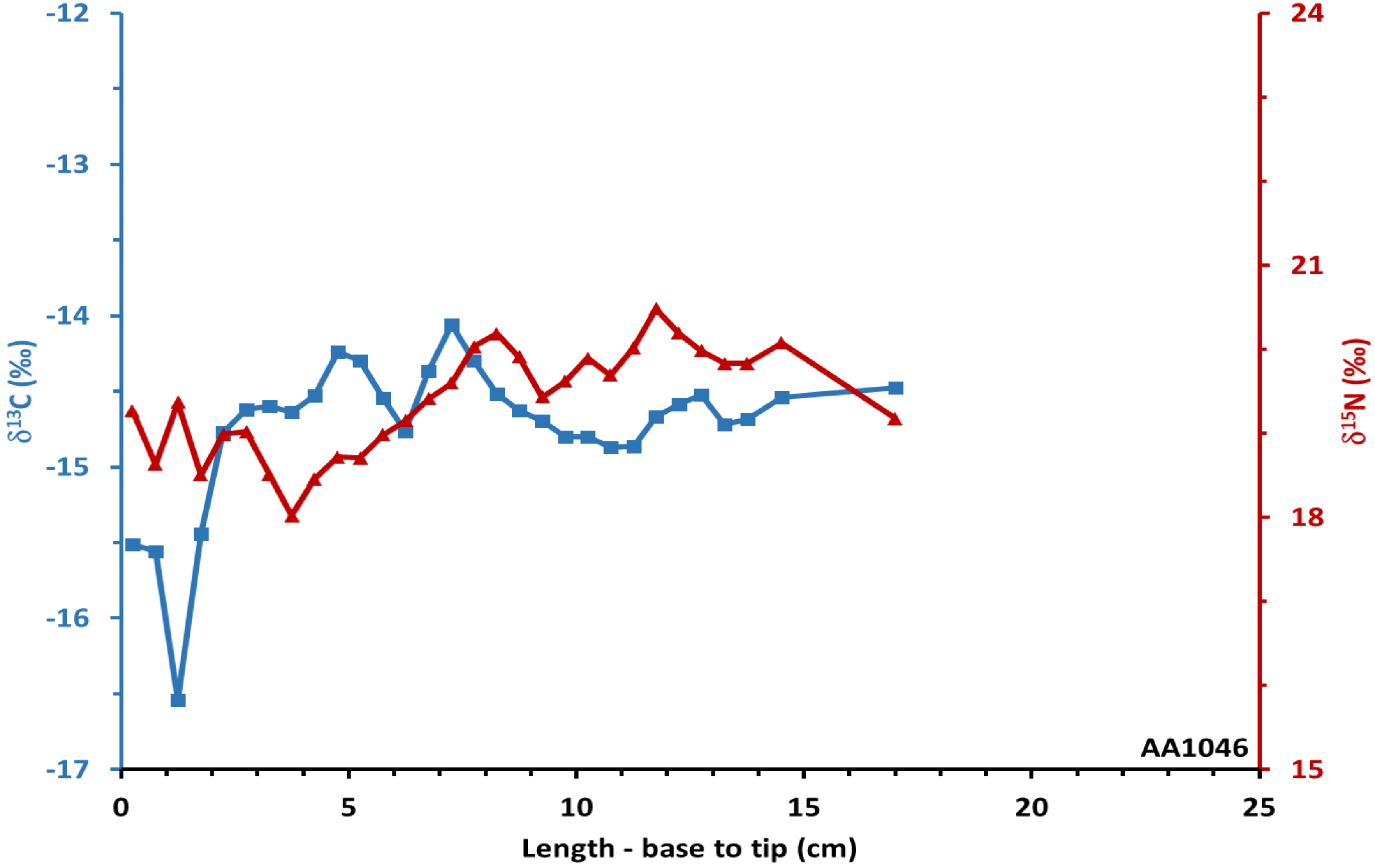

Figure B-23. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1046), 2010.

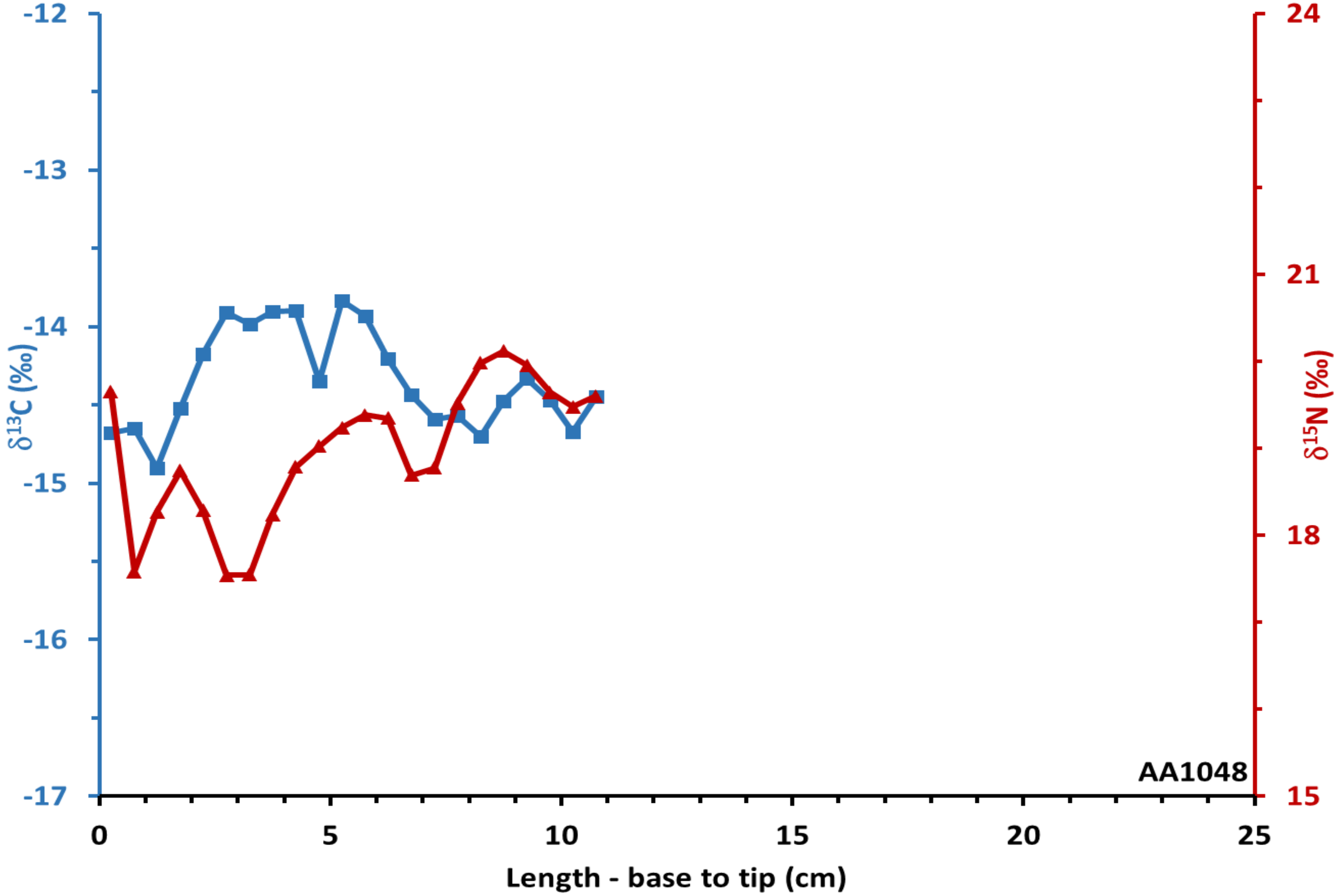

Figure B-24. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1048), 2010.

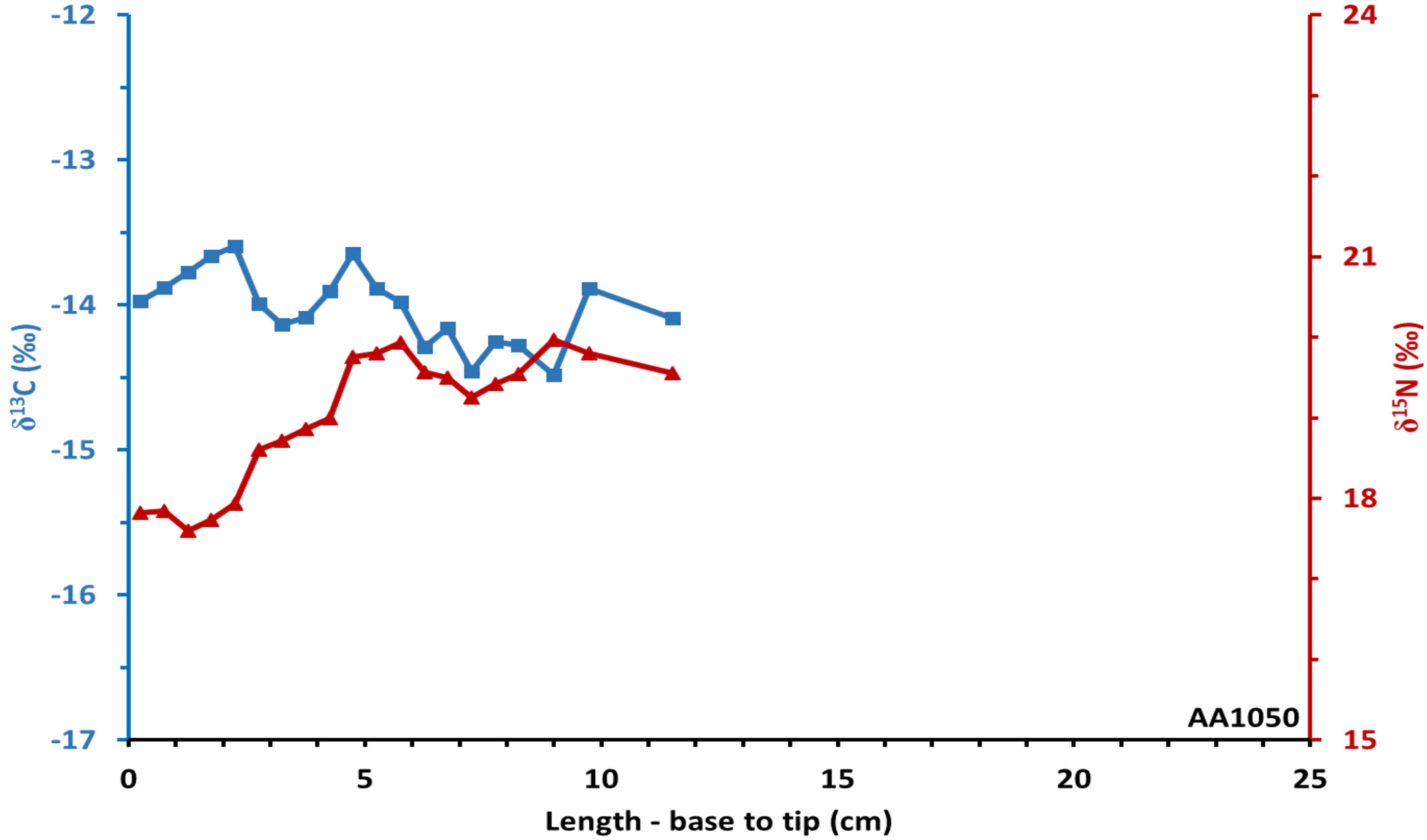

Figure B-25. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1050), 2010.

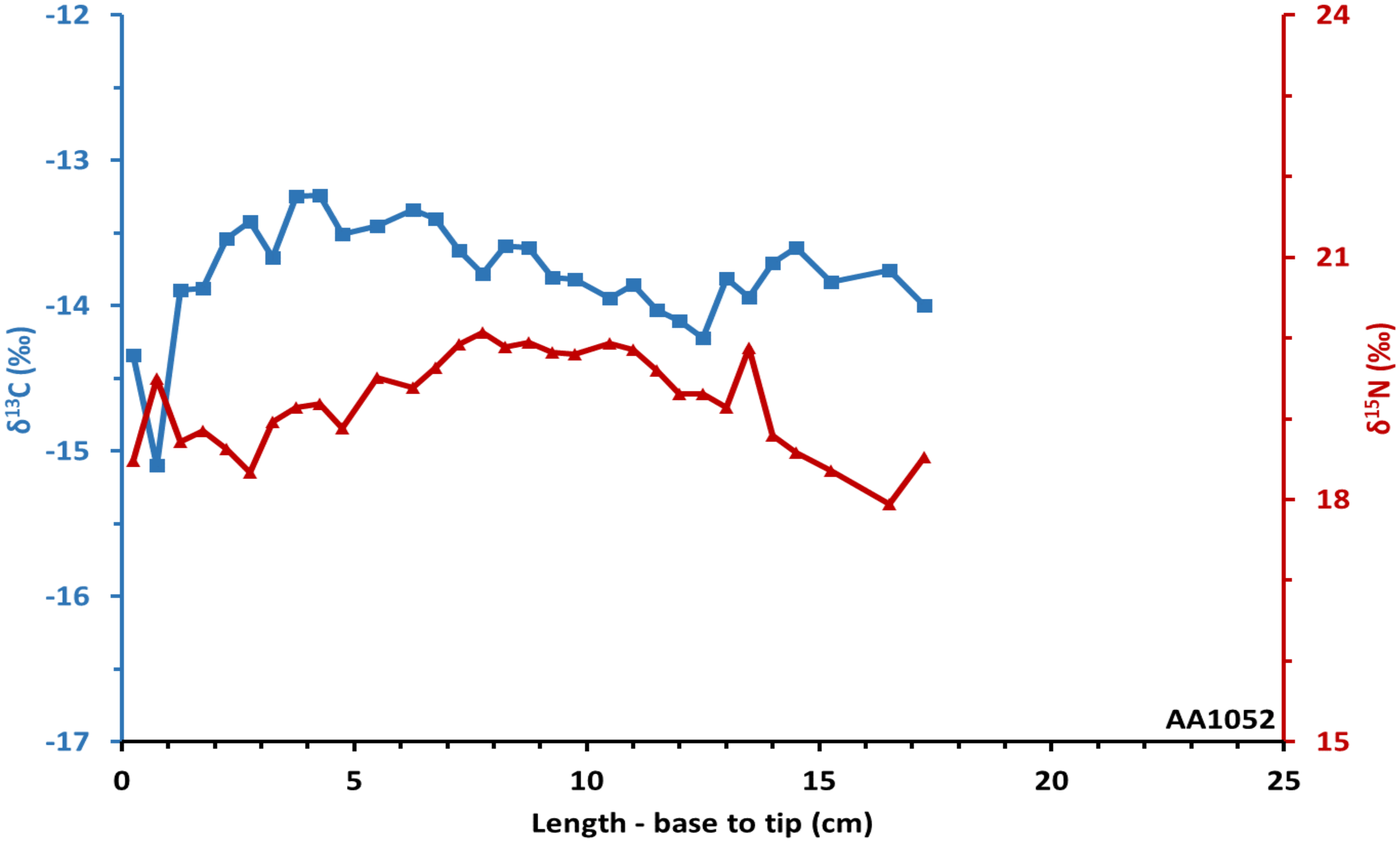

Figure B-26. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1052), 2010.

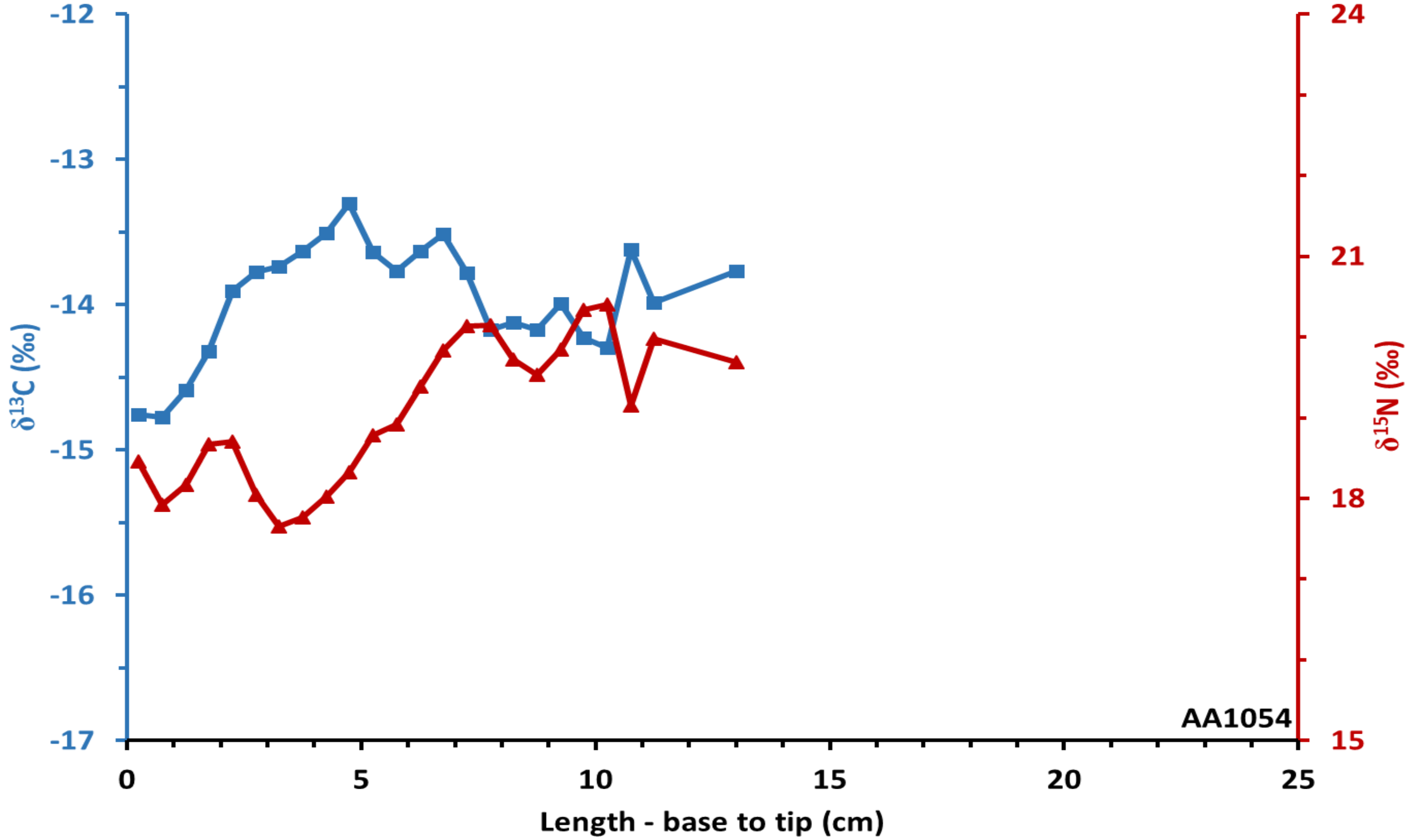

Figure B-27. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1054), 2010.

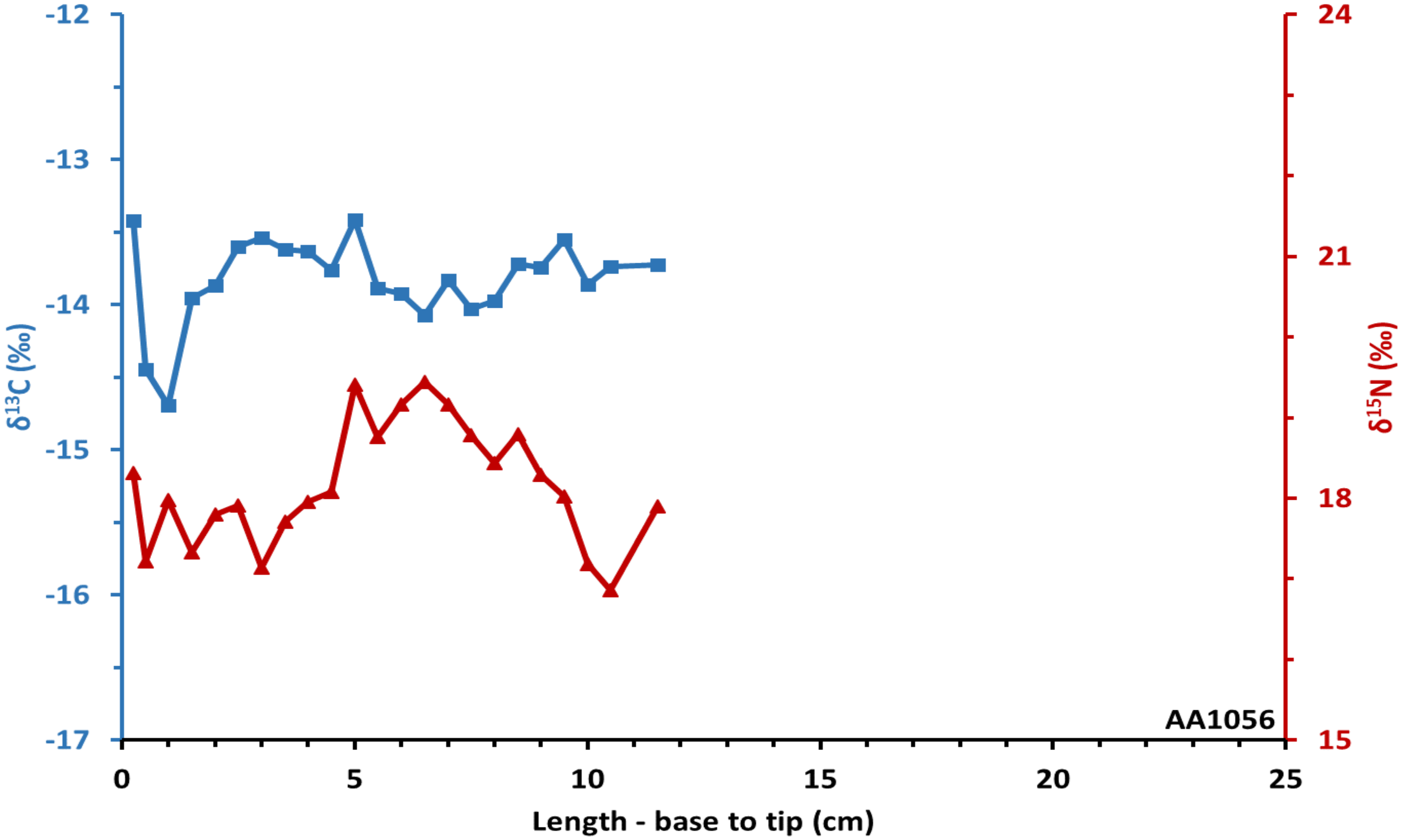

Figure B-28. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1056), 2010.

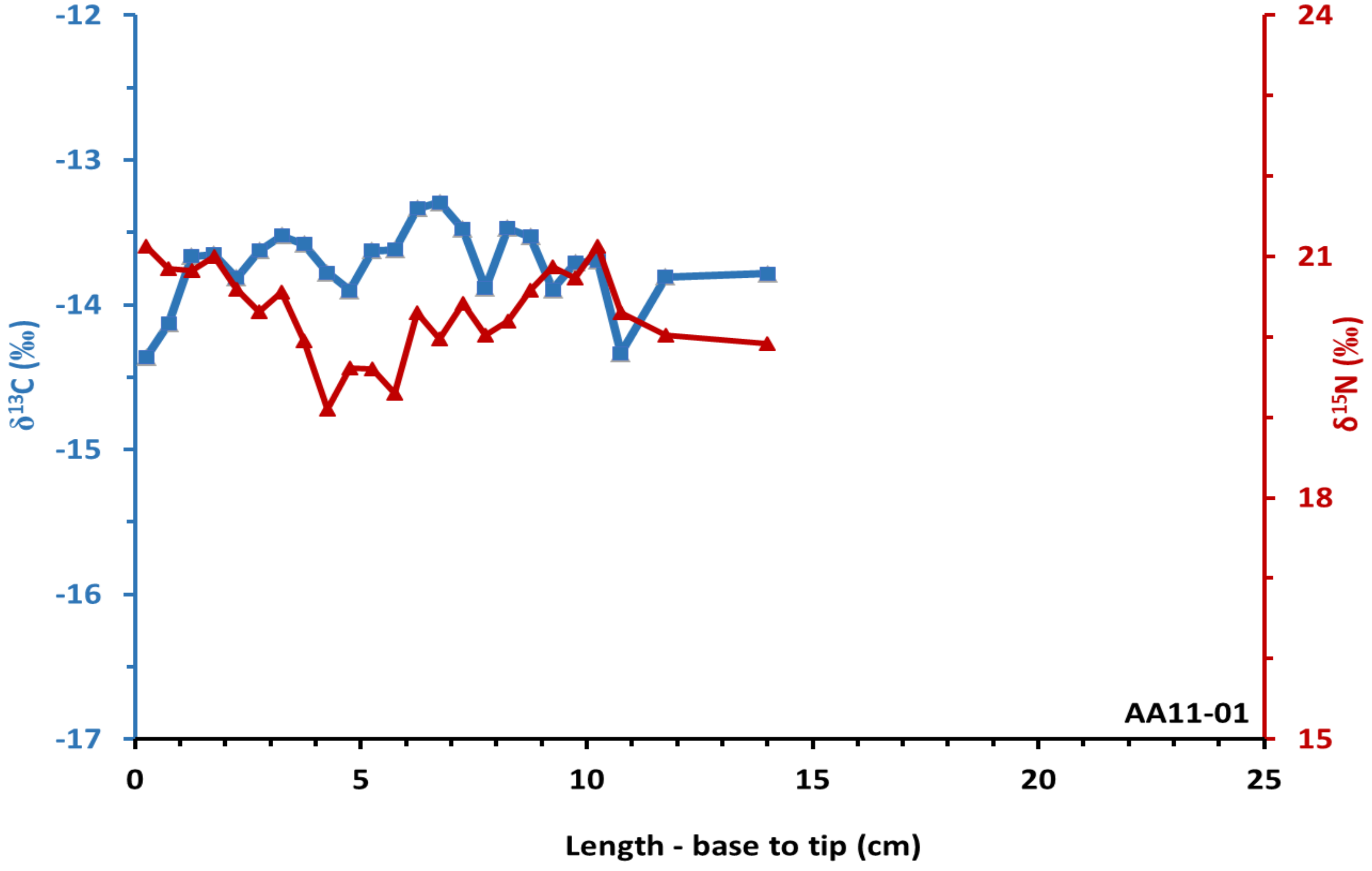

Figure B-29. Subadult male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA11-01), 2011.

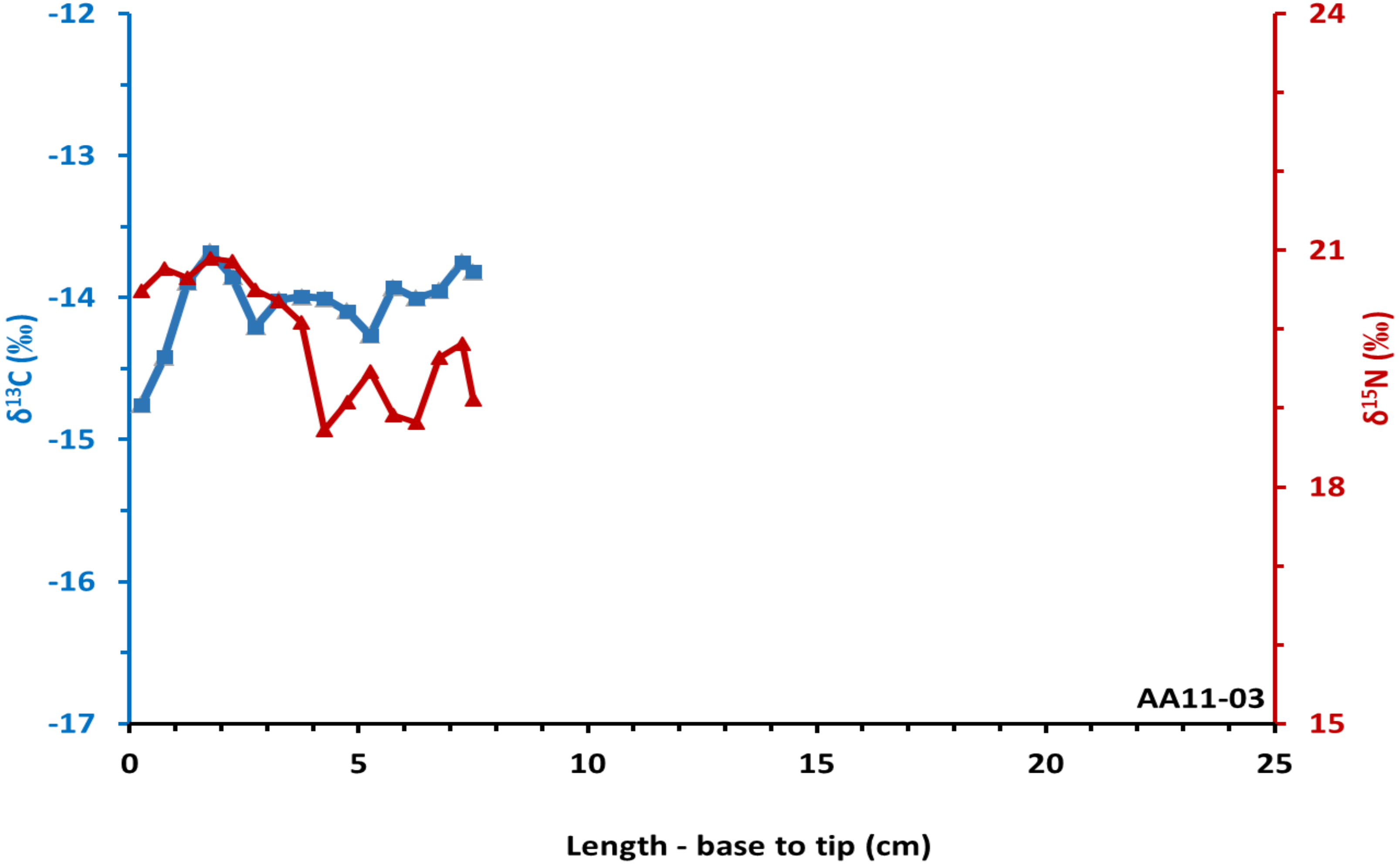

Figure B-30. Subadult male Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA11-03), 2011.

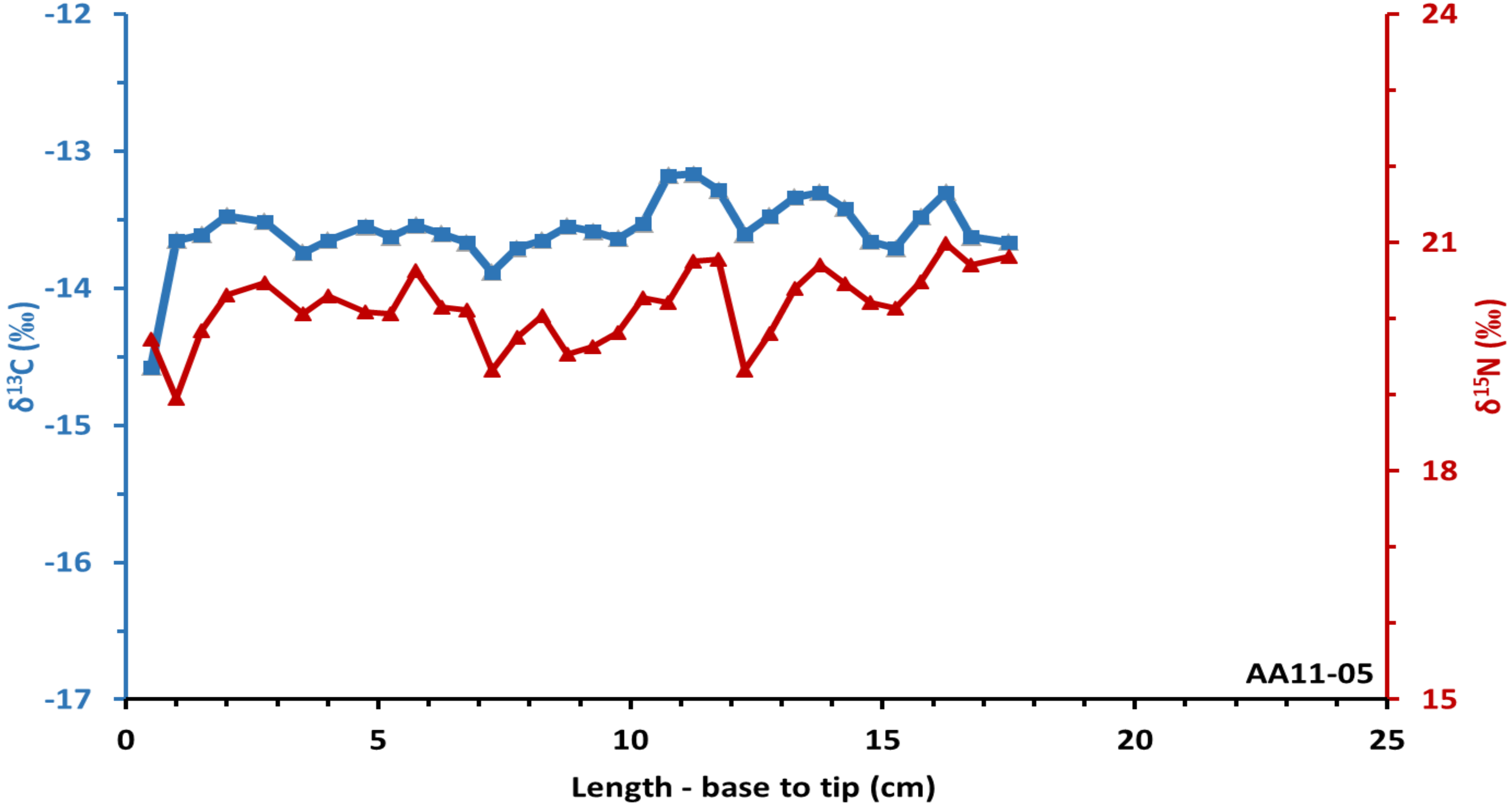

Figure B-31. Subadult male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA11-05), 2011.

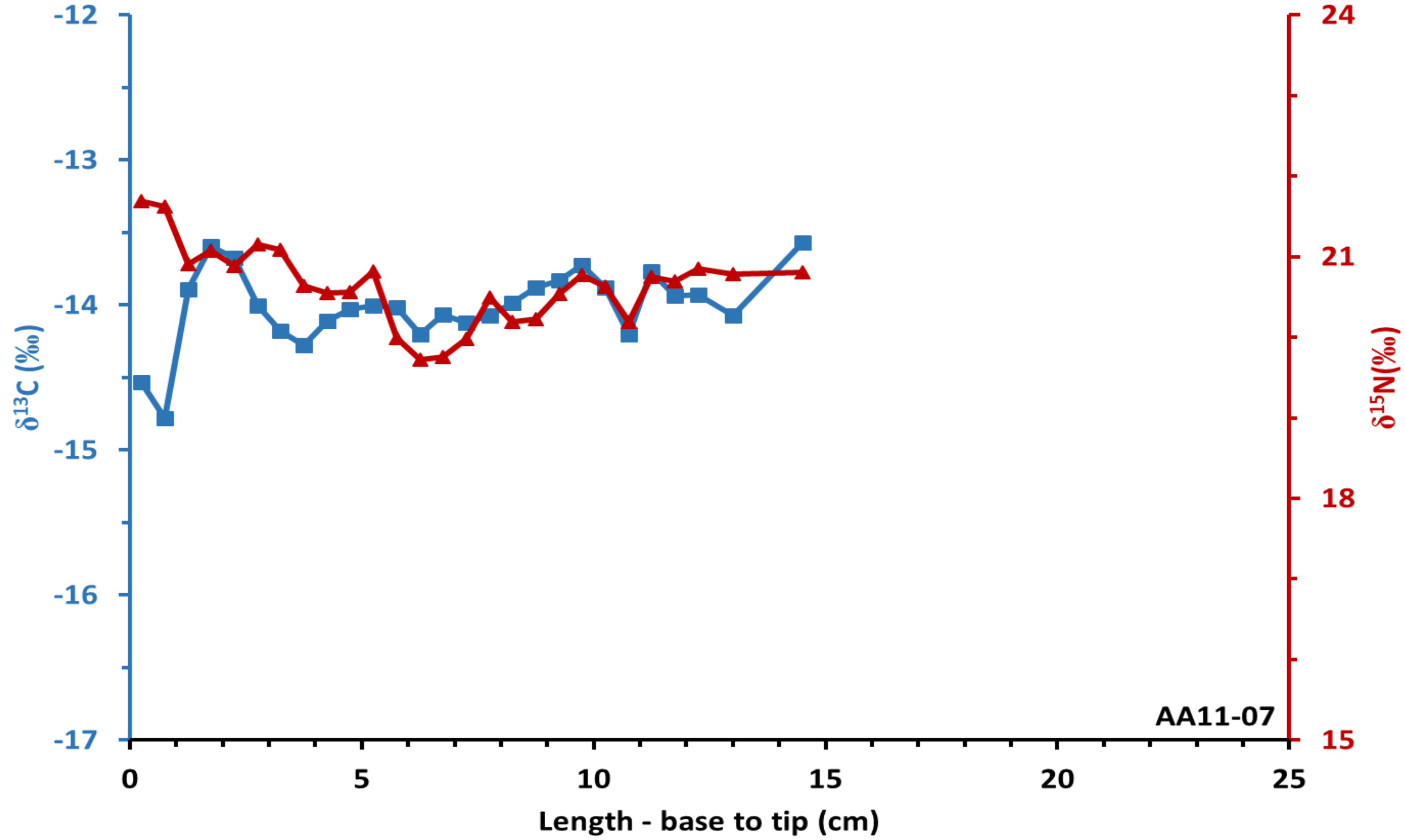

Figure B-32. Subadult male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA11-07), 2011.

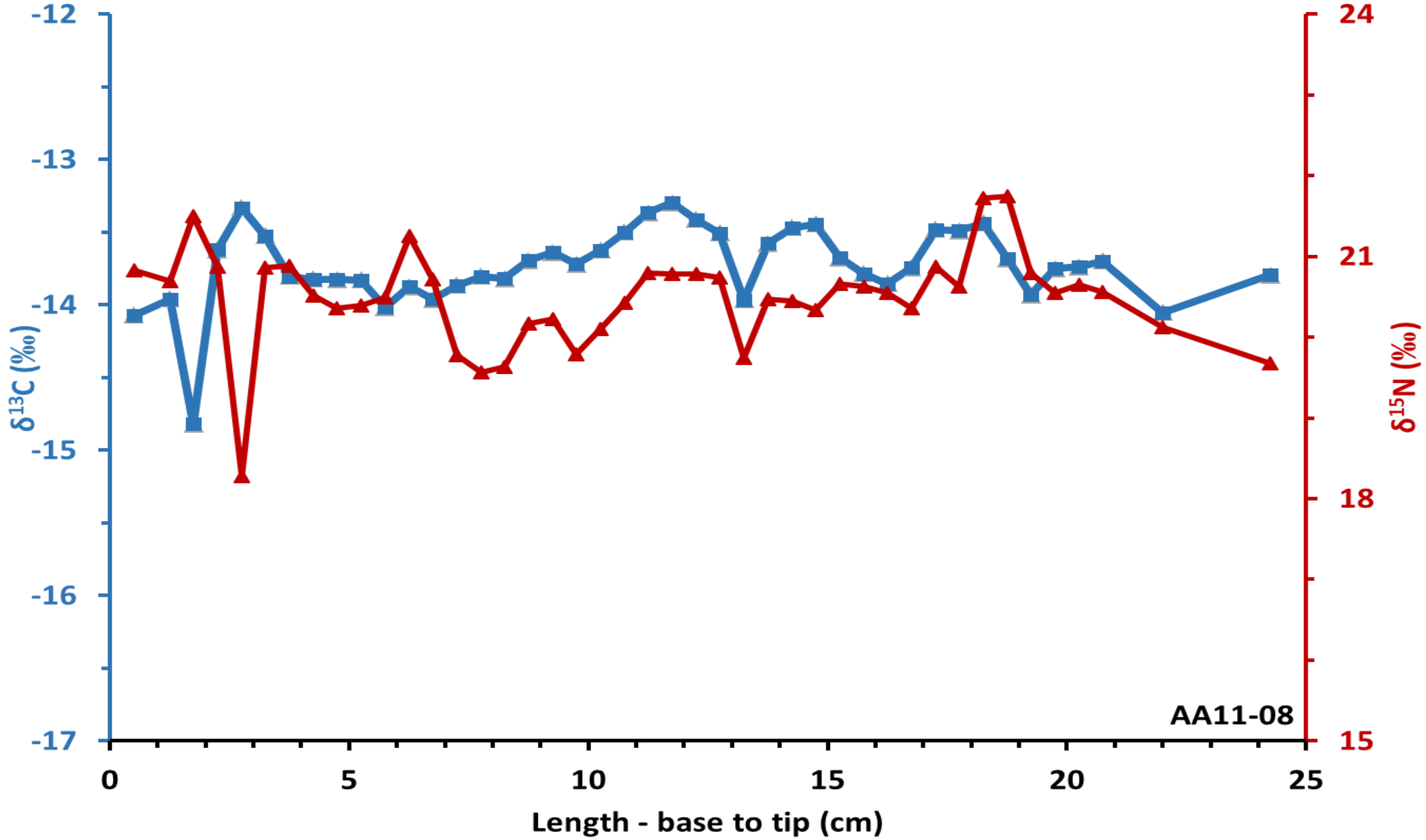

Figure B-33. Subadult male Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA11-08), 2011.

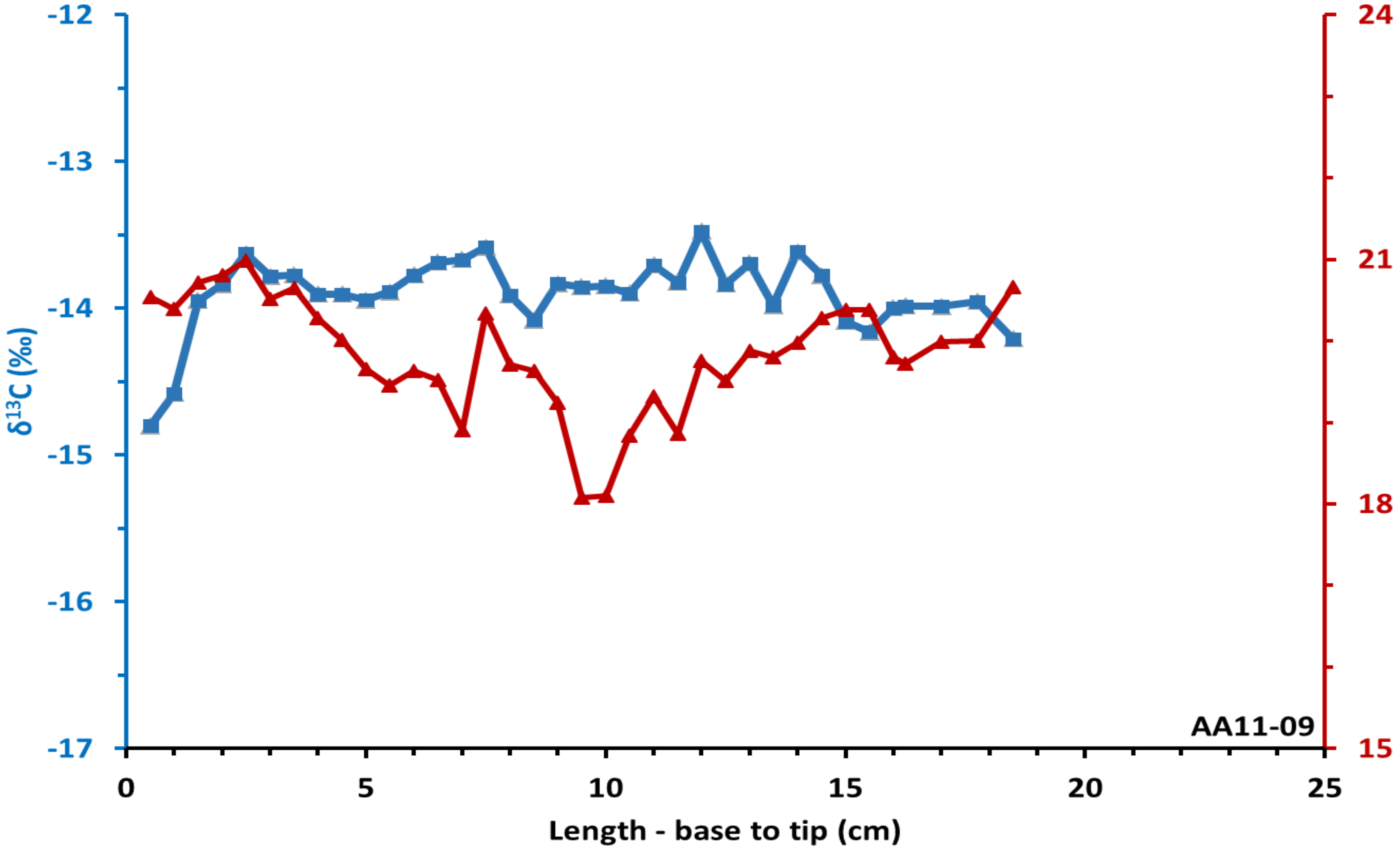

Figure B-34. Subadult male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA11-09), 2011.

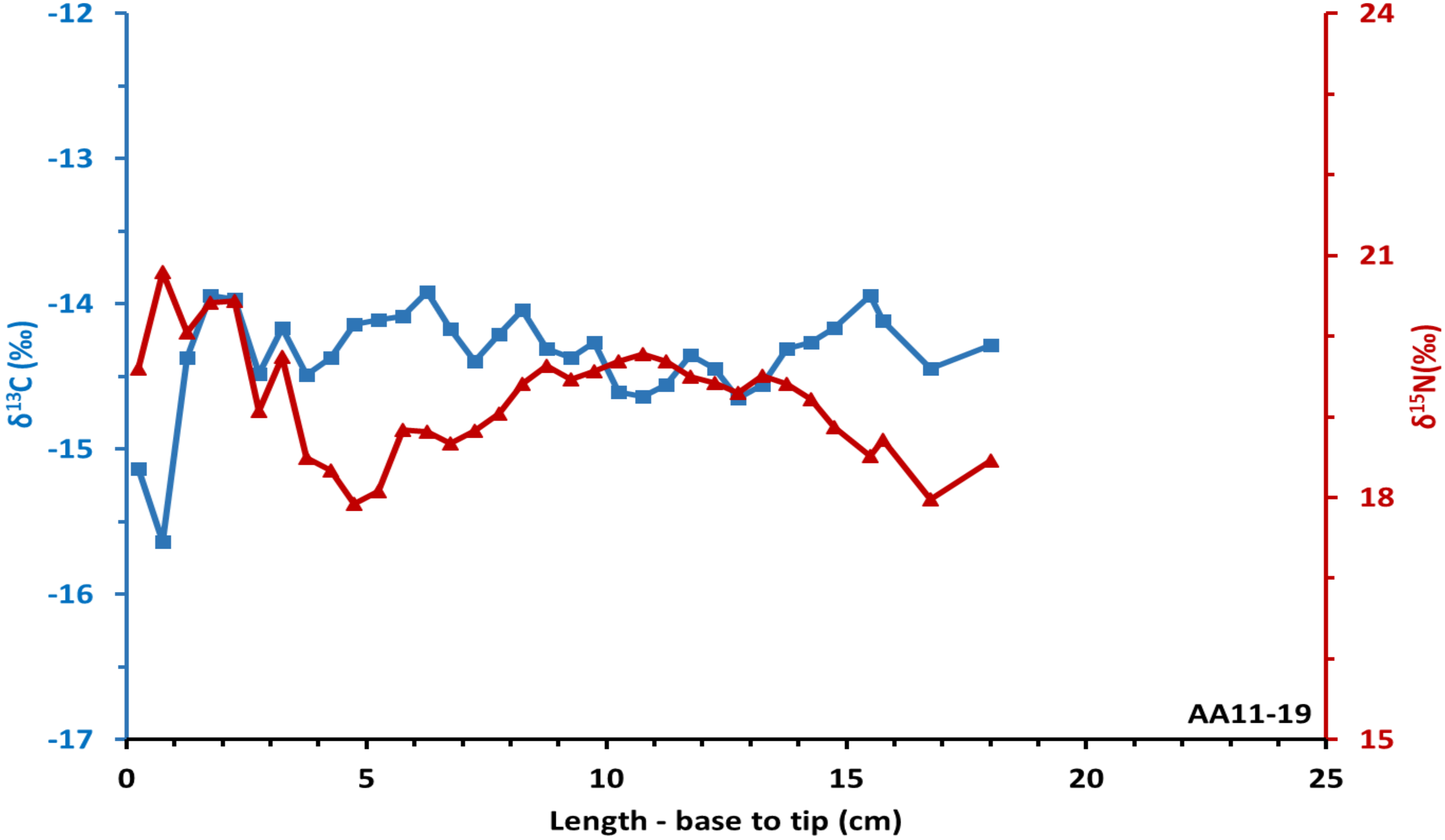

Figure B-35. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA11-19), 2011.

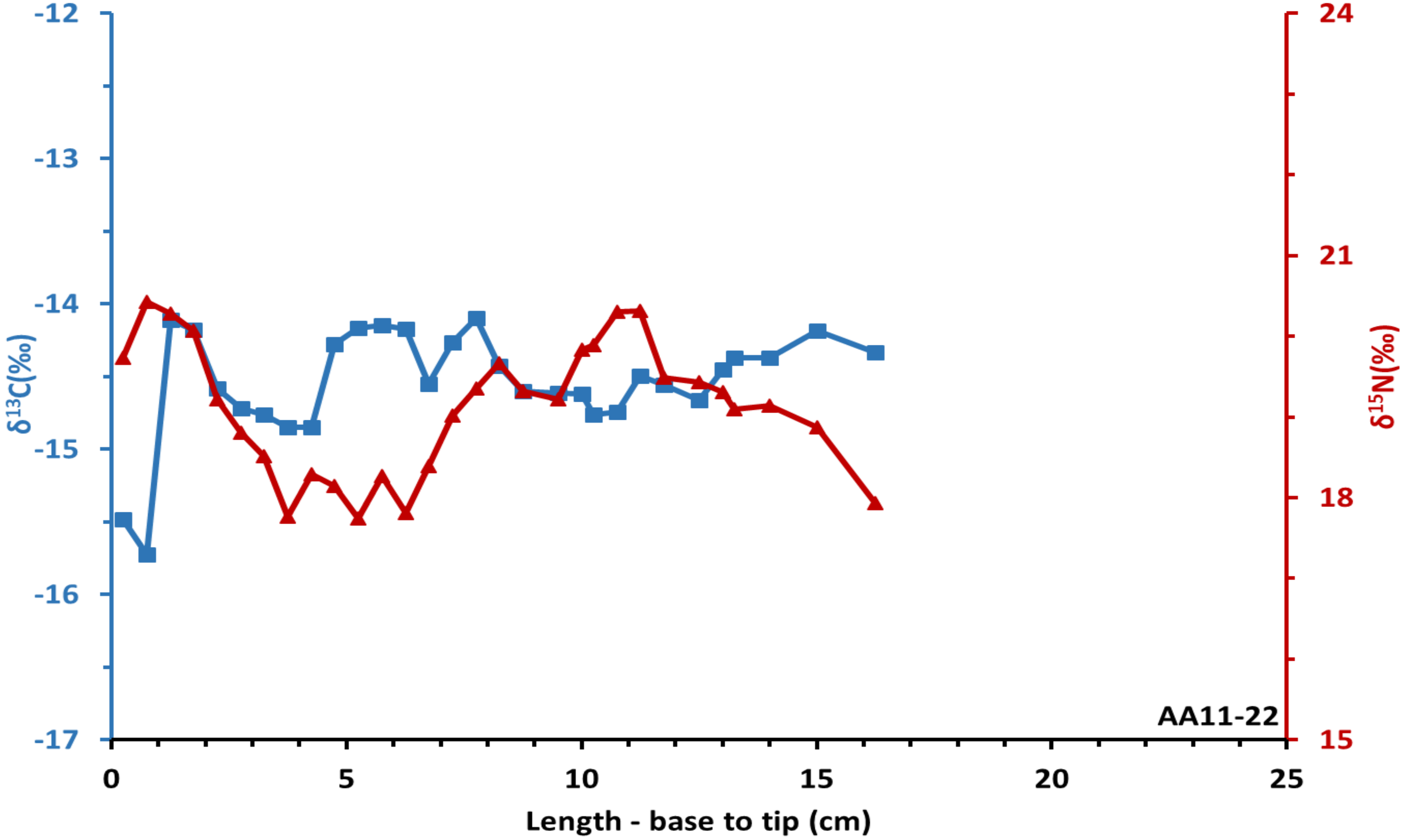

Figure B-36. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA11-22), 2011.

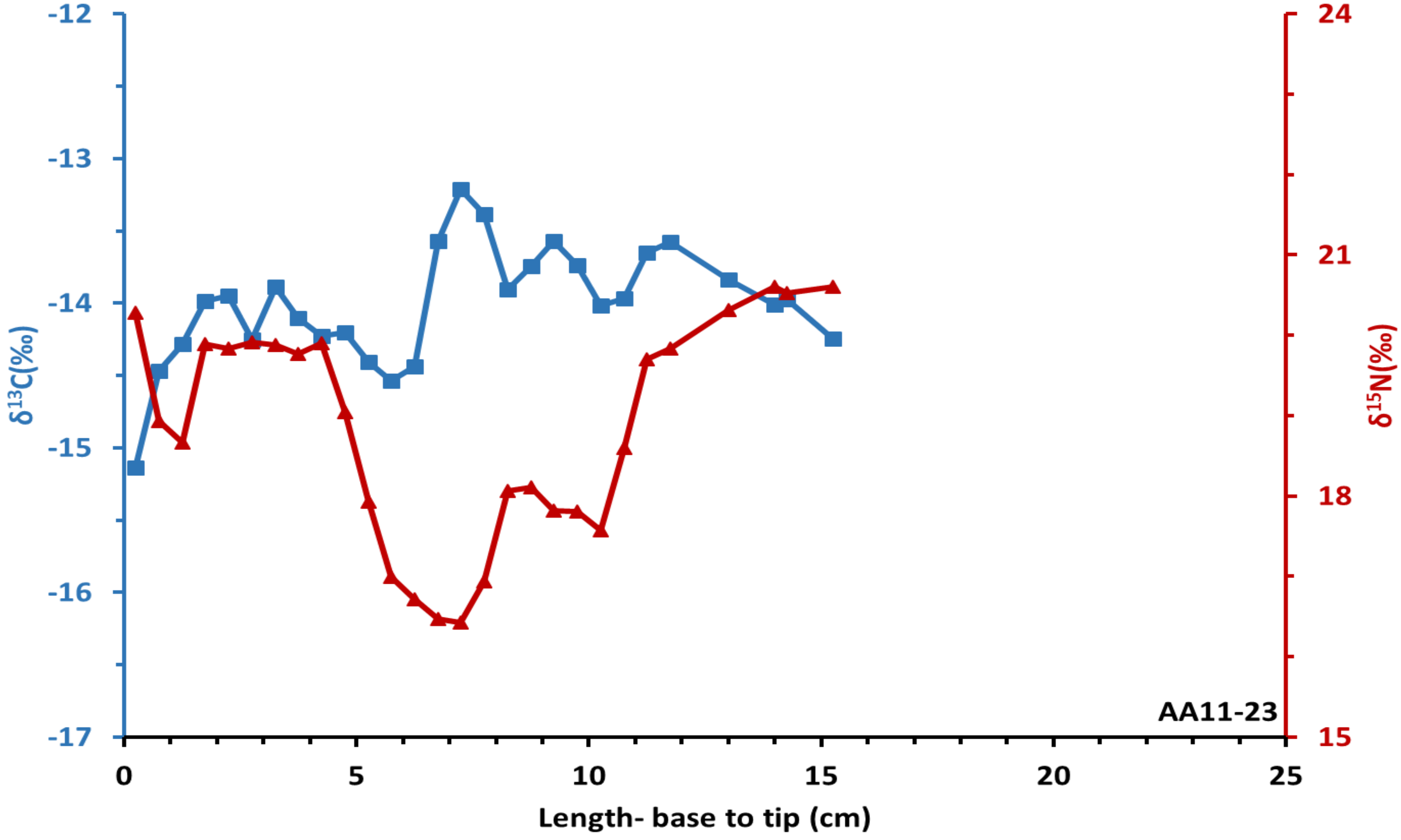

Figure B-37. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA11-23), 2011.

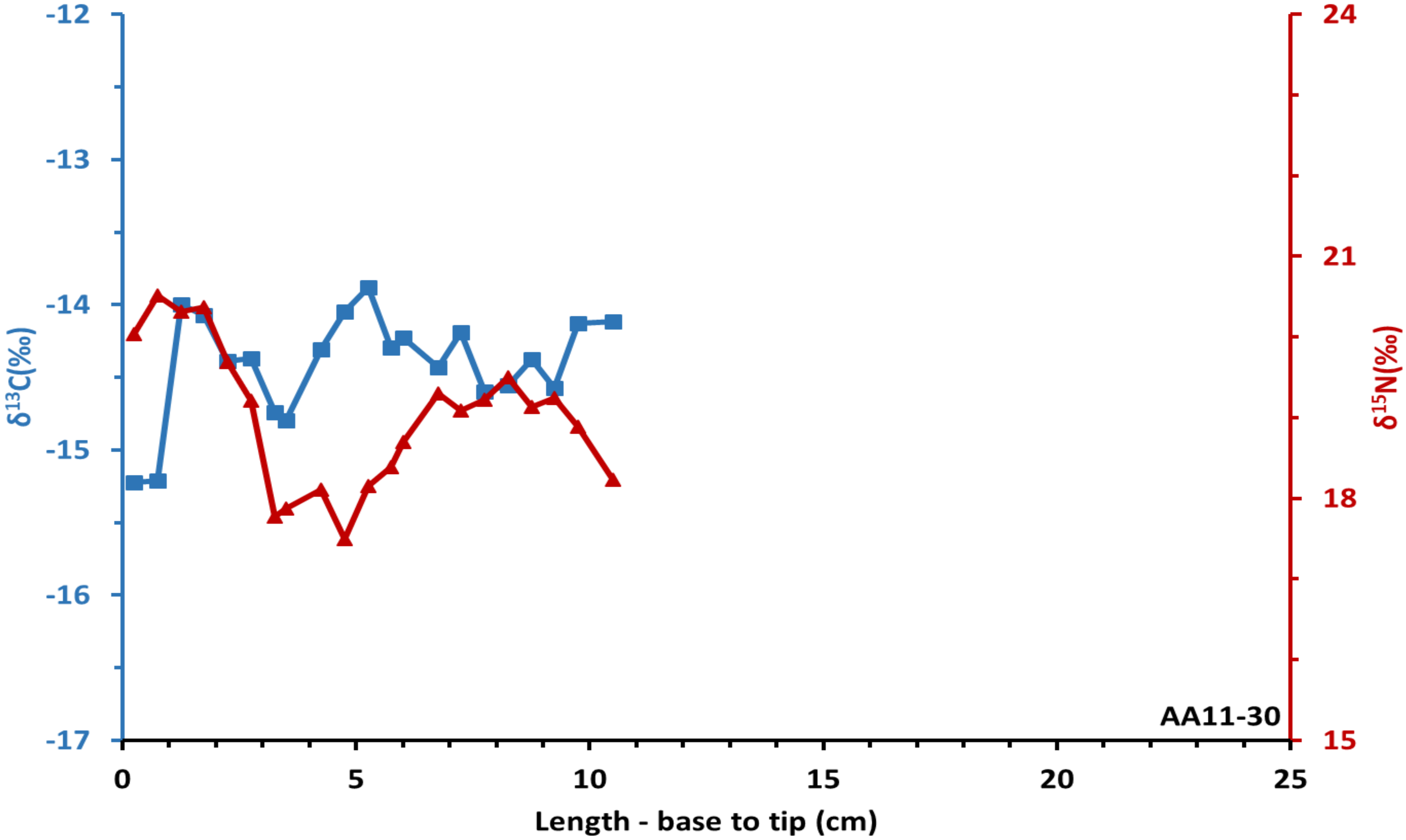

Figure B-38. Adult female Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA11-30), 2011.

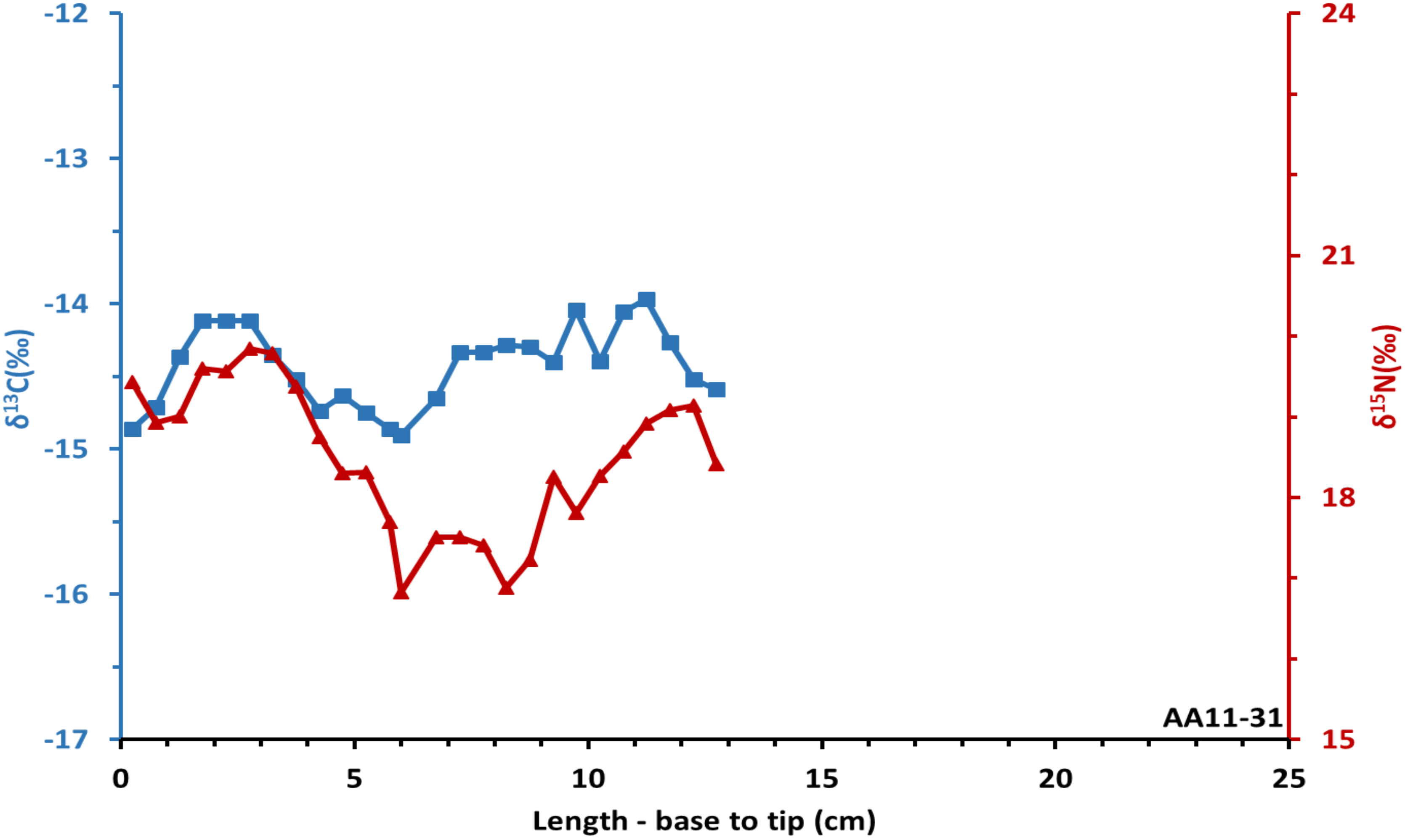

Figure B-39. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA11-31), 2011.

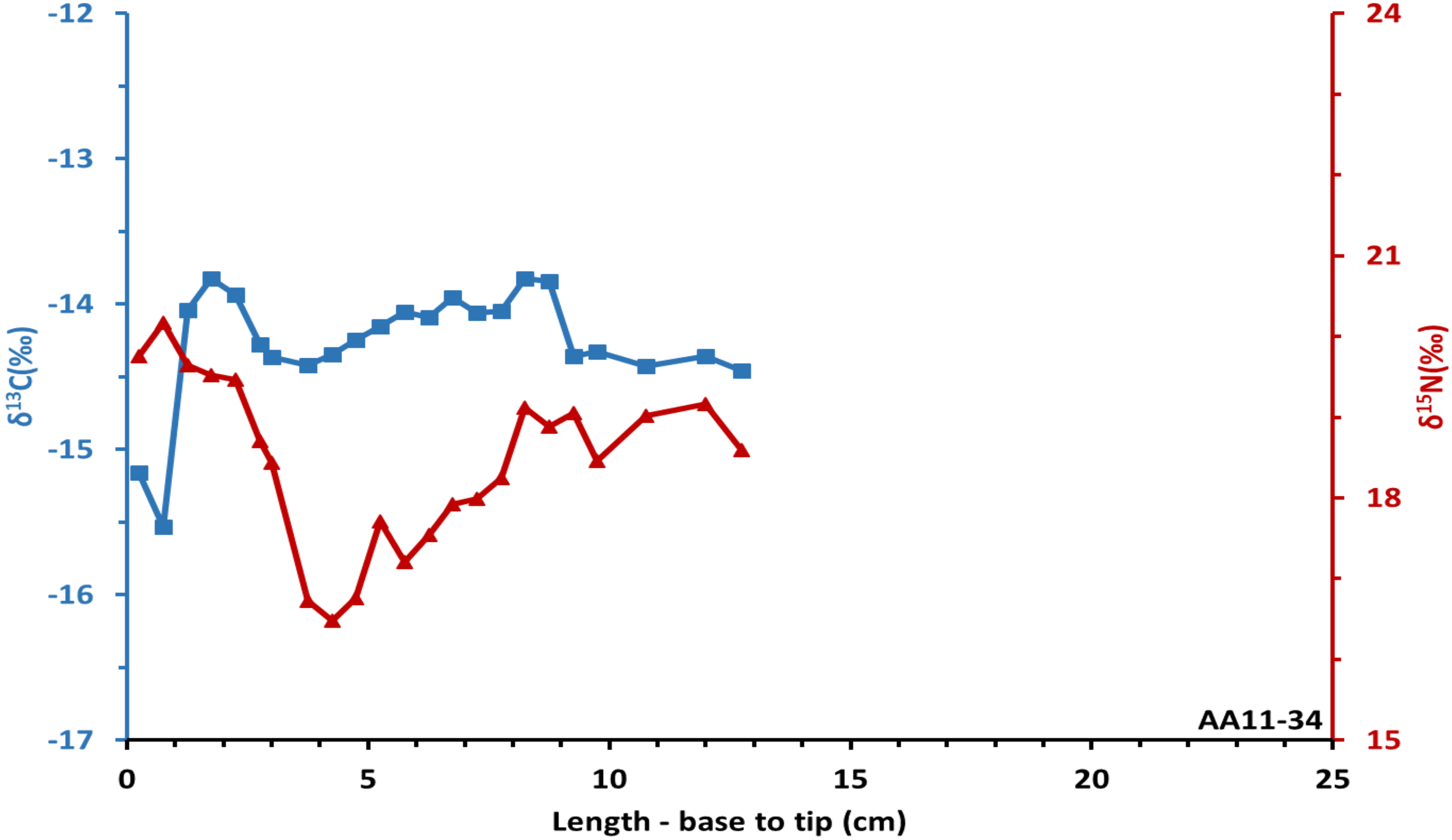

Figure B-40. Adult female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA11-34), 2011.

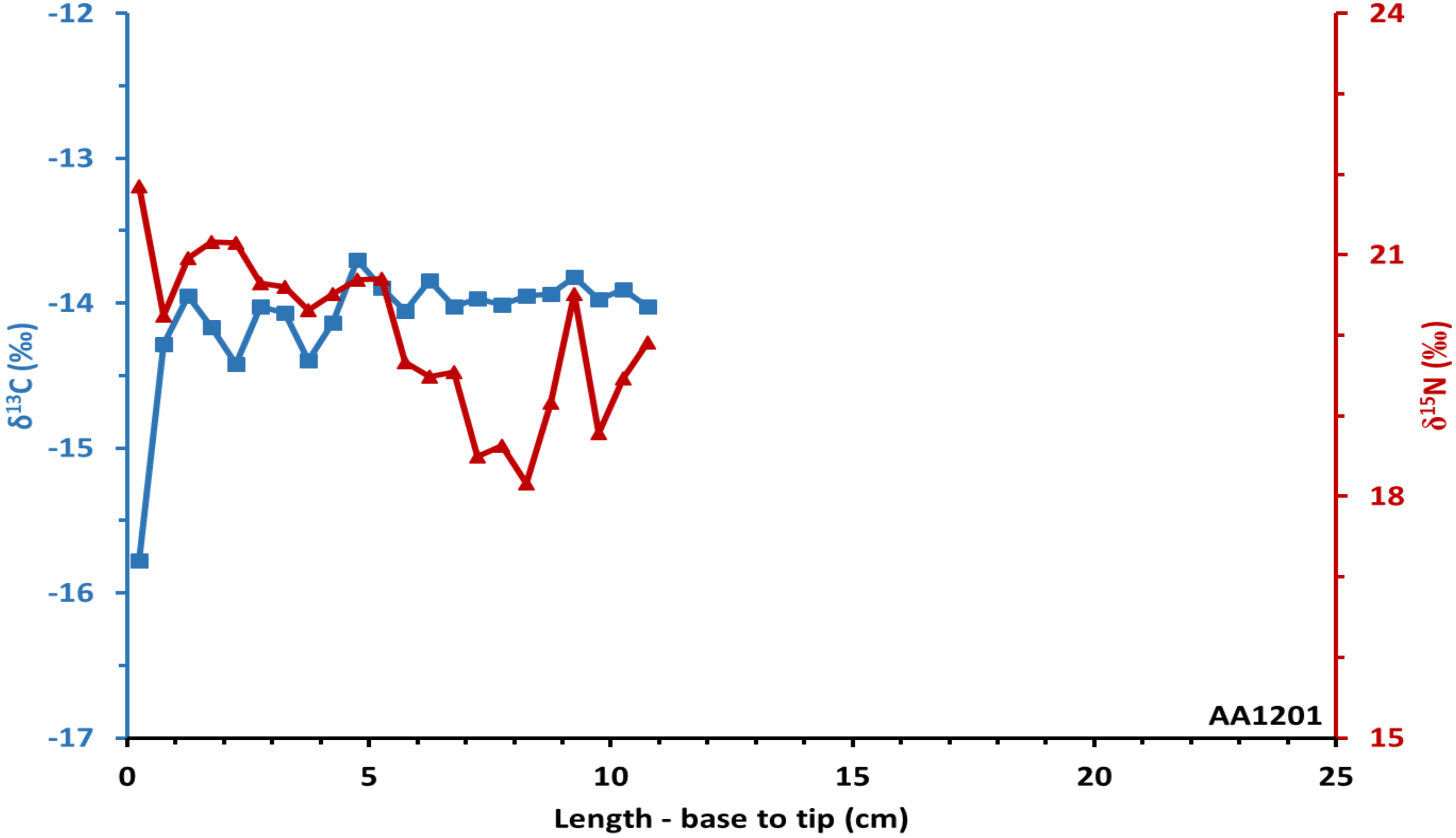

Figure B-41. Subadult male Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1201), 2012.

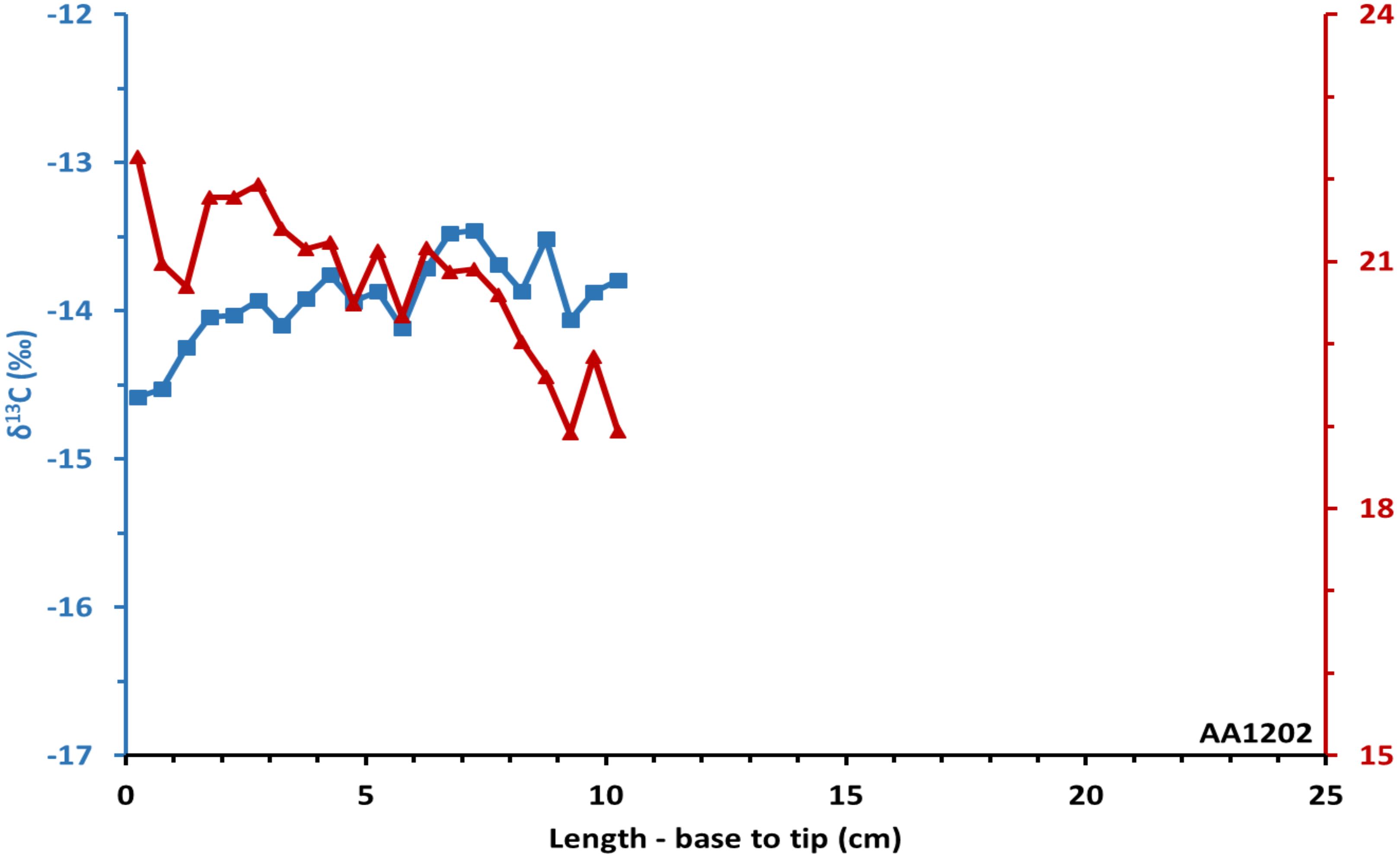

Figure B-42. Subadult male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1202), 2012.

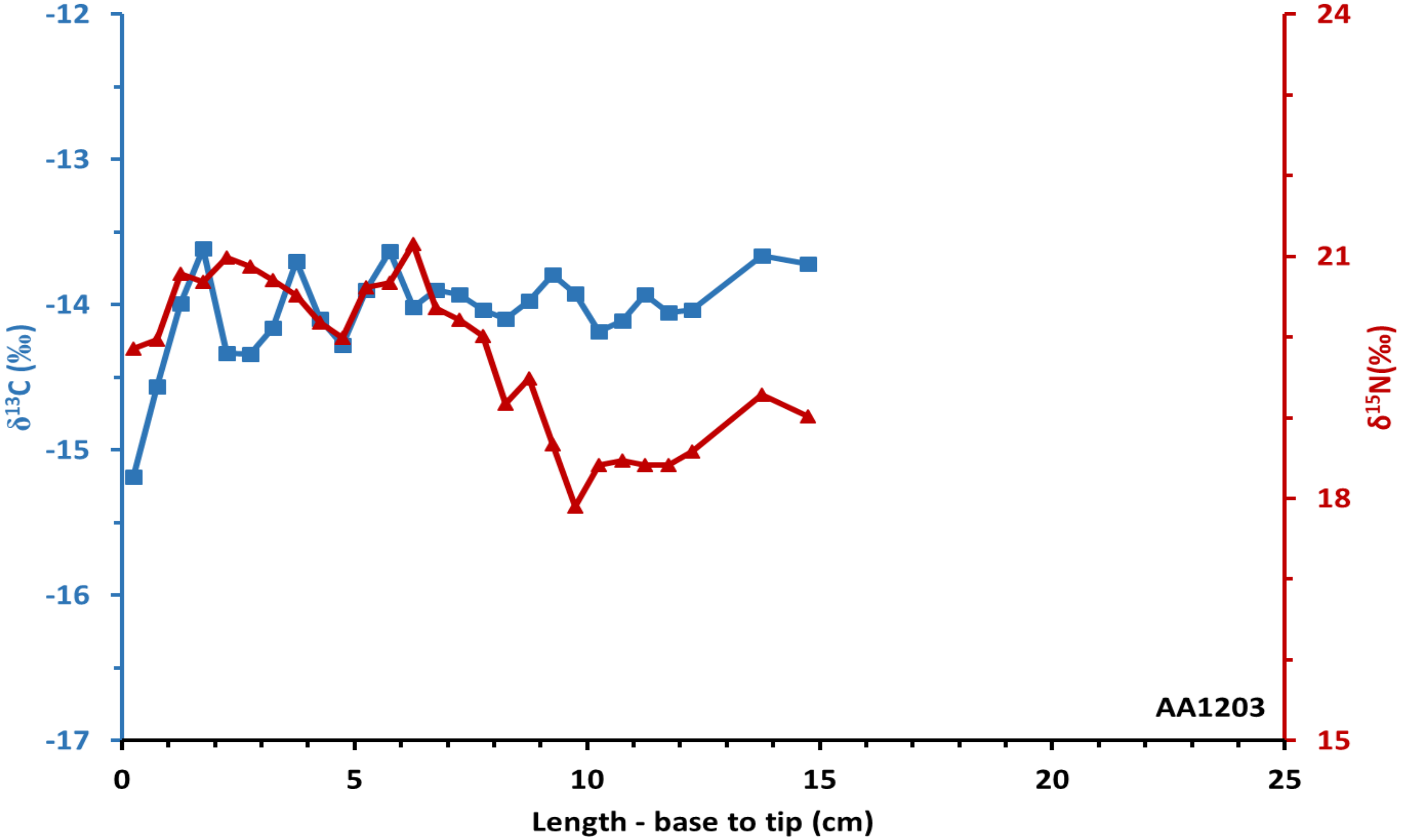

Figure B-43. Subadult male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1203), 2012.

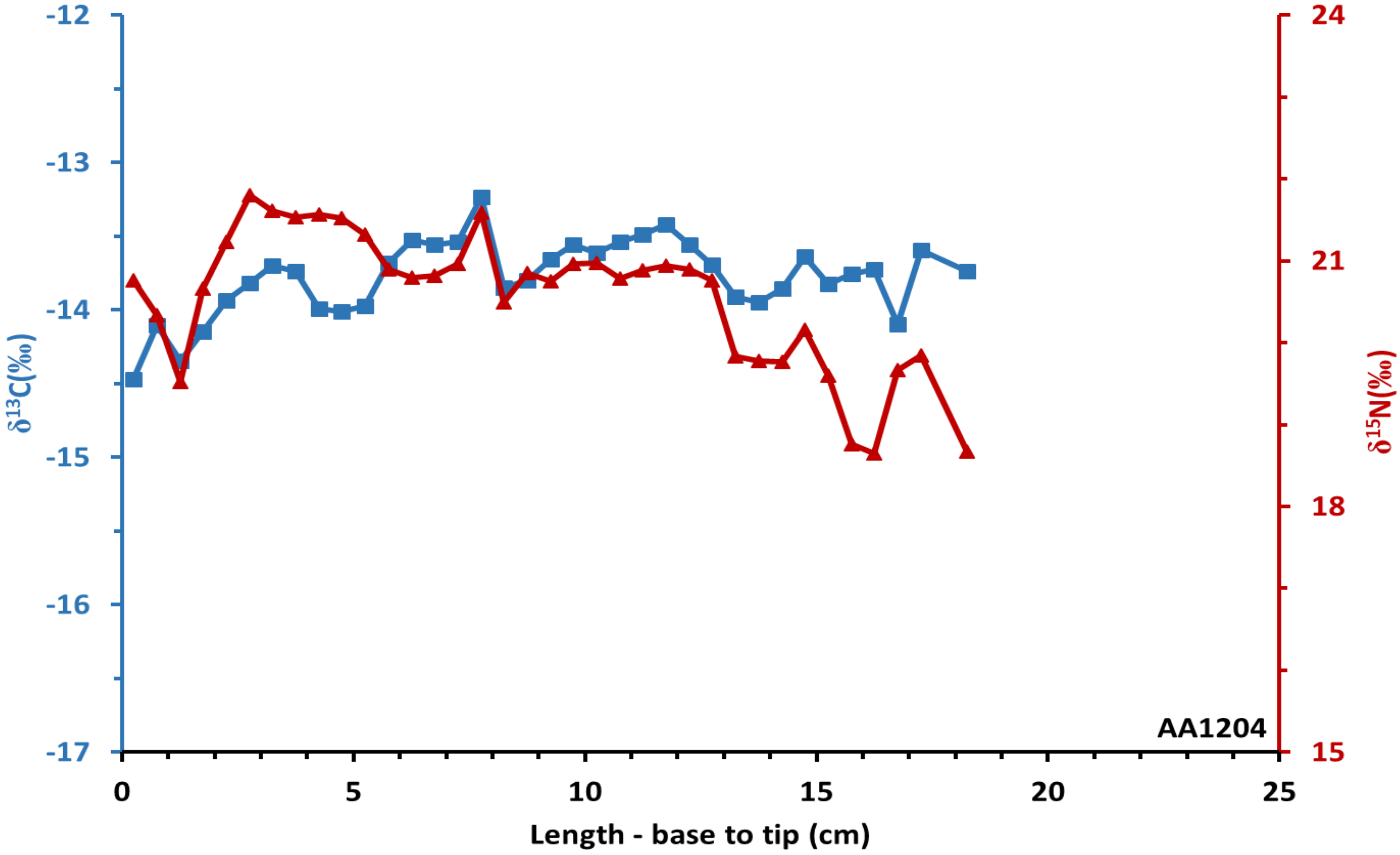

Figure B-44. Subadult male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1204), 2012.

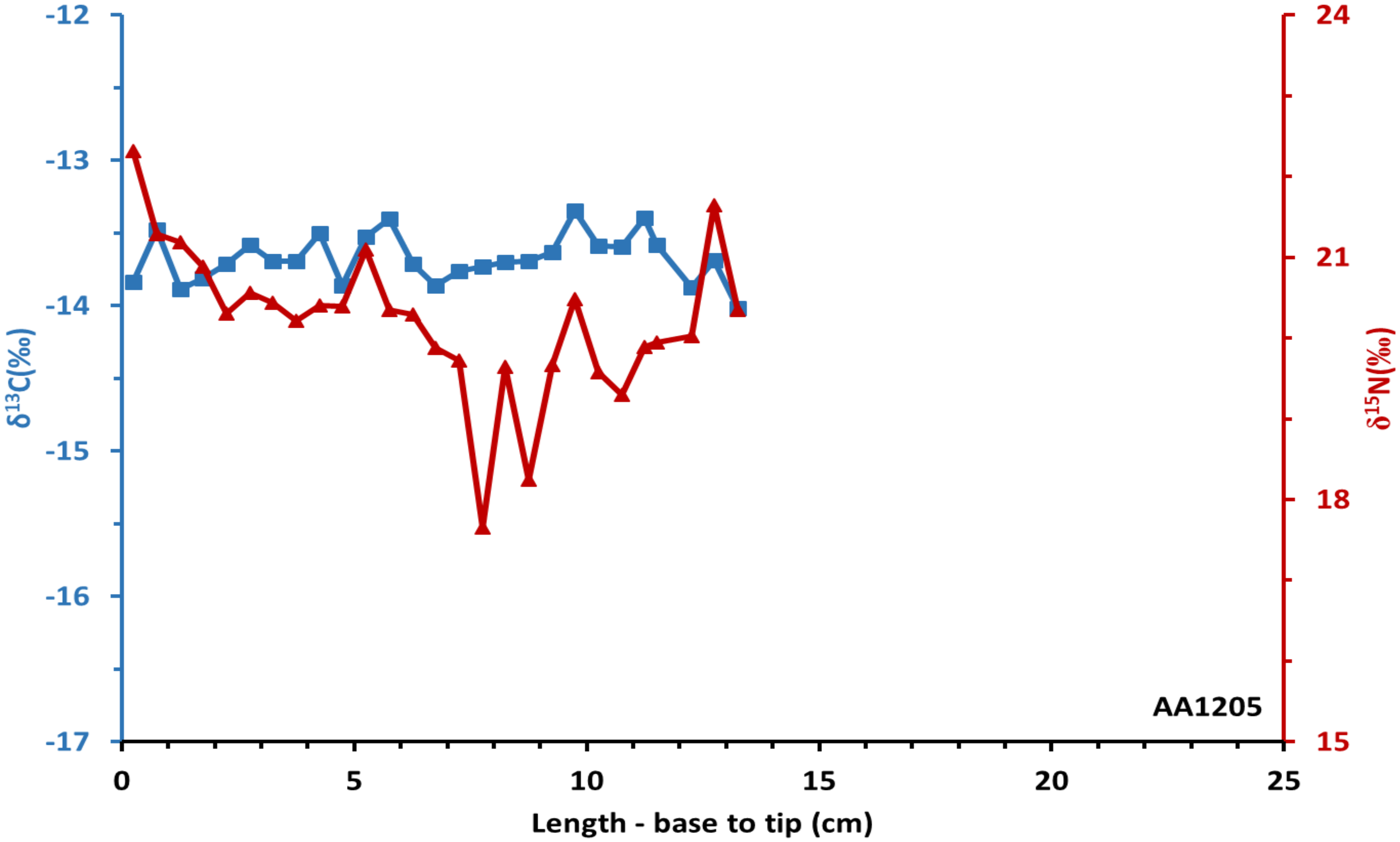

Figure B-45. Subadult male Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1205), 2012.

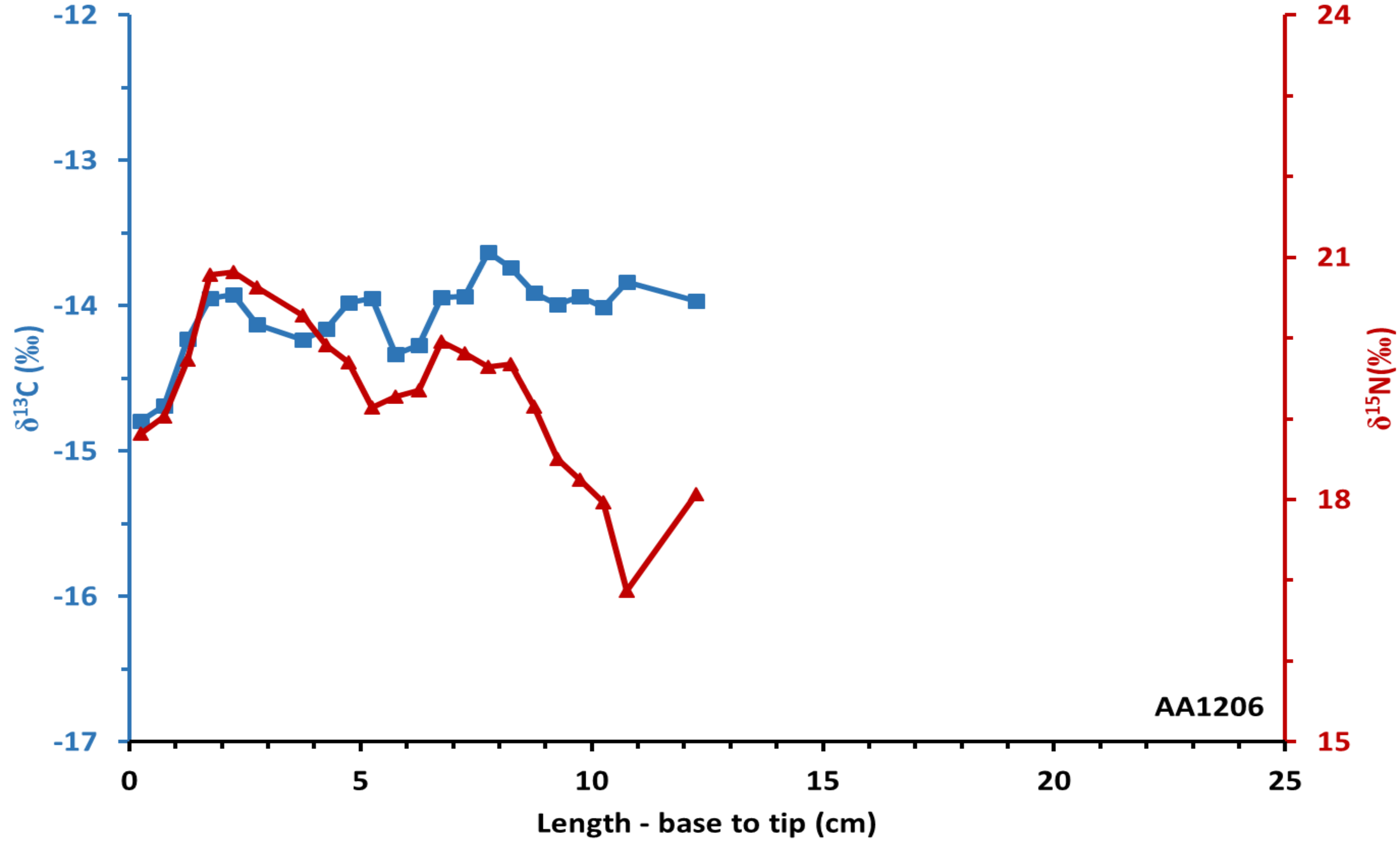

Figure B-46. Adult Female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1206), 2012.

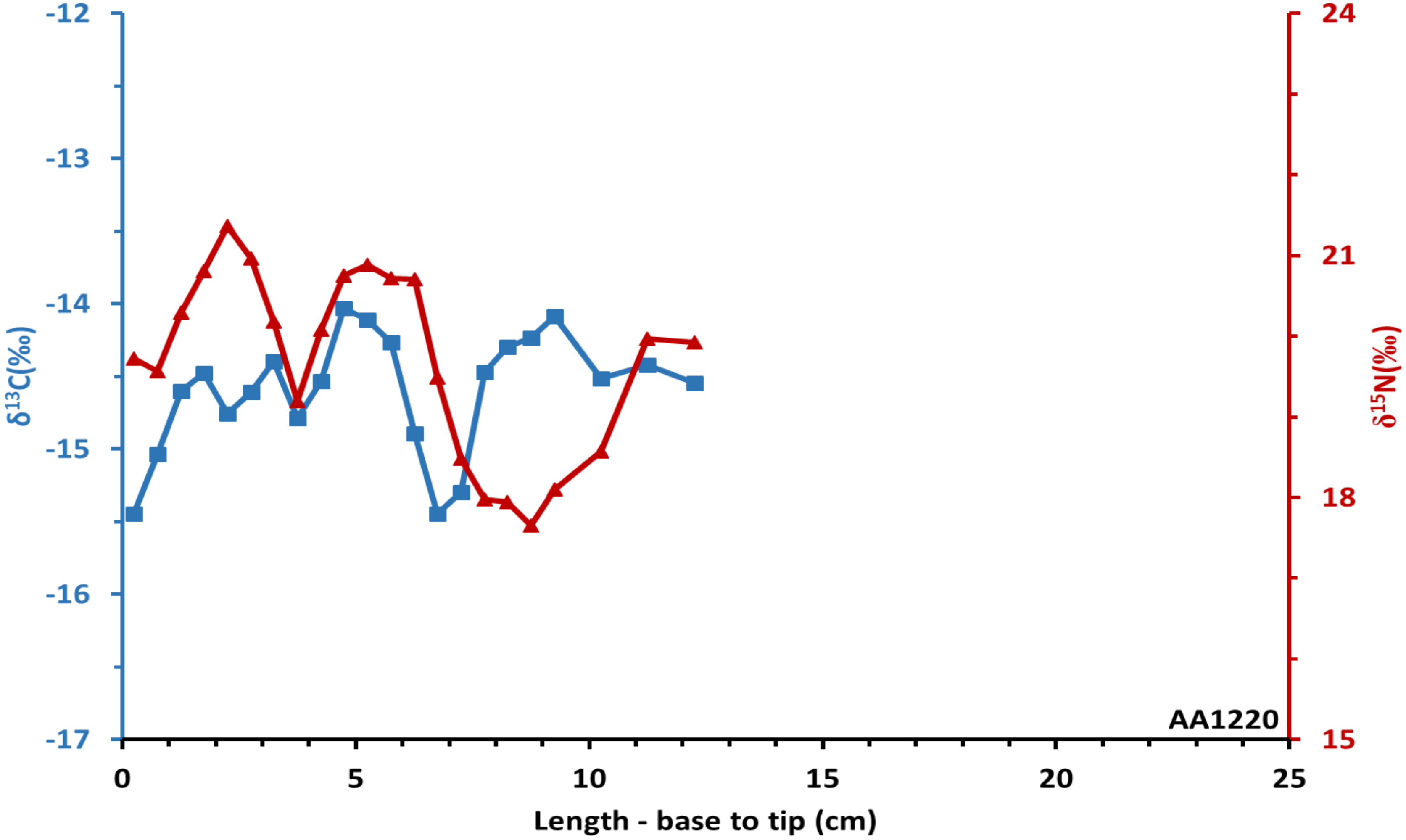

Figure B-47. Adult Female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1220), 2012.

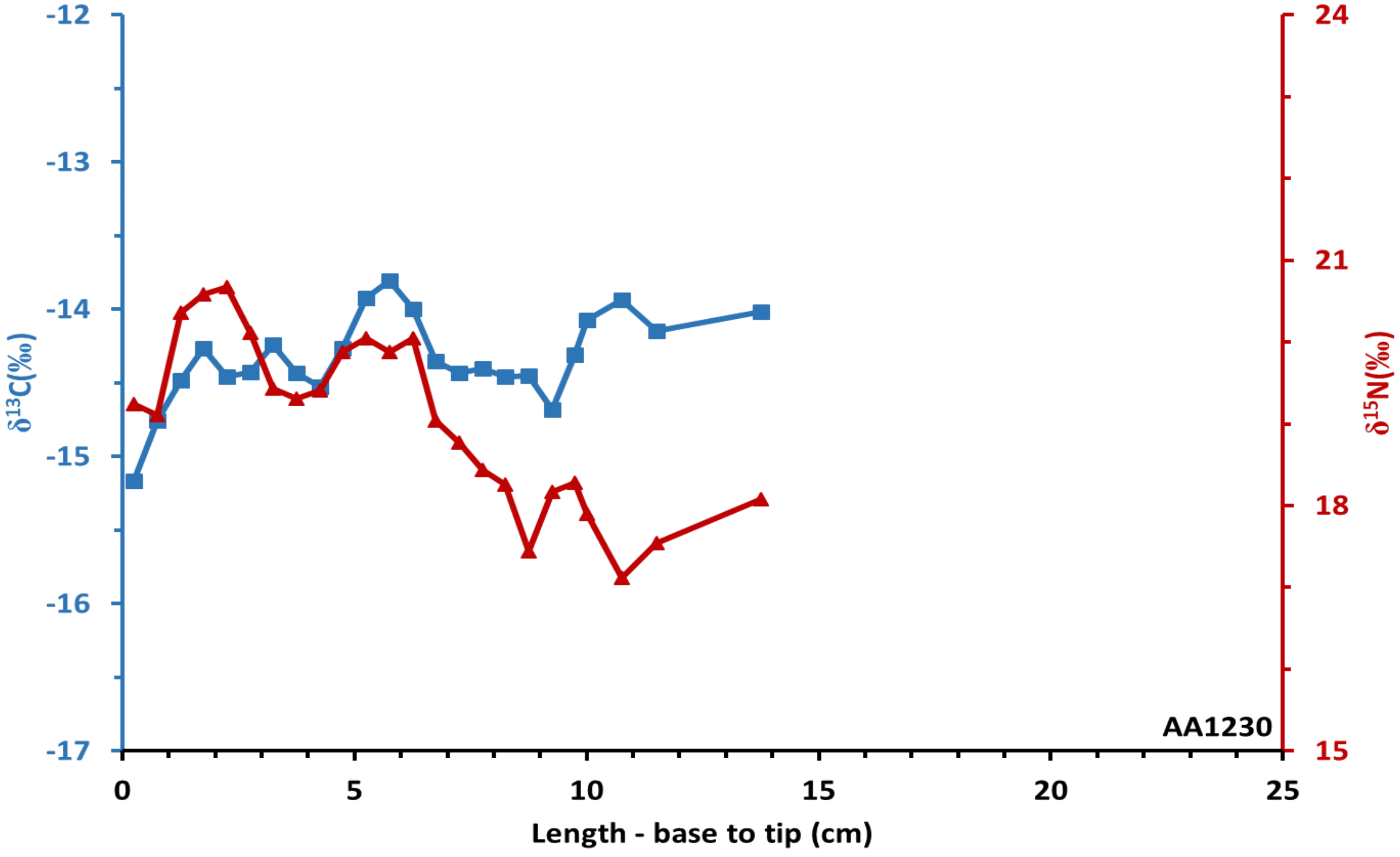

Figure B-48. Adult Female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1230), 2012.

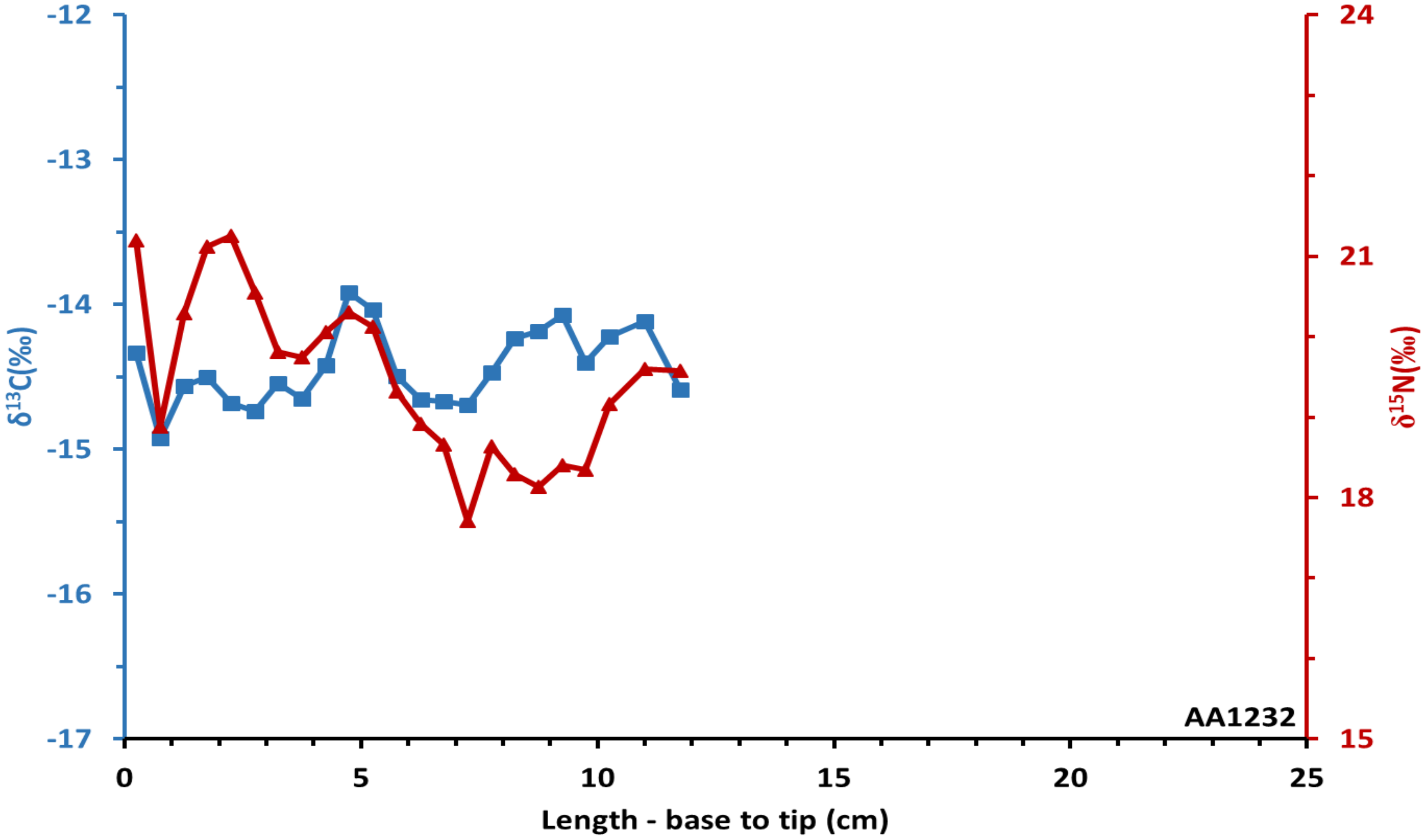

Figure B-49. Adult Female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1232), 2012.

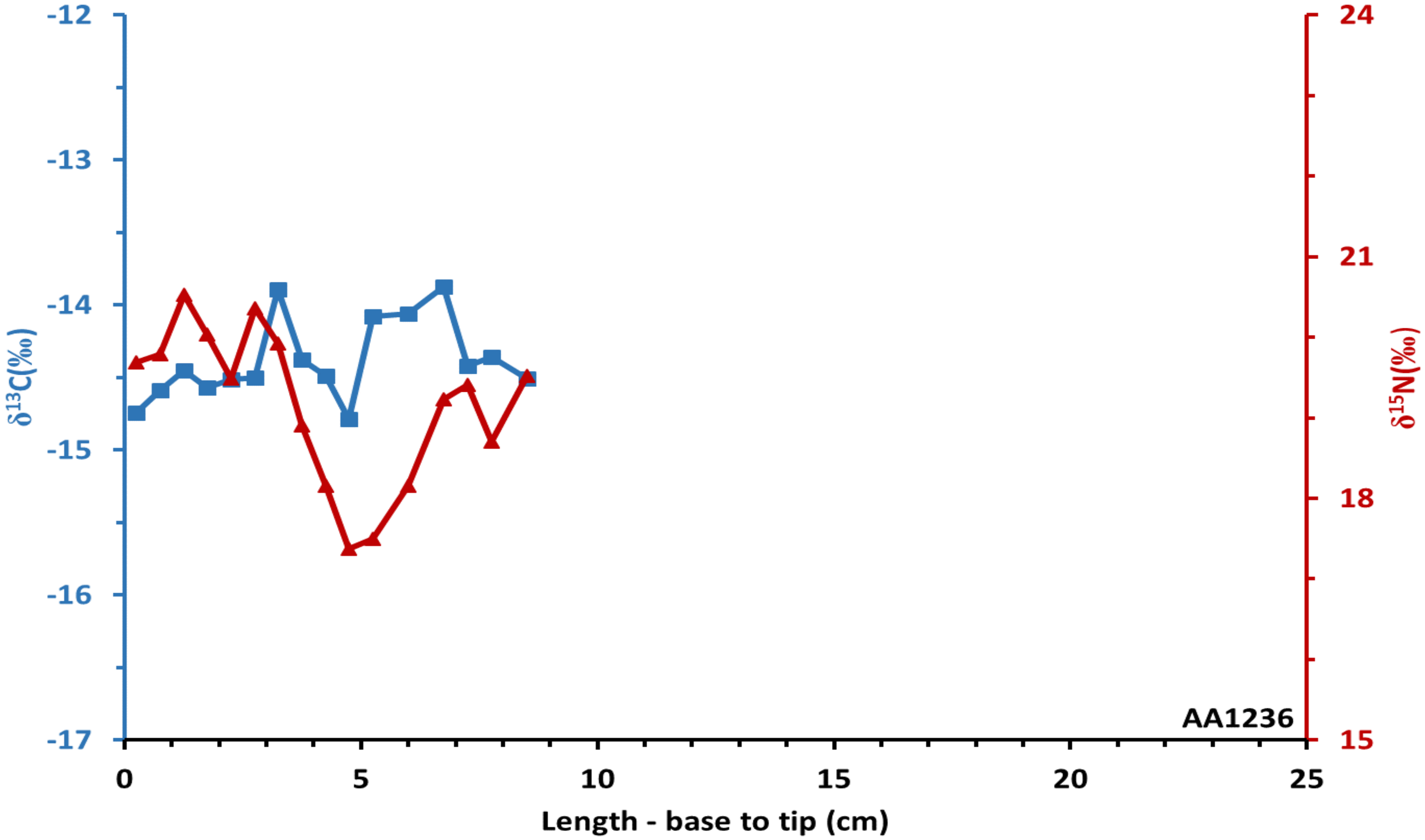

Figure B-50. Adult Female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1236), 2012.

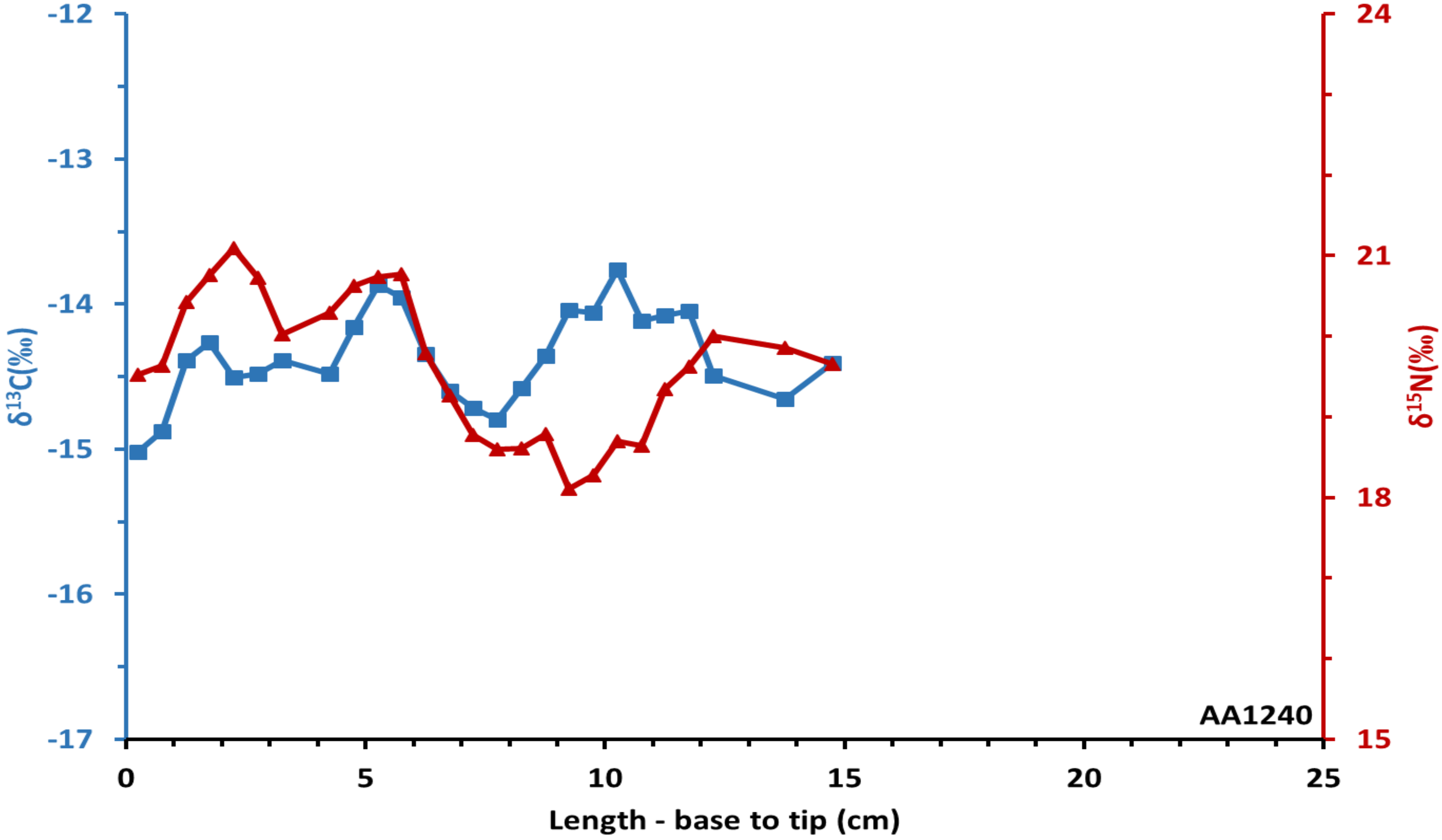

Figure B-51. Adult Female Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1240), 2012.

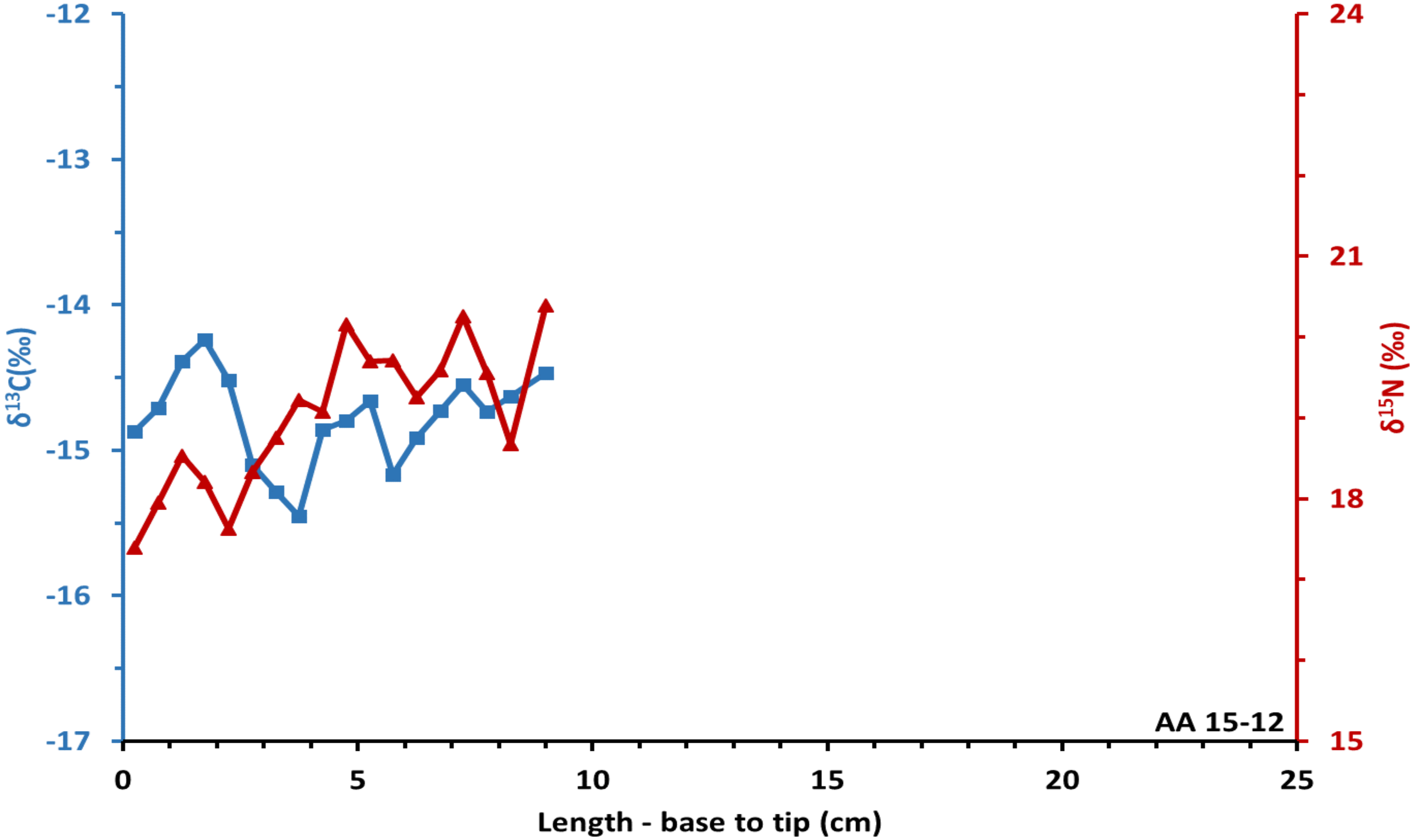

Figure B-52. Adult Female (Dam) Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA15-12), 2015.

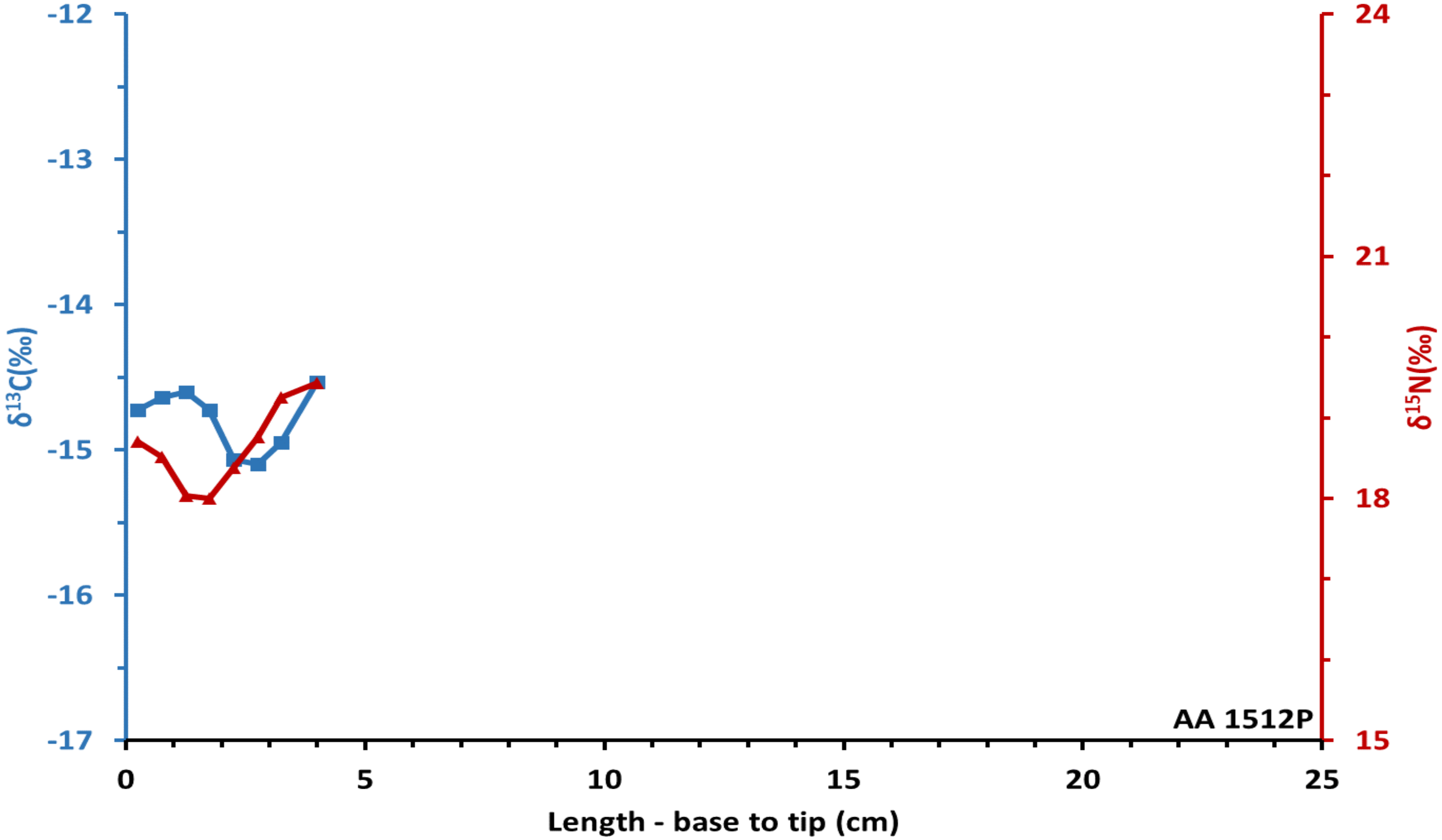

Figure B-53. Pup of (Dam AA15-12) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA15-12P), 2015.

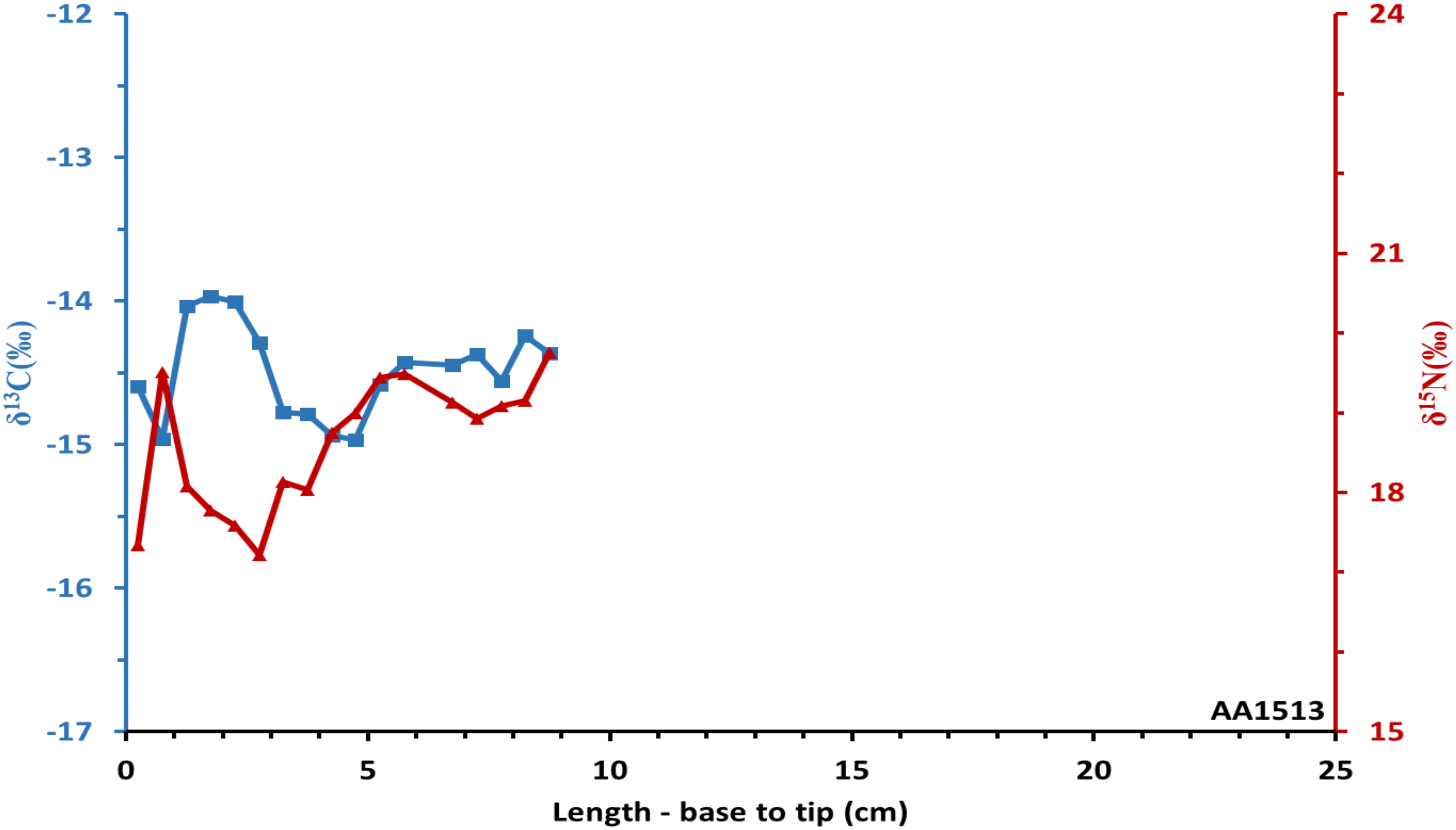

Figure B-54. Adult Female (Dam) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1513), 2015.

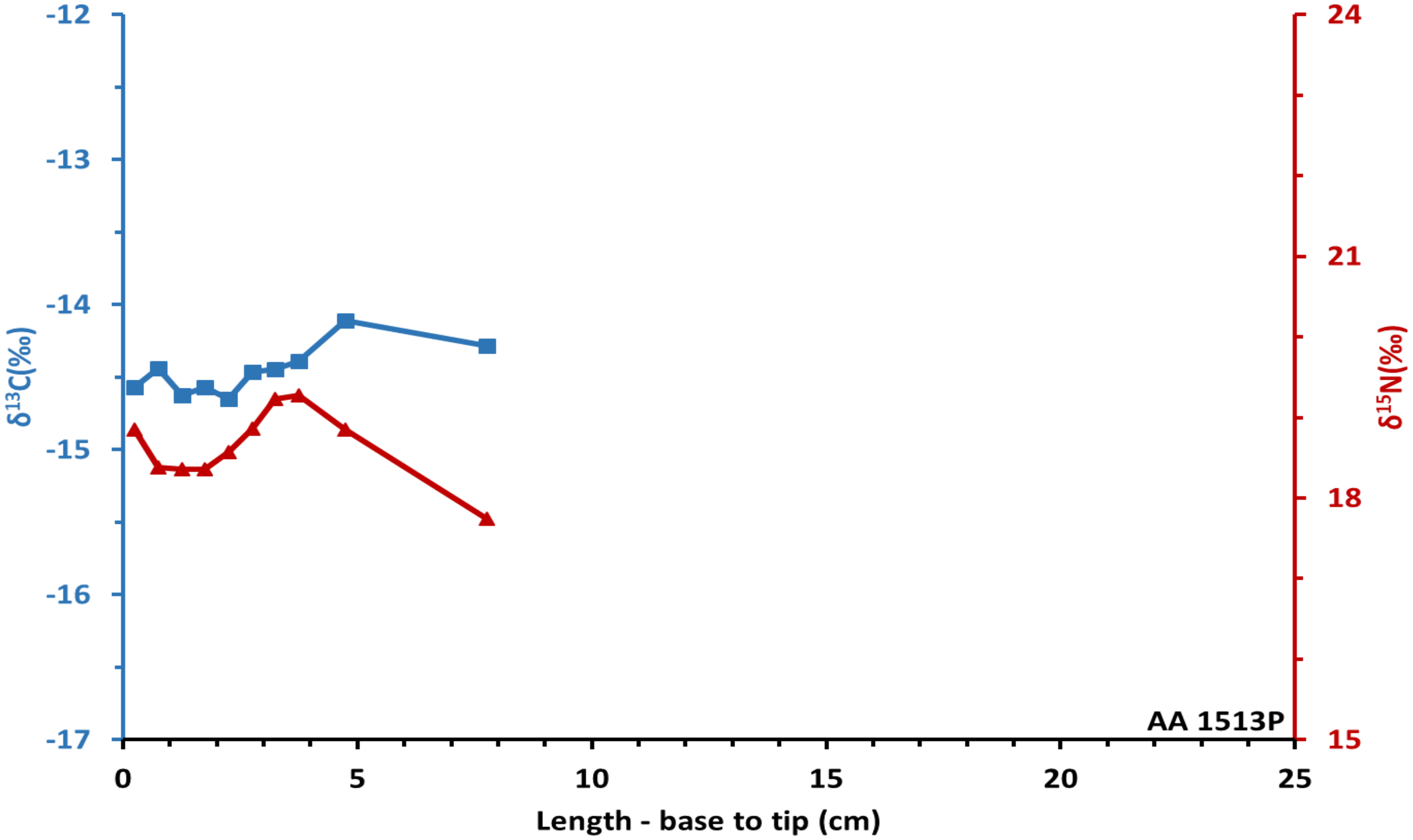

Figure B-55. Pup of (Dam AA1513) Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1513P), 2015

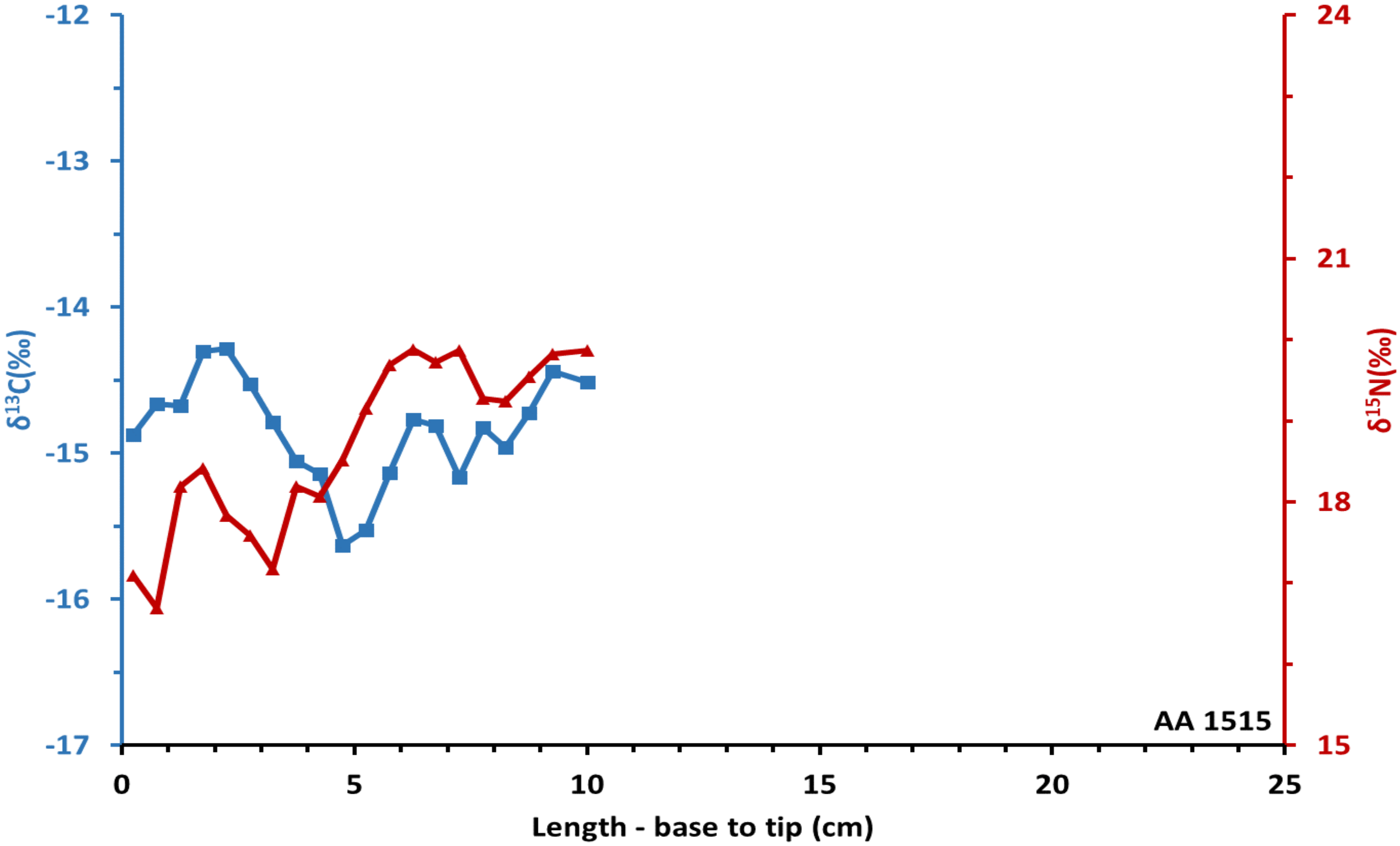

Figure B-56. Adult Female (Dam) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1515), 2015.

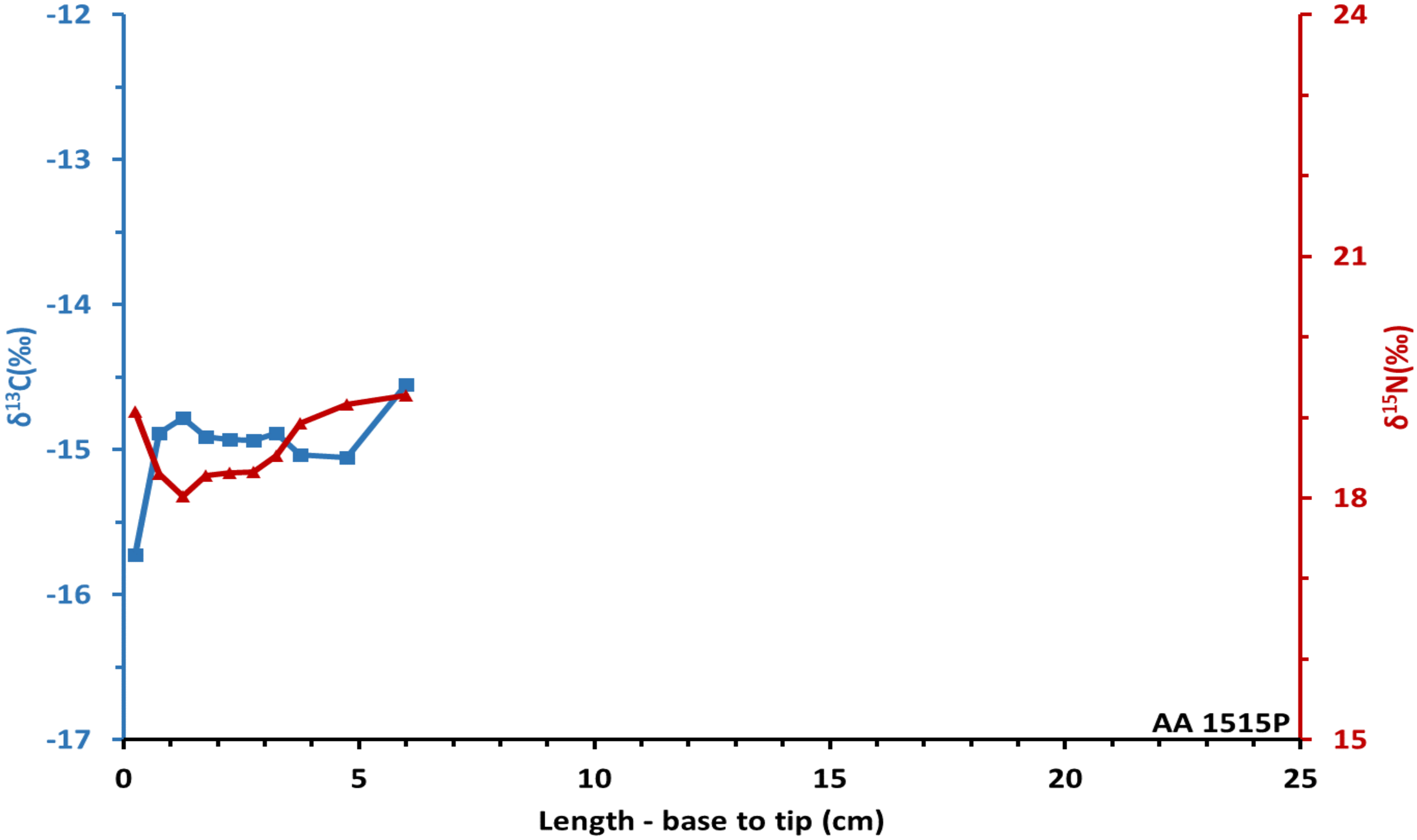

Figure B-57. Pup of (Dam AA1515) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1515P), 2015

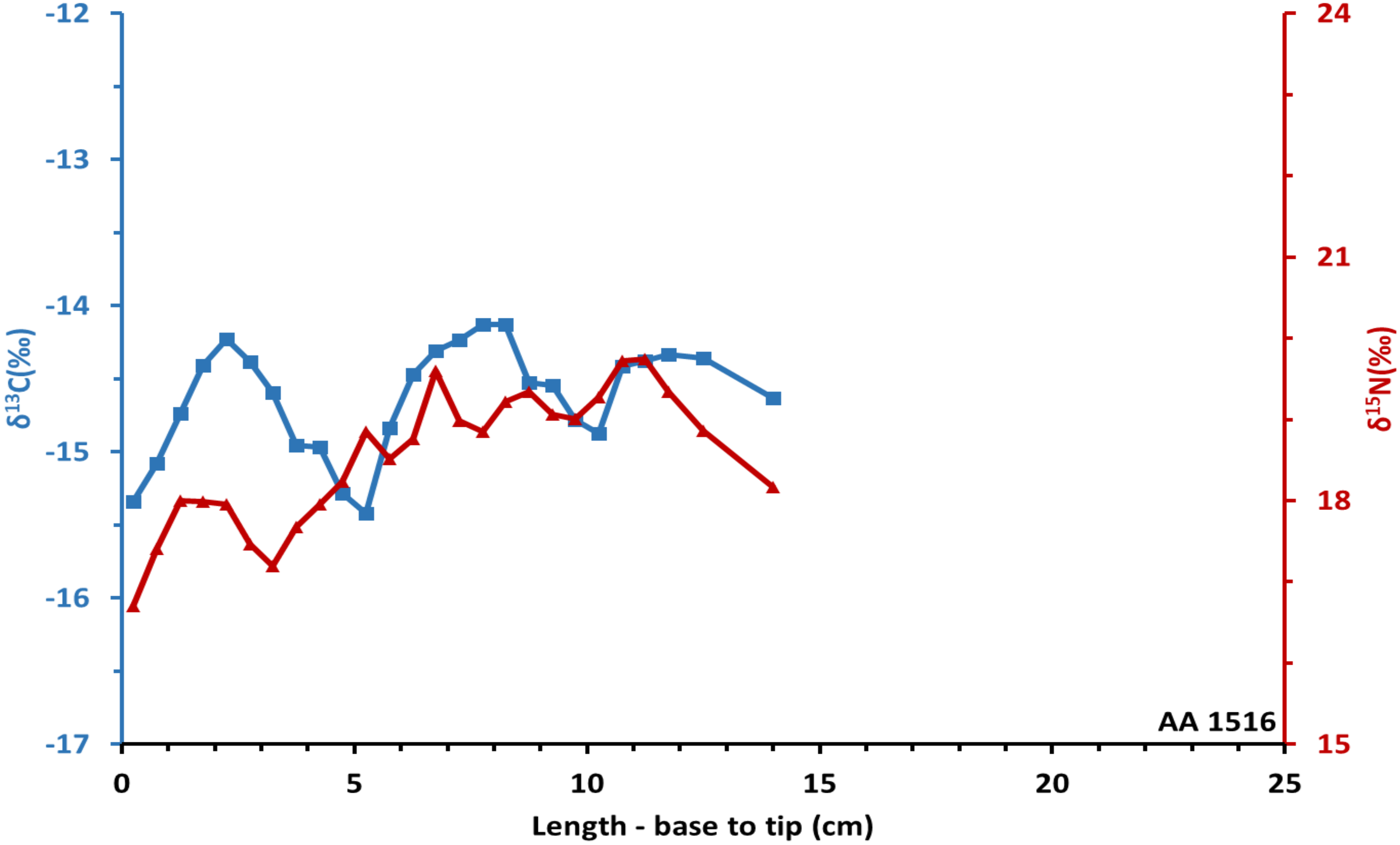

Figure B-58. Adult Female (Dam) Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1516), 2015.

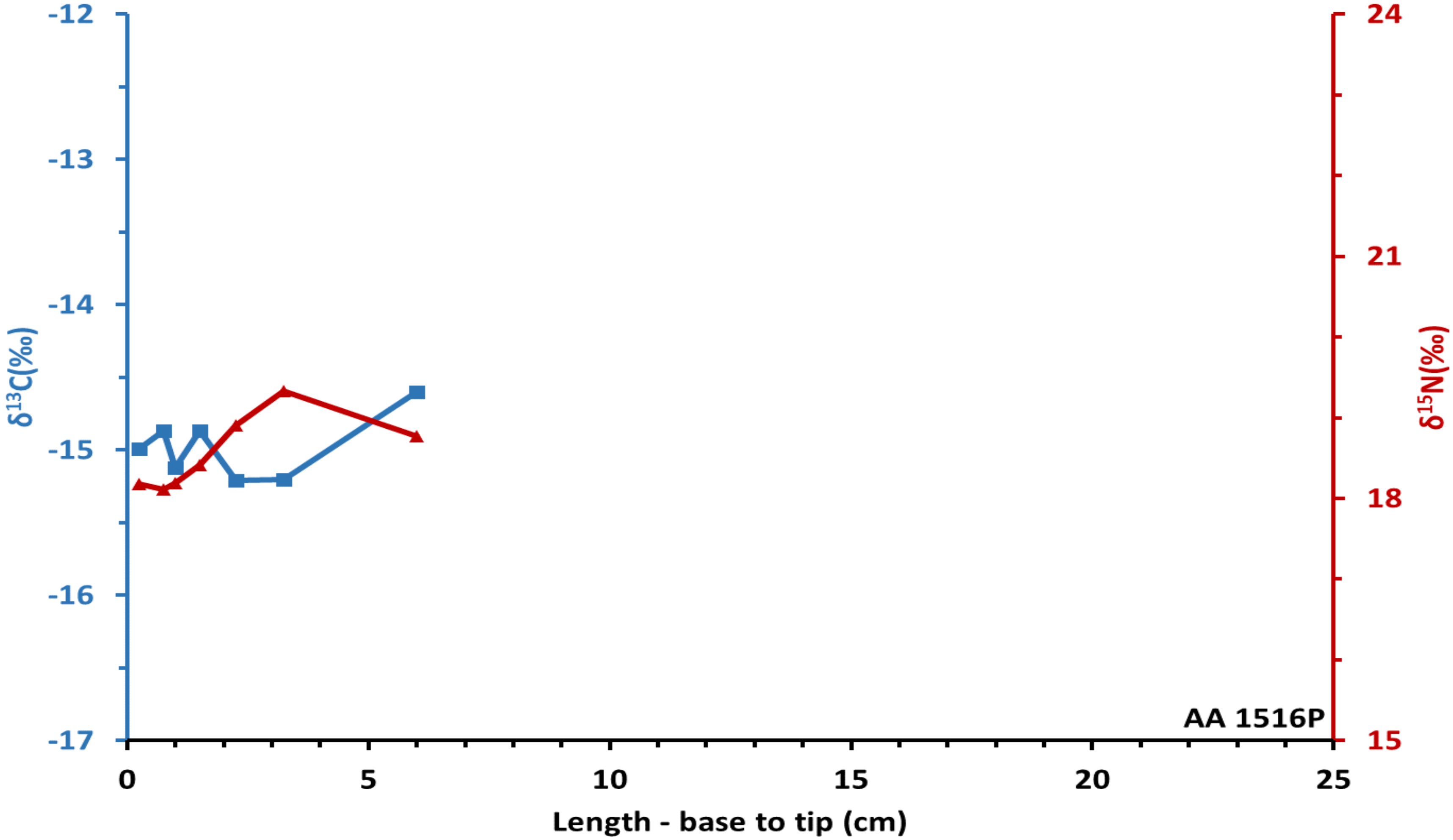

Figure B-59. Pup of Dam 1516 sampled in 2015. Pup of (Dam AA1516) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1516P), 2015

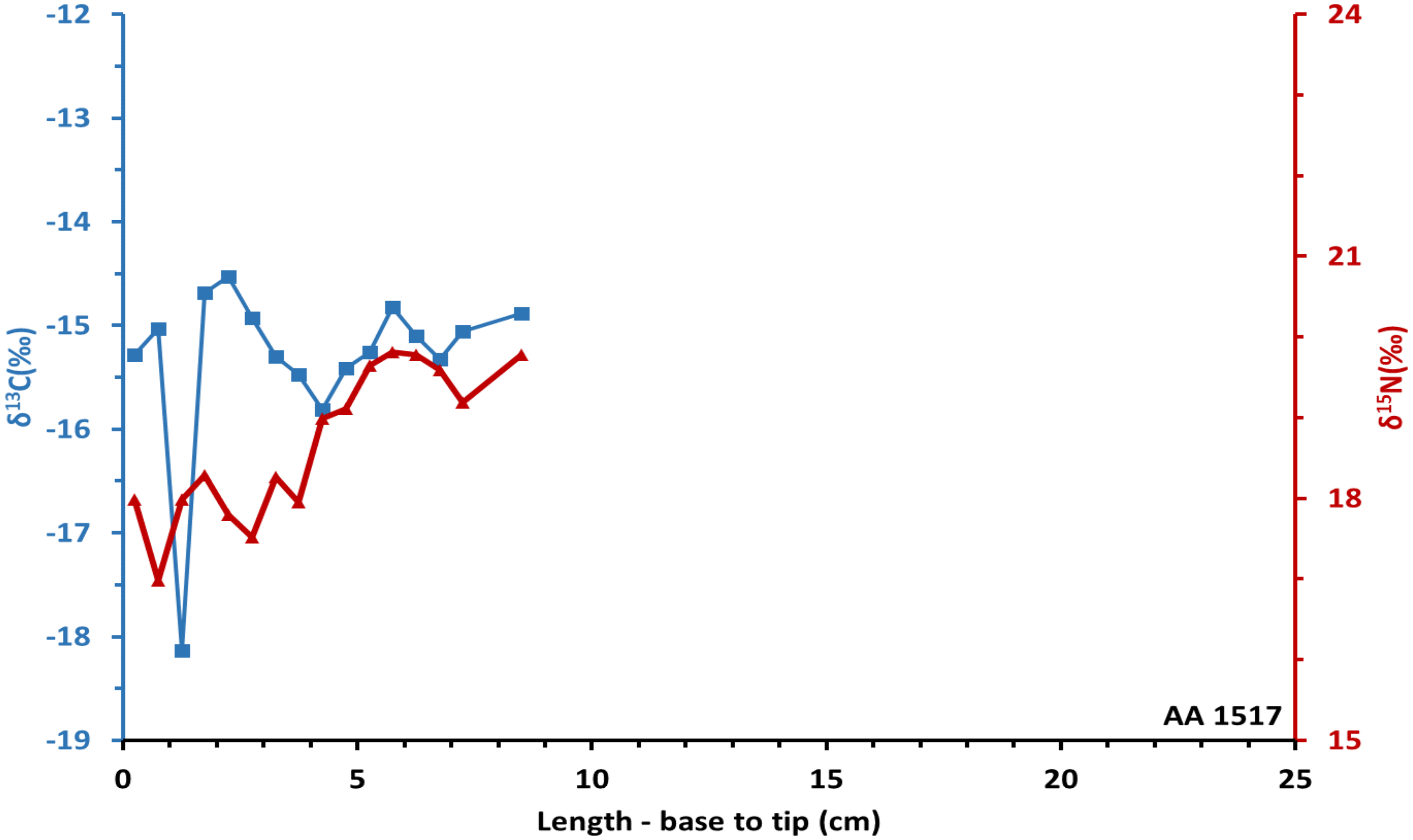

Figure C-60. Adult Female (Dam) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1517), 2015.

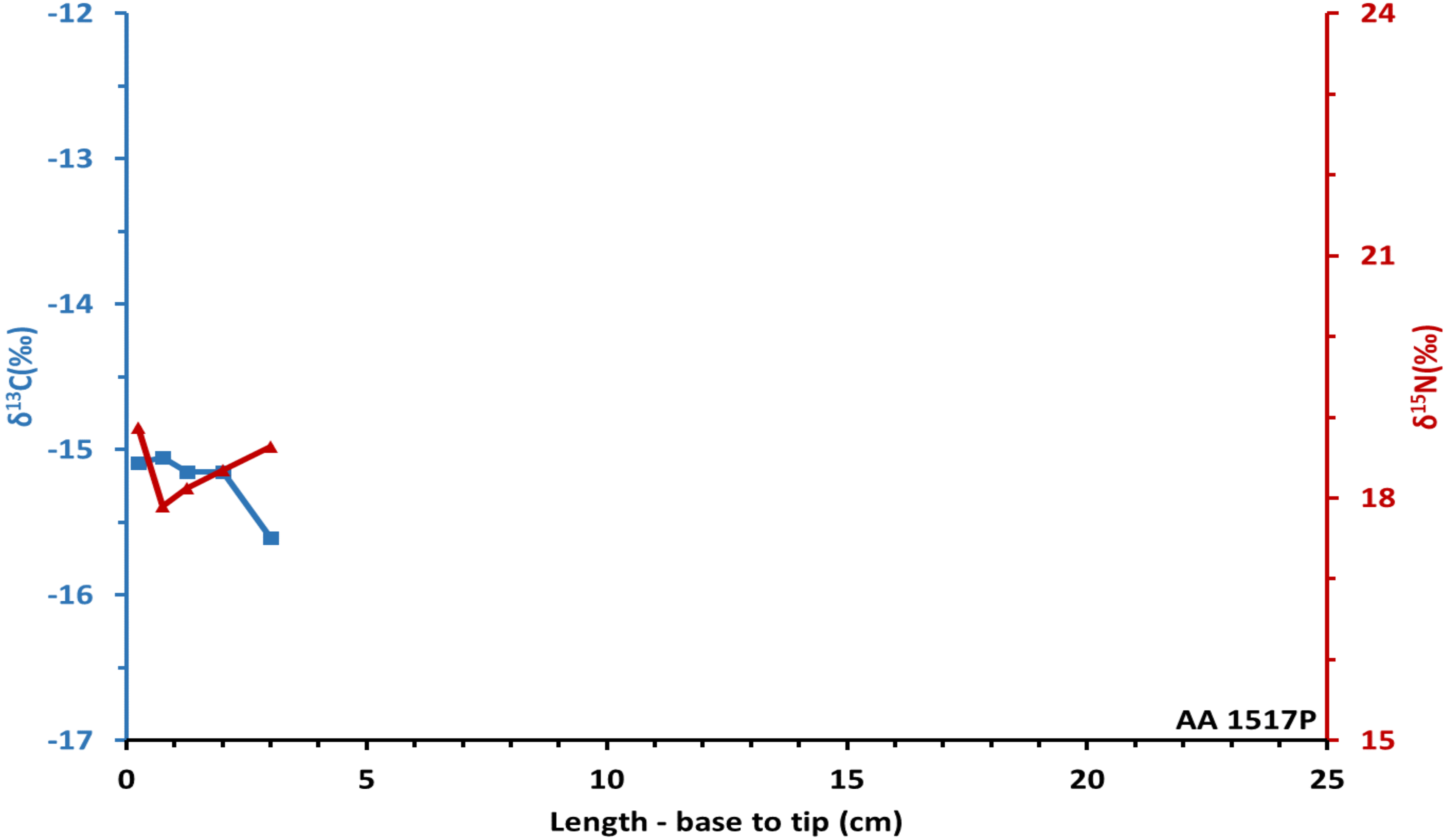

Figure B-61. Pup of (Dam AA1517) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1517P), 2015

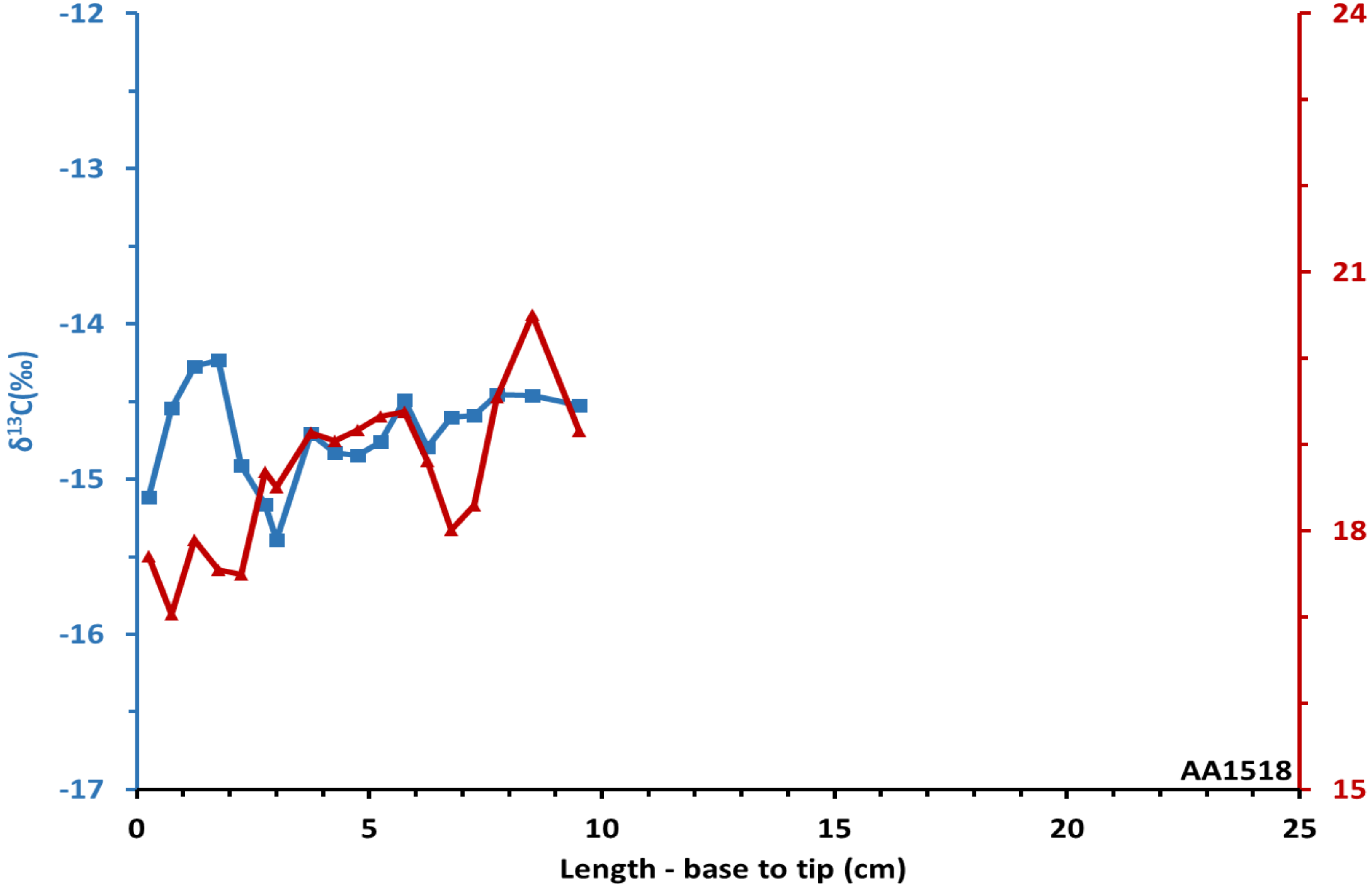

Figure B-62. Adult Female (Dam) Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA1518), 2015

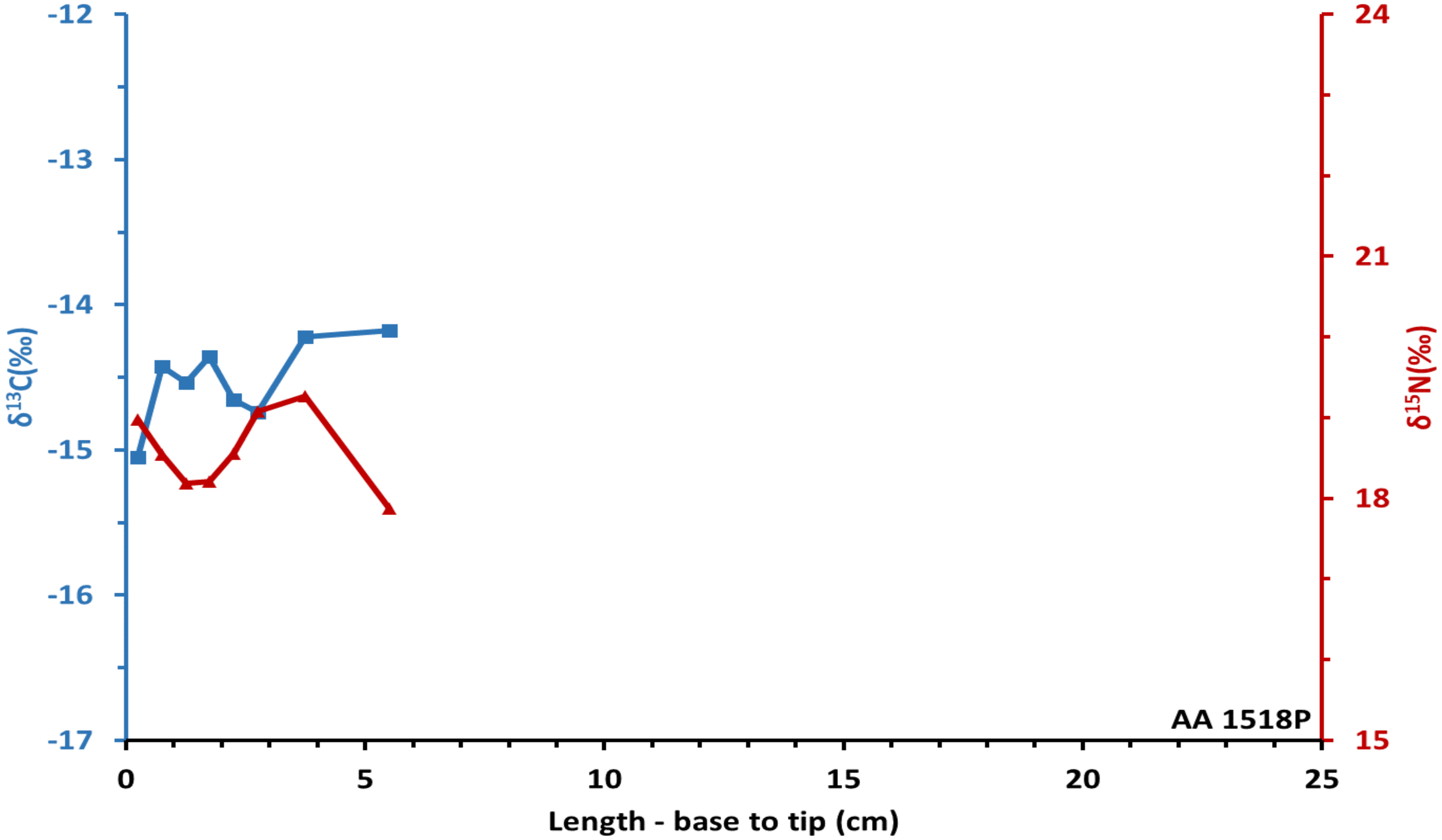

Figure B-63. Pup of (Dam AA1518) Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA1518P), 2015

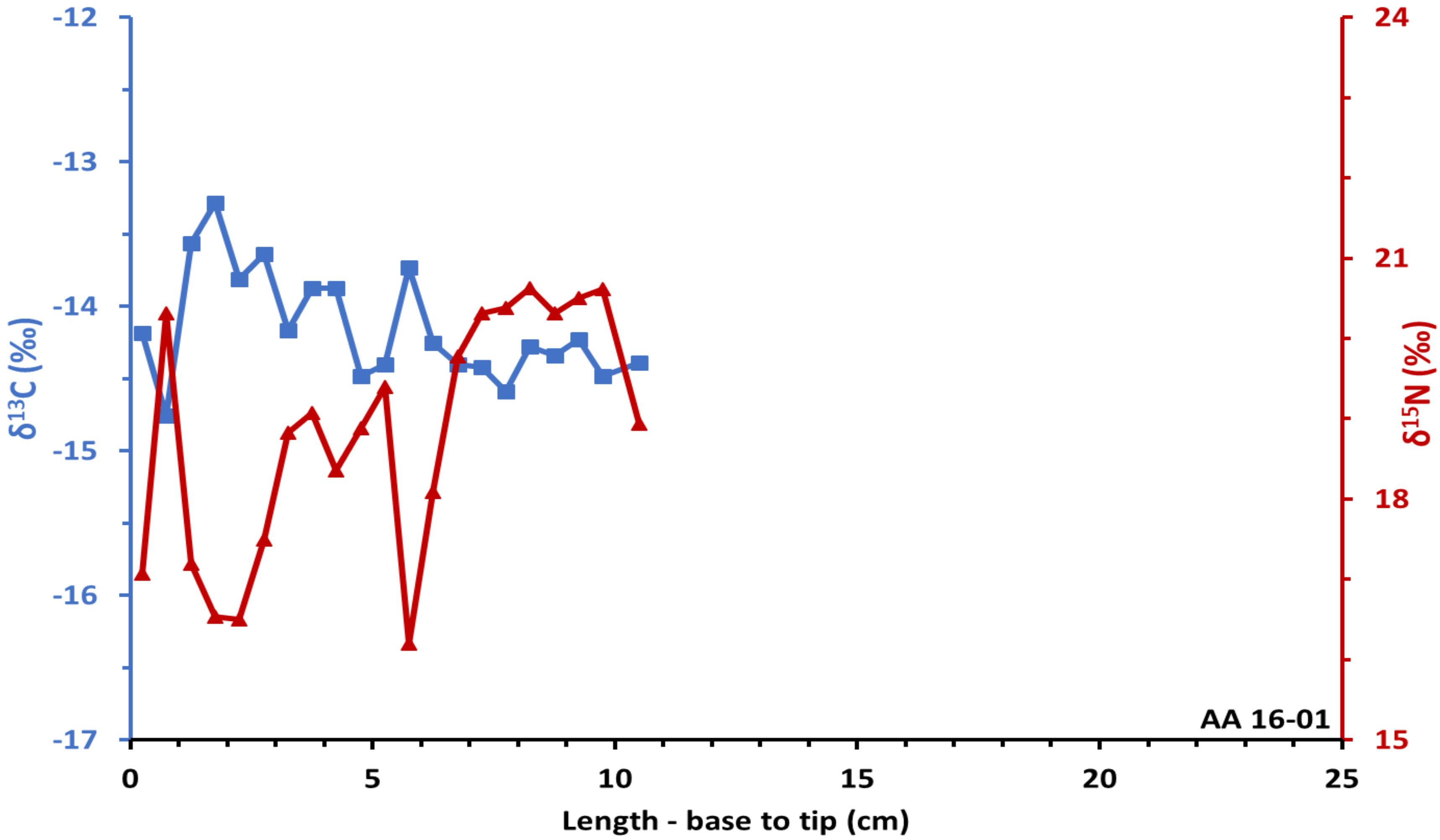

Figure B-64. Adult Bull male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA16-01), 2016.

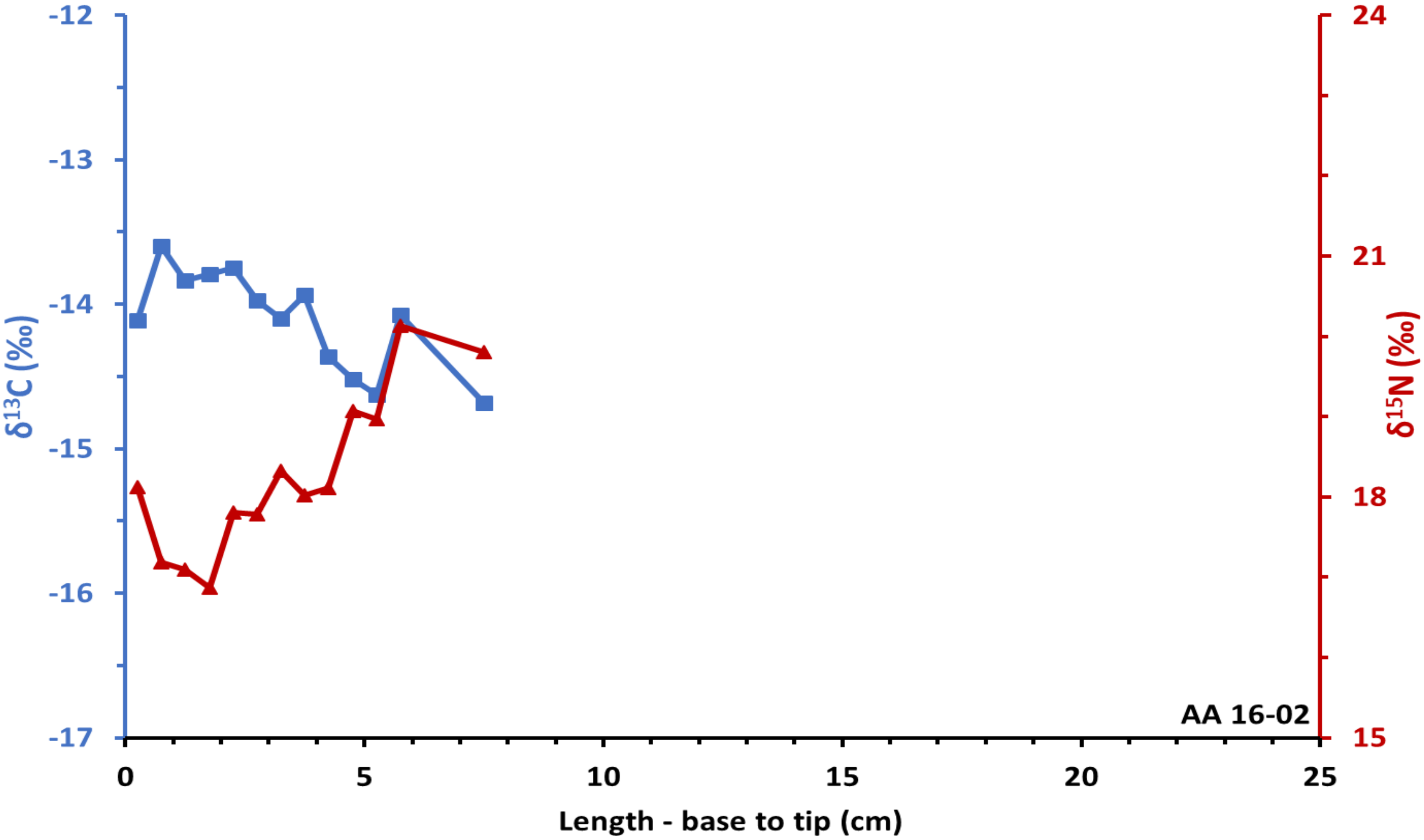

Figure B-65. Adult Bull male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA16-02), 2016.

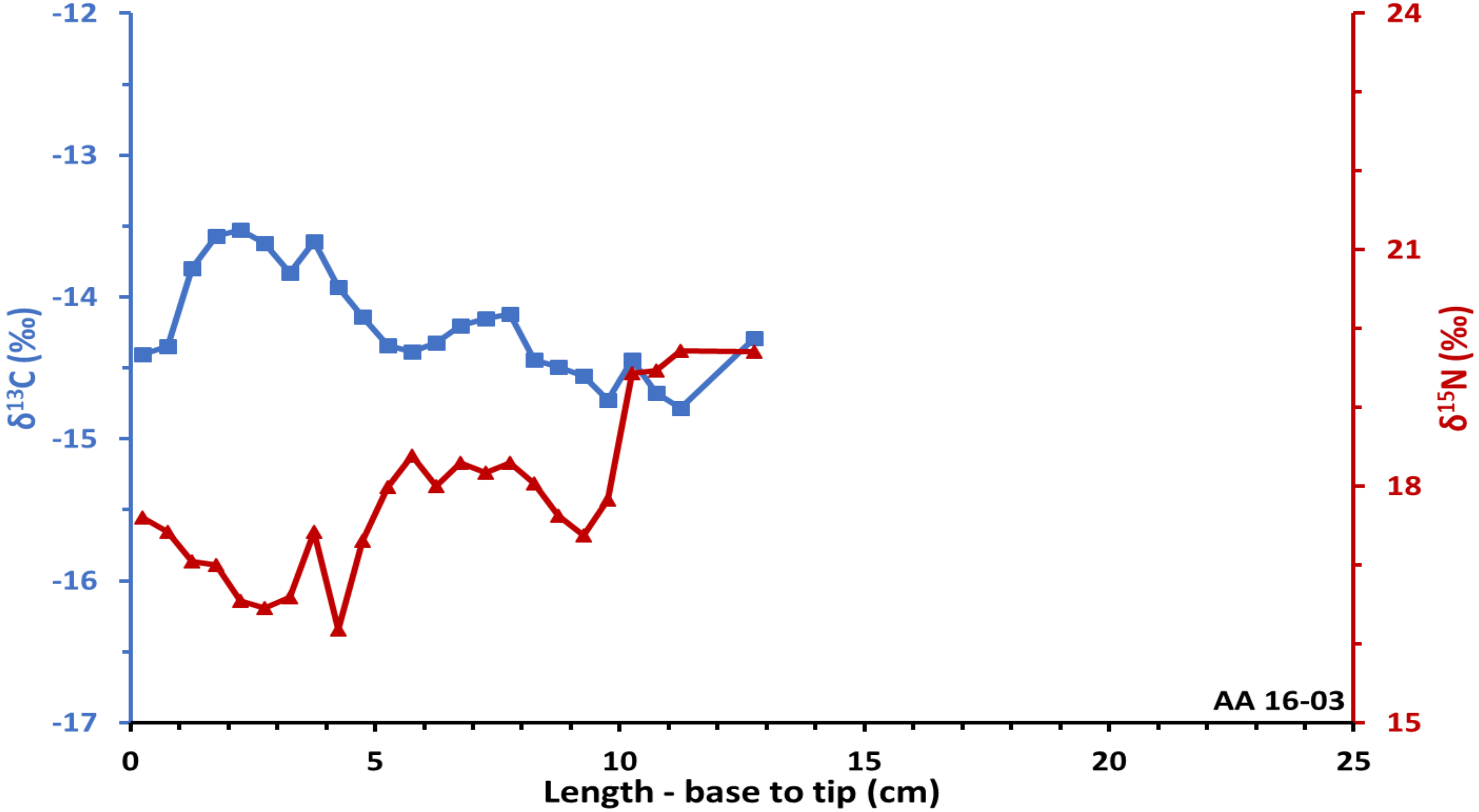

Figure B-66. Adult Bull male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA16-03), 2016.

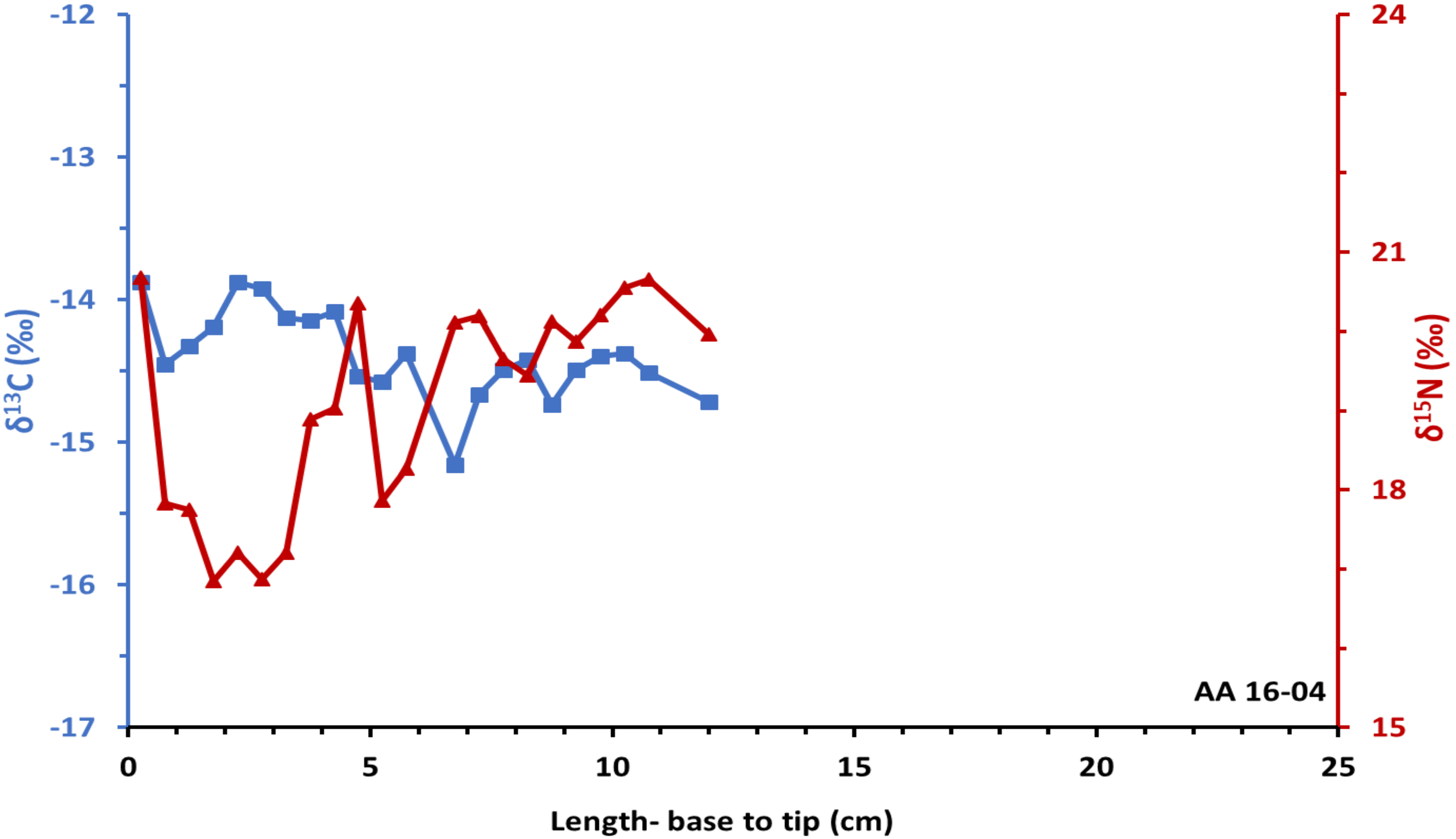

Figure B-67. Adult Bull male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA16-04), 2016.

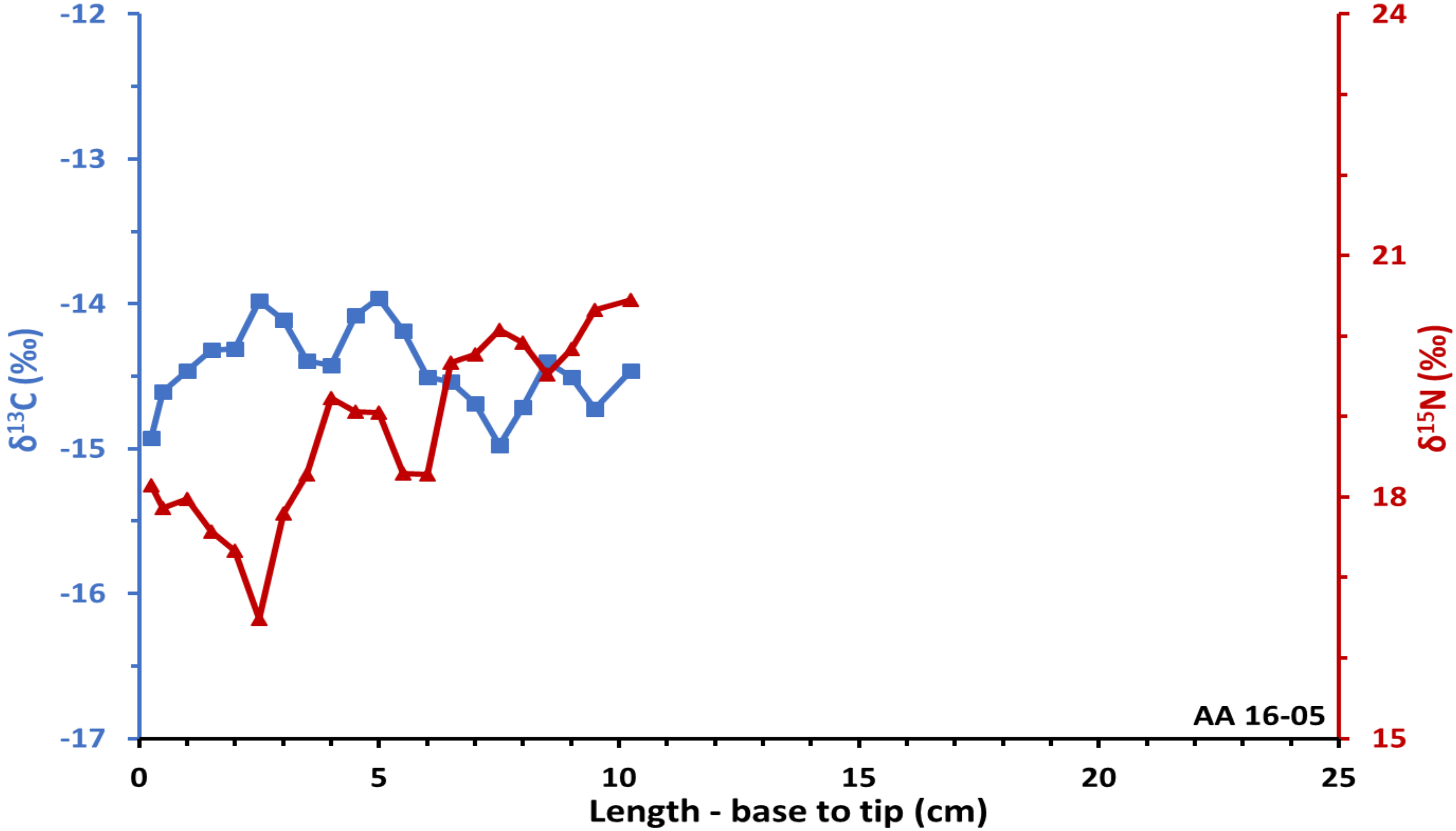

Figure B-68. Adult Bull male Peruvian fur seal vibrissae $\delta^{13}C$ and $\delta^{15}N$ (AA16-05), 2016.

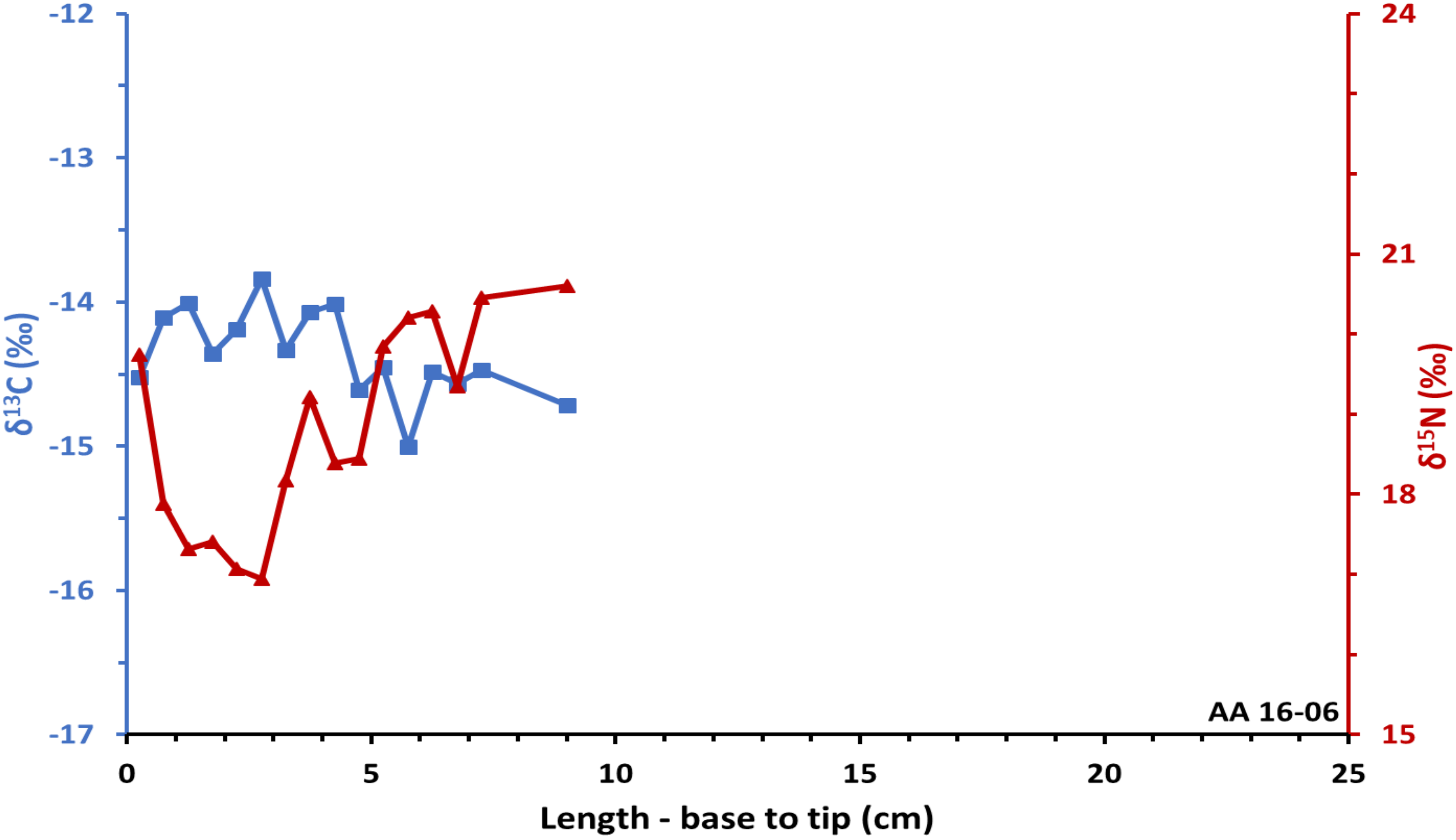

Figure B-69. Adult Bull male Peruvian fur seal vibrissae δ^{13}C and δ^{15}N (AA16-06), 2016.

Appendix C: Vibrissae Plots (South American Sea Lion)

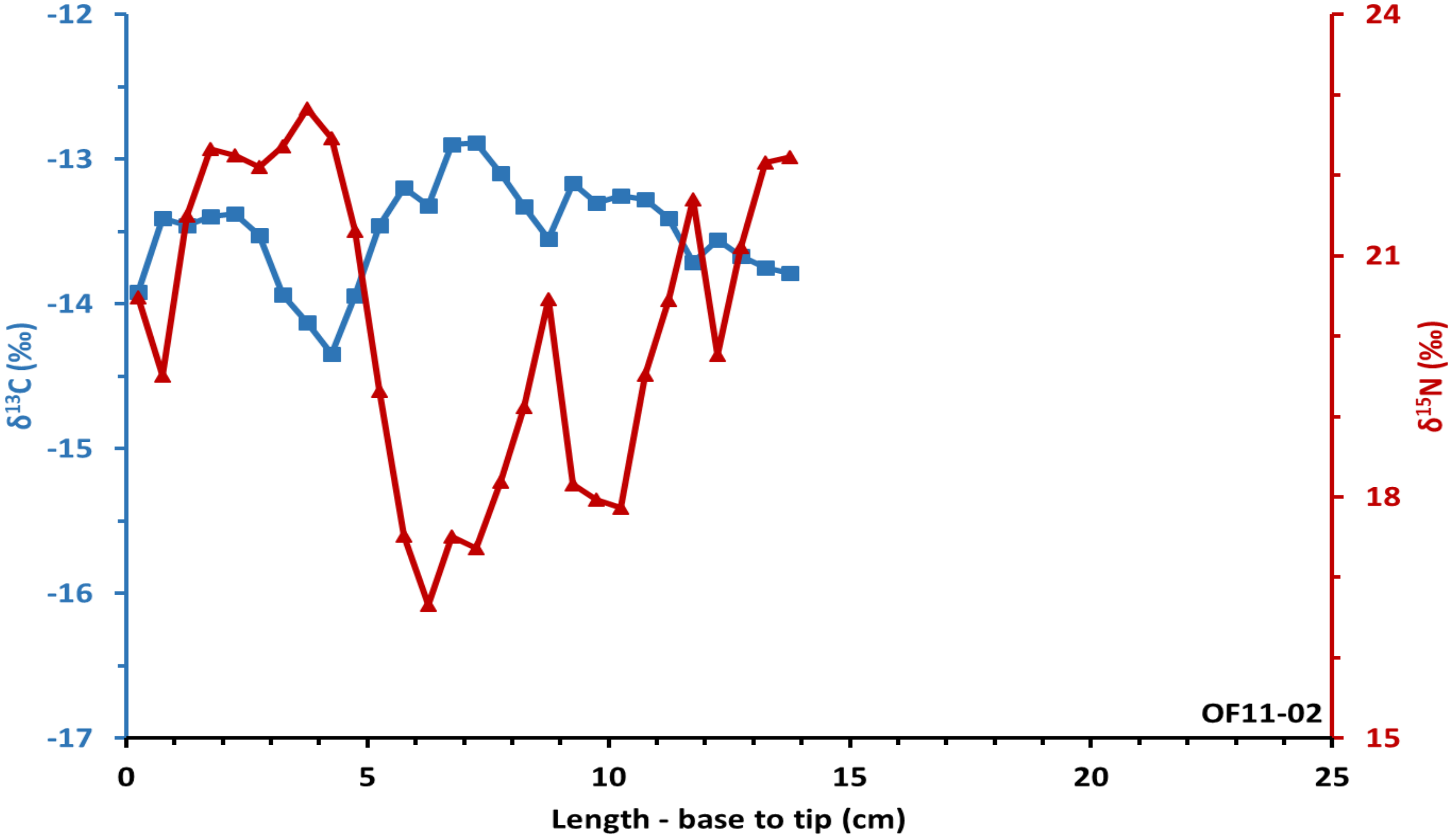

Figure C-1.Subadult South American sea lion vibrissae δ^{13}C and δ^{15}N (OF11-02), 2011.

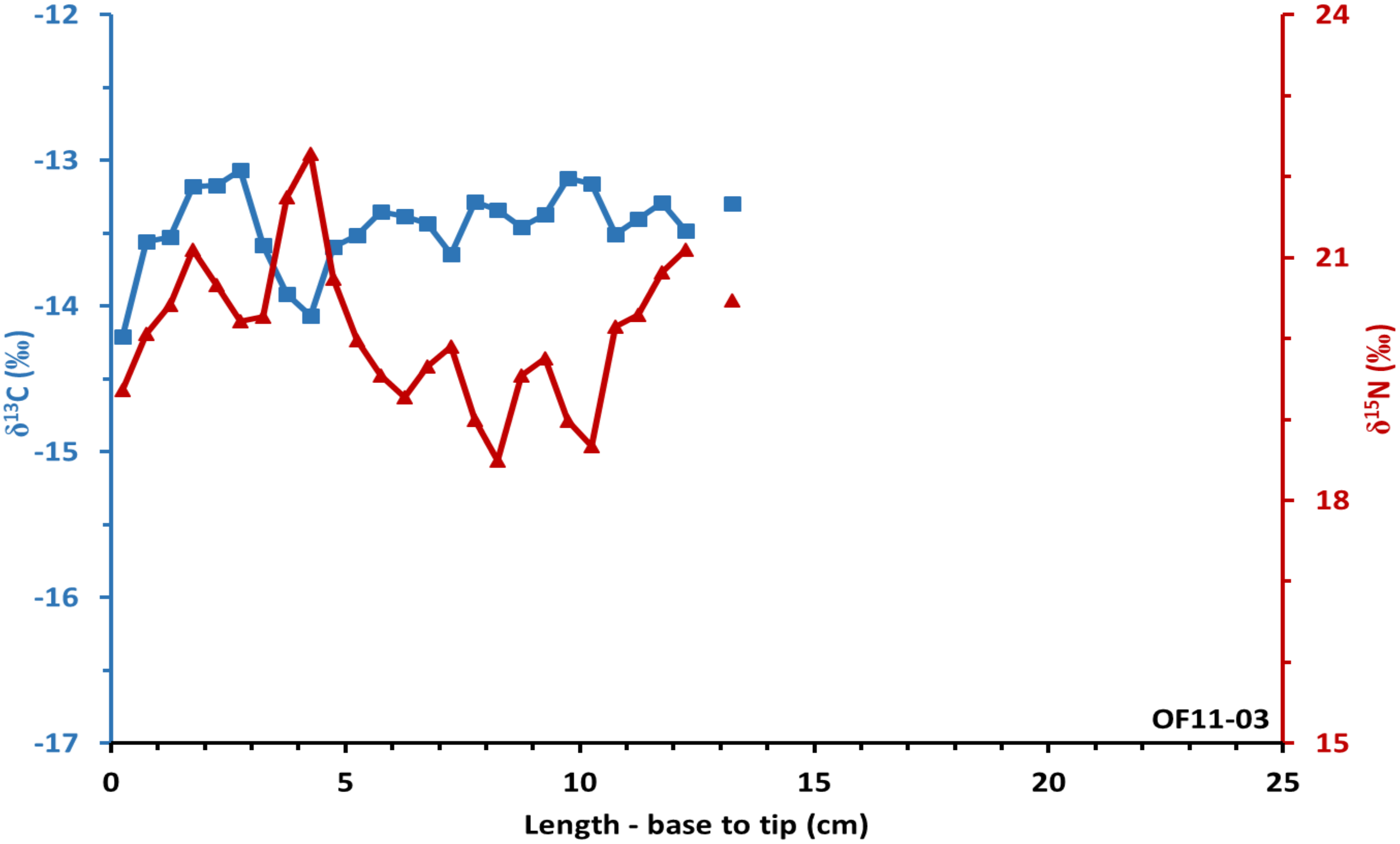

Figure C-2. Subadult South American sea lion vibrissae δ^{13}C and δ^{15}N (OF11-03), 2011.

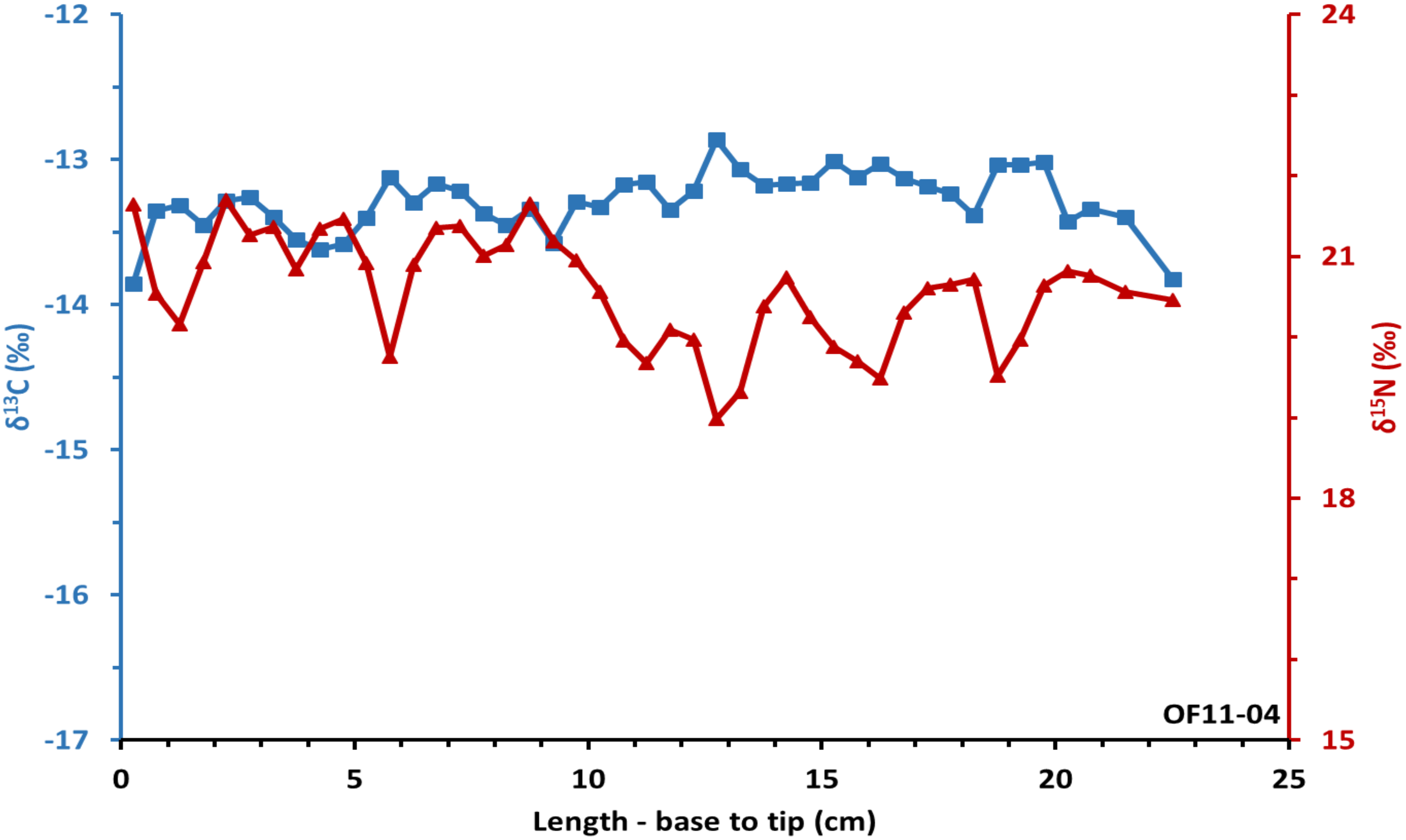

Figure C-3 Subadult South American sea lion vibrissae δ^{13}C and δ^{15}N (OF11-04), 2011.

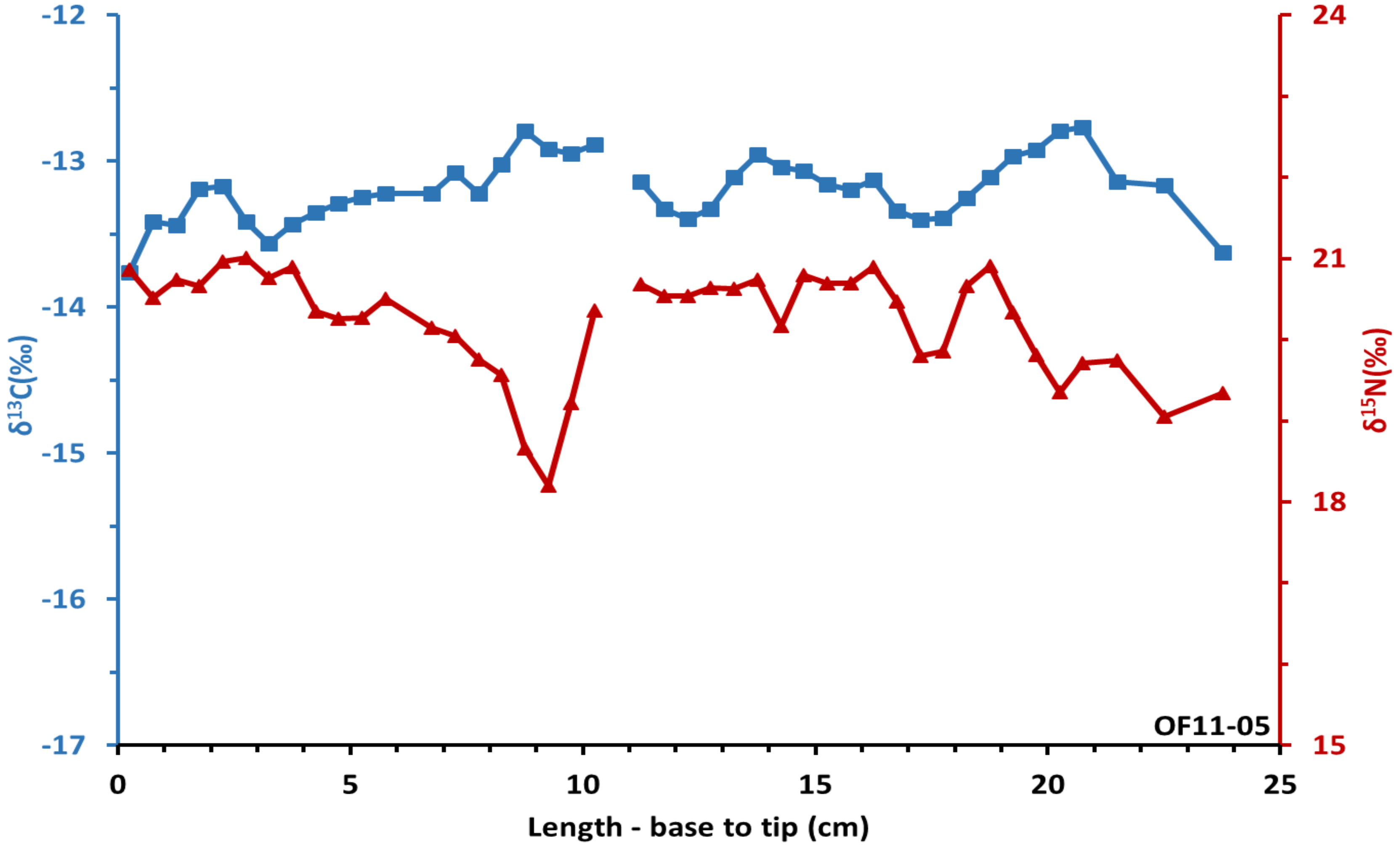

Figure C-4. Subadult South American sea lion vibrissae δ^{13}C and δ^{15}N (OF11-05), 2011.

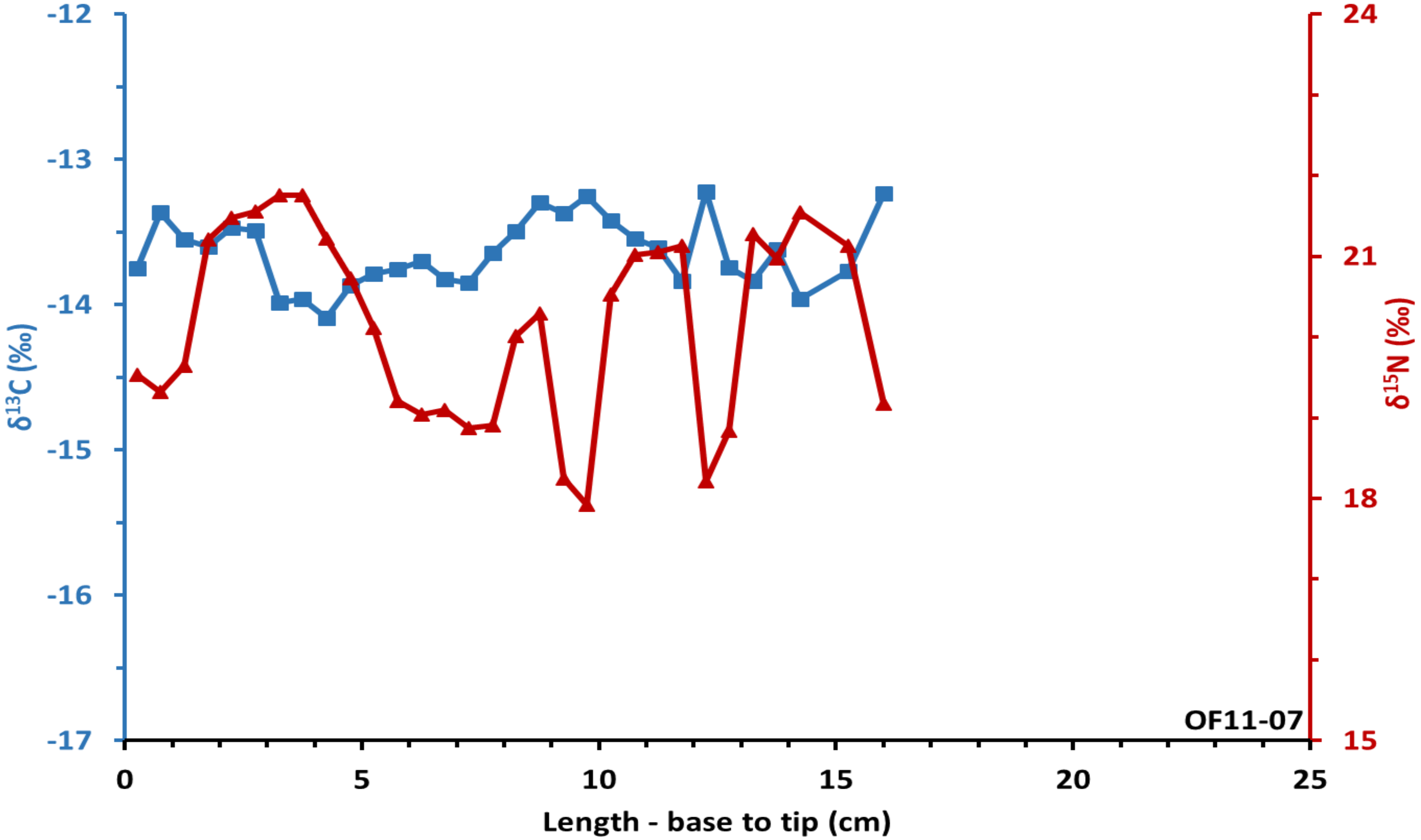

Figure C-5. Subadult South American sea lion vibrissae $\delta^{13}C$ and $\delta^{15}N$ (OF11-07), 2011.

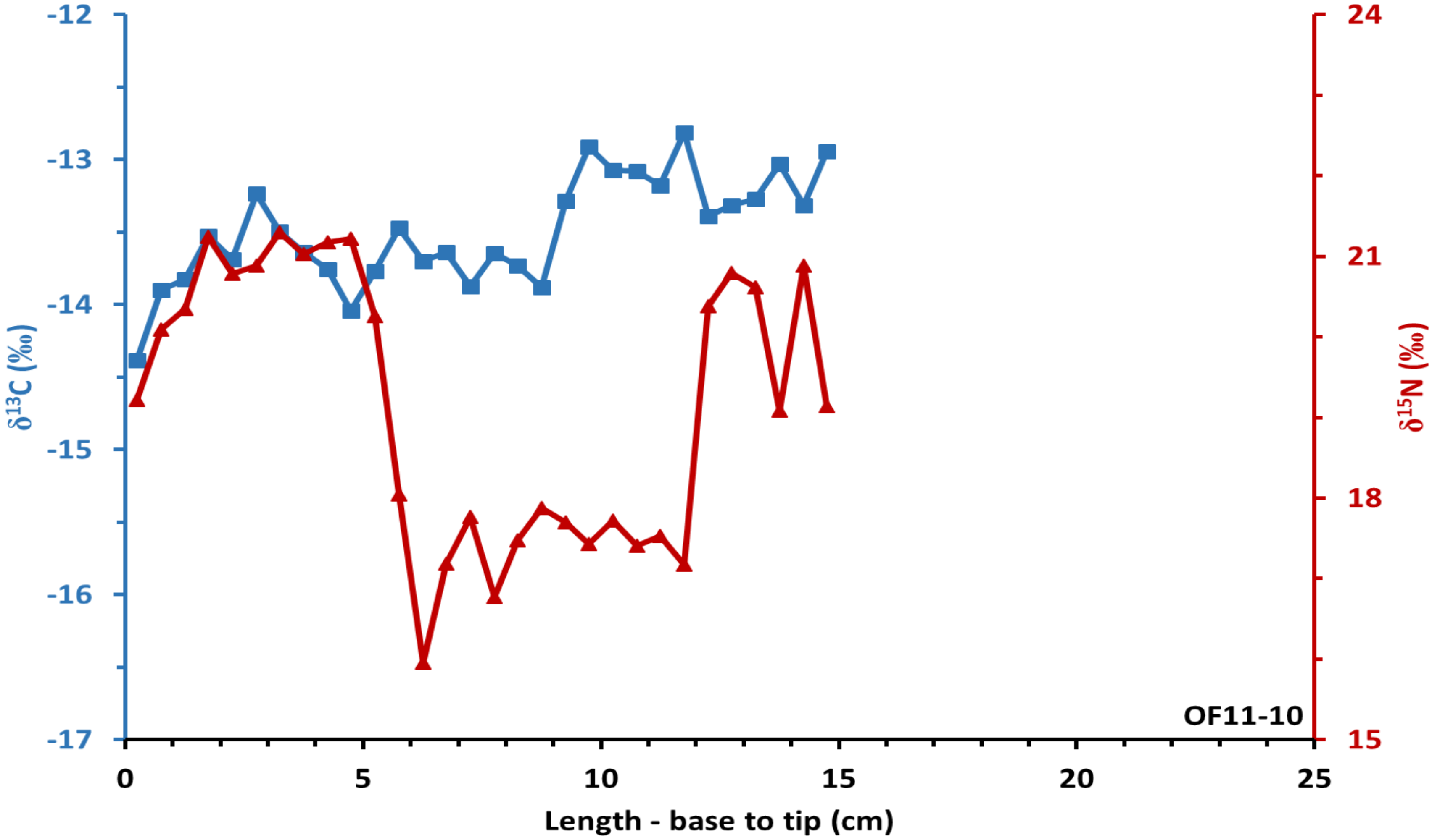

Figure C-6. Subadult South American sea lion vibrissae $\delta^{13}C$ and $\delta^{15}N$ (OF11-10), 2011.

Appendix D: Vibrissae Tables

Table 4. Minimum, maximum, range, and mean $\delta^{13}C$ and $\delta^{15}N$ (‰) in Peruvian fur seal (*Arctocephalus australis* unnamed ssp.) vibrissae, Punta San Juan, Peru, 2010-2016. Gender (Male=M, Female=F, Unknown =UNK) and Age (Adult=AD, Pup=PUP).

Individual	Year	Gender	Age	Min $\delta^{13}C$	Max $\delta^{13}C$	Range $\delta^{13}C$	x $\delta^{13}C$	Min $\delta^{15}N$	Max $\delta^{15}N$	Range $\delta^{15}N$	x $\delta^{15}N$
AA 1002	2010	F	AD	-14.97	-14.02	0.95	-14.44	15.83	19.95	4.12	18.87
AA 1003	2010	F	AD	-14.84	-13.61	1.23	-14.23	17.09	19.87	2.78	18.49
AA 1006	2010	F	AD	-15.35	-13.77	1.58	-14.38	17.58	20.85	3.27	19.29
AA 1008	2010	F	AD	-14.87	-13.71	1.16	-14.16	17.26	20.13	2.87	18.70
AA 1010	2010	F	AD	-15.50	-13.67	1.83	-14.19	17.81	20.49	2.68	19.11
AA 1012	2010	F	AD	-15.12	-13.96	1.16	-14.65	17.76	21.55	3.79	19.74
AA 1014	2010	F	AD	-15.28	-13.80	1.48	-14.25	17.15	19.98	2.83	18.61
AA 1016	2010	F	AD	-15.22	-14.03	1.19	-14.48	17.42	19.61	2.19	18.68
AA 1018	2010	F	AD	-14.12	-13.76	0.36	-14.12	18.50	20.43	1.93	19.36
AA 1020	2010	F	AD	-15.02	-14.09	0.93	-14.54	17.26	19.65	2.39	18.91
AA 1022	2010	F	AD	-15.07	-13.66	1.41	-14.19	17.47	19.68	2.21	18.84
AA 1024	2010	F	AD	-15.47	-14.03	1.44	-14.44	17.26	19.95	2.69	18.79
AA 1026	2010	F	AD	-14.74	-13.78	0.96	-14.28	17.47	19.75	2.28	18.81
AA 1028	2010	F	AD	-14.69	-13.91	0.78	-14.35	17.41	20.03	2.62	19.08
AA 1030	2010	F	AD	-15.51	-14.02	1.49	-14.60	17.44	20.78	3.34	19.04
AA 1032	2010	F	AD	-14.53	-13.77	0.76	-14.19	17.58	19.96	2.38	18.87
AA 1034	2010	F	AD	-14.22	-13.73	0.49	-13.97	16.17	18.12	1.95	17.40
AA 1036	2010	F	AD	-14.58	-13.87	0.71	-14.19	18.48	20.30	1.82	19.38
AA 1038	2010	F	AD	-15.11	-14.01	1.10	-14.43	17.31	19.91	2.60	18.45
AA 1040	2010	F	AD	-15.52	-13.80	1.72	-14.37	17.35	19.74	2.39	18.55
AA 1042	2010	F	AD	-14.86	-14.06	0.80	-14.46	17.91	20.19	2.28	19.31
AA 1044	2010	F	AD	-16.00	-13.74	2.26	-14.36	17.43	20.26	2.83	18.97
AA 1046	2010	F	AD	-16.54	-14.06	2.48	-14.74	18.02	20.48	2.46	19.39

Table 4. Continued.

Individual	**Year**	**Gender**	**Age**	**Min $\delta^{13}C$**	**Max $\delta^{13}C$**	**Range $\delta^{13}C$**	**x $\delta^{13}C$**	**Min $\delta^{15}N$**	**Max $\delta^{15}N$**	**Range $\delta^{15}N$**	**X $\delta^{15}N$**
AA 1048	2010	F	AD	-14.91	-13.83	1.08	-14.35	17.54	20.12	2.58	18.97
AA 1050	2010	F	AD	-14.48	-13.59	0.89	-14.09	17.60	19.97	2.37	19.01
AA 1052	2010	F	AD	-15.10	-13.24	1.86	-13.78	17.94	20.07	2.13	19.22
AA 1054	2010	F	AD	-14.78	-13.30	1.48	-13.96	17.65	20.40	2.75	19.07
AA 1056	2010	F	AD	-14.69	-13.42	1.27	-13.83	16.86	19.45	2.59	18.16
AA 1058	2010	F	AD	-14.23	-13.19	1.04	-13.64	17.72	20.92	3.20	18.87
AA1101	2011	M	AD	-14.37	-13.29	1.08	-13.73	19.10	21.13	2.03	20.30
AA1103	2011	M	AD	-14.75	-13.68	1.07	-14.04	18.73	20.90	2.17	19.88
AA1105	2011	M	AD	-14.58	-13.17	1.41	-13.57	18.96	20.99	2.03	20.15
AA1107	2011	M	AD	-14.01	-13.57	0.44	-14.01	19.72	21.69	1.97	20.64
AA1108	2011	M	AD	-14.82	-13.30	1.52	-13.73	18.28	21.75	3.47	20.49
AA1109	2011	M	AD	-14.80	-13.48	1.32	-13.90	18.08	20.99	2.91	19.84
AA1119	2011	F	AD	-15.64	-13.92	1.72	-14.36	17.93	20.80	2.87	19.23
AA1122	2011	F	AD	-15.72	-14.53	1.19	-14.53	17.74	20.42	2.68	19.07
AA1123	2011	F	AD	-15.14	-13.21	1.93	-14.02	16.42	20.61	4.19	18.70
AA1130	2011	F	AD	-15.22	-13.88	1.34	-14.39	17.49	20.52	3.03	19.09
AA1131	2011	F	AD	-14.86	-13.97	0.89	-14.41	16.89	19.84	2.95	18.54
AA1134	2011	F	AD	-15.53	-13.82	1.71	-14.25	16.48	20.17	3.69	18.54
AA1201	2012	M	AD	-15.77	-13.70	2.07	-14.11	18.16	21.85	3.69	20.03
AA1202	2012	M	AD	-14.58	-13.46	1.12	-13.93	18.91	22.27	3.36	20.76
AA1203	2012	M	AD	-15.18	-13.61	1.57	-14.04	17.90	21.16	3.26	19.76
AA1204	2012	M	AD	-14.47	-13.23	1.24	-13.78	18.65	21.80	3.15	20.55
AA1205	2012	M	AD	-14.02	-13.34	0.68	-13.68	17.65	22.31	4.66	20.22
AA1206	2012	F	AD	-14.07	-13.63	0.44	-14.07	16.88	20.82	3.94	19.33
AA1220	2012	F	AD	-15.45	-14.03	1.42	-14.60	17.65	21.37	3.72	19.70
AA1230	2012	F	AD	-15.17	-13.80	1.37	-14.35	17.11	20.67	3.56	19.09

Table 4. Continued.

Individual	**Year**	**Gender**	**Age**	**Min δ^{13}C**	**Max δ^{13}C**	**Range δ^{13}C**	**x δ^{13}C**	**Min δ^{15}N**	**Max δ^{15}N**	**Range δ^{15}N**	**x δ^{15}N**
AA1232	2012	F	AD	-14.92	-13.92	1.00	-14.44	17.71	21.25	3.54	19.48
AA1236	2012	F	AD	-14.79	-13.88	0.91	-14.41	17.38	20.52	3.14	19.24
AA1240	2012	F	AD	-15.02	-13.77	1.25	-14.35	18.11	21.09	2.98	19.63
AA1512	2015	F	AD	-15.46	-14.24	1.22	-14.78	17.40	20.40	3.00	19.02
AA1512	2015	UNK	PUP	-15.10	-14.53	0.57	-14.79	18.00	19.44	1.44	18.64
AA1513	2015	F	AD	-14.97	-13.97	1.00	-14.49	17.22	19.75	2.53	18.61
AA1513	2015	UNK	PUP	-14.65	-14.11	0.54	-14.45	17.74	19.28	1.54	18.65
AA1515	2015	F	AD	-15.63	-14.28	1.35	-14.84	16.69	19.88	3.19	18.69
AA1515	2015	UNK	PUP	-15.72	-14.55	1.17	-14.97	18.03	19.27	1.24	18.62
AA1516	2015	F	AD	-15.42	-14.13	1.29	-14.63	16.71	19.74	3.03	18.53
AA1516	2015	UNK	PUP	-15.21	-14.60	0.61	-14.97	18.66	19.33	0.67	18.66
AA1517	2015	F	AD	-18.13	-14.53	3.60	-15.31	16.98	19.81	2.83	18.67
AA1517	2015	UNK	PUP	-15.21	-15.05	0.16	-15.21	17.90	18.87	0.97	18.37
AA1518	2015	F	AD	-15.16	-14.23	0.93	-14.67	17.03	20.51	3.48	18.63
AA1518	2015	UNK	PUP	-15.05	-14.18	0.87	-14.52	17.88	19.26	1.38	18.59
AA1601	2016	M	AD	-14.75	-13.28	1.47	-14.15	16.20	20.62	4.42	18.83
AA1602	2016	M	AD	-14.68	-13.60	1.08	-14.10	16.87	20.13	3.26	18.25
AA1603	2016	M	AD	-14.20	-13.52	0.68	-14.20	16.18	19.72	3.54	17.83
AA1604	2016	M	AD	-15.16	-13.88	1.28	-14.38	16.85	20.68	3.83	19.07
AA1605	2016	M	AD	-14.98	-13.96	1.02	-14.44	16.49	20.45	3.96	18.81
AA1606	2016	M	AD	-14.36	-13.84	0.52	-14.36	16.94	20.60	3.66	18.83

Table 5. Minimum, maximum, range, and mean of δ^{13}C and δ^{15}N (‰) in South American sea lion (*Otaria byronia*) vibrissae, Punta San Juan, Peru, 2011. Gender: Male=M, Age: SA=Subadult

Individual	**Year**	**Gender**	**Age**	**Min δ13C**	**Max δ^{13}C**	**Range δ^{13}C**	**x δ^{13}C**	**Min δ^{15}N**	**Max δ^{15}N**	**Range δ^{15}N**	**x δ15N**
OF11-02	2011	M	SA	-14.35	-12.89	1.46	-13.50	16.66	22.82	6.16	20.15
OF11-03	2011	M	SA	-14.21	-13.07	1.14	-13.46	18.49	22.28	3.79	20.09
OF11-04	2011	M	SA	-13.85	-12.86	0.99	-13.29	18.98	21.70	2.72	20.58
OF11-05	2011	M	SA	-13.76	-12.77	0.99	-13.19	18.20	21.01	2.81	20.23
OF11-07	2011	M	SA	-14.09	-13.22	0.87	-13.64	17.92	21.76	3.84	20.15
OF11-10	2011	M	SA	-14.38	-12.81	1.57	-13.49	15.95	21.30	5.35	19.15