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Evidence of Intermittent Residency in the Northern Fur Seal (Callorhinus ursinus).

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

Evidence of Intermittent Residency in the Northern Fur Seal (*Callorhinus ursinus*).

BY

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Abstract

This study found evidence of intermittent, multi-year residency periods in northern fur seals (*Callorhinus ursinus*) using stable isotope ratios in vibrissae and canine teeth. Northern fur seals migrate from the Bering Sea during summer months to lower latitudes and slightly warmer waters of the northeastern Pacific Ocean and California Current in the winter. To determine the length of time spent away from the Bering Sea, growth rate was estimated using the covarying oscillations $\delta^{13}C$ and $\delta^{15}N$, estimated to be 0.09 mm/day. The $\delta^{13}C$ and $\delta^{15}N$ in vibrissae from 30 male fur seals showed a minimum of 13 separate periods of stable covariance covering 3.25+ cm, indicating at least 1 year in warmer, less productive waters of the northeastern Pacific Ocean. The vibrissae isotope ratios were used in conjunction with $\delta^{18}O$ from tooth dentin growth layer groups of 20 male northern fur seals; they showed significant enrichment in $\delta^{18}O$ in 50% of the animals at age 1-2 years, which indicates extended periods of time spent in lower latitudes in the North Pacific Ocean as $\delta^{18}O$ is typically enriched in warmer, less productive waters. Significant changes in $\delta^{18}O$ were found to be ~ 0.2‰ enrichment per 10º south latitude, while longitude was found to have 0.2‰ enrichment per 50˚ East longitude. These data show that latitudinal changes, those related to the southerly migration from the Bering Sea to the northeastern Pacific Ocean, are a stronger factor in the shifts in dentinal $\delta^{18}O$ than longitudinal shifts. These intermittent periods of occupation are important when estimating population abundance of northern fur seals, especially pups and juveniles.

Keywords: Northern Fur Seal, Stable Isotopes, Migration, $\delta^{18}O$, $\delta^{13}C$, $\delta^{15}N$

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Introduction

Northern fur seals

Northern fur seals are a long-distance, migratory species of otariid found in the North Pacific Ocean and Bering Sea. They show strong sexual dimorphism with the males up to four times larger than the females (Wickens and York 1997; Perrin et al. 2009; Sterling 2009; Call and Ream 2011). Northern fur seals range throughout the northeastern Pacific Ocean from Japan to southern California (Figure 1). Northern fur seals breed only on offshore islands, though historical data suggest that they once bred on the coastlines of California. The shift from the coastlines has been hypothesized to have been related to human hunting (Burton et al. 2001). The Pribilof Islands in the Bering Sea serve as rookeries for more than half of the entire northern fur seal population (Baker et al. 1995; Towell et al. 2006; Baker et al. 2007; Perrin et al. 2009; Testa 2012; Benoit-Bird et al. 2013) and have been used for approximately 10,000 years (Fang 2009; Dickerson 2010). The Pribilof Islands, comprise St. Paul and St. George Islands, support several colonies of pinnipeds, many bird species, and a small human population (Veltre and Douglas 2002). Bogoslof Island is a small, volcanic island in the southern Bering Sea which supports a small, but increasing, population of northern fur seals (Ream and York 2006; Lee 2014). It was identified as a northern fur seal rookery in 1980 (Loughlin and Miller 1989; Ream and York 2006).

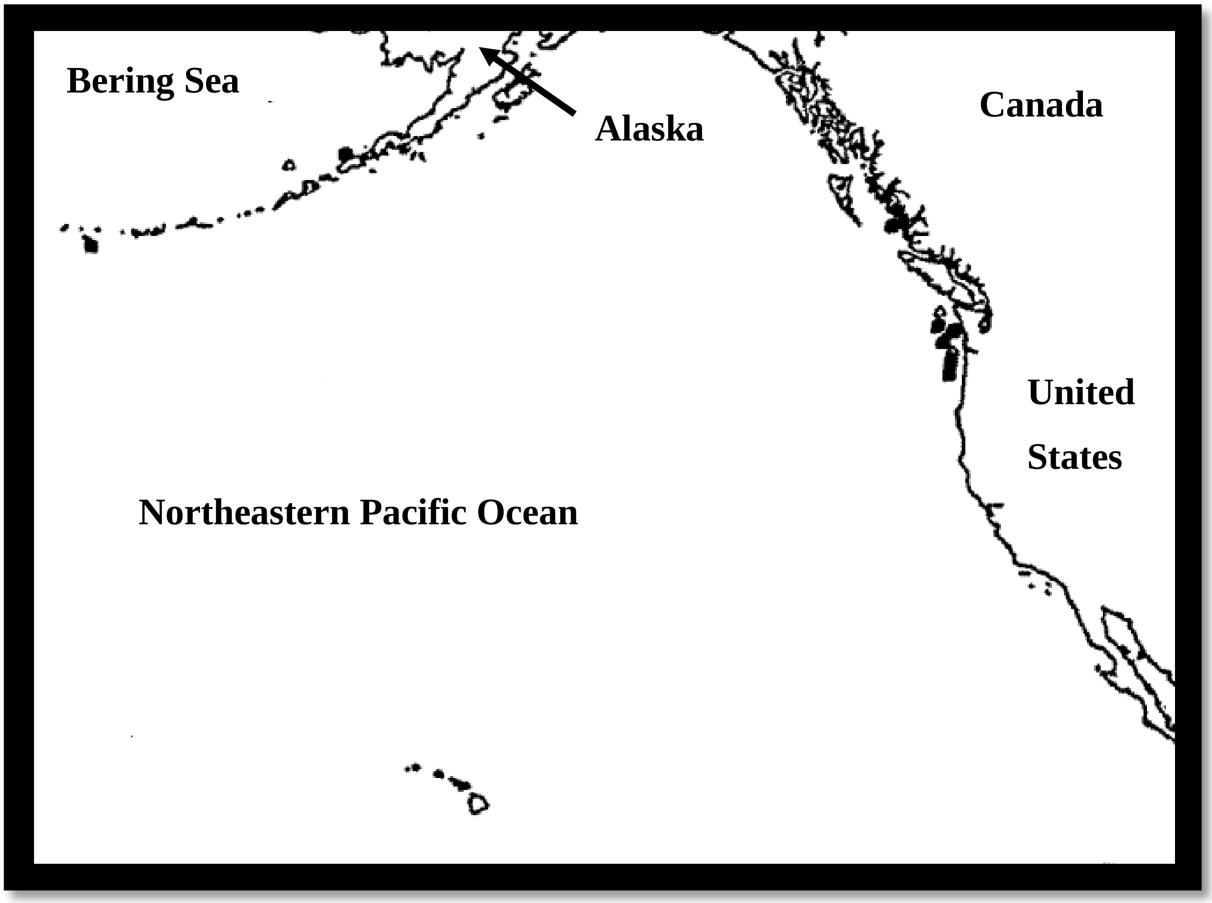

Figure 1. Bering Sea and northeastern Pacific Ocean (Fowler 1987).

Fur seals show strong site fidelity to their rookeries and typically return to the same rookery each year (Baker et al. 1995; Perrin et al. 2009; Sterling 2009). The juvenile seals spend the majority of their first three years of life at sea but are also observed in the waters around the rookeries during the summer months (Baker et al 1970; Trites and Antonelis 1994). Rookery selection appears be related to the female fur seals' ability to access food resources while breeding and nursing, as well as areas that are protected from tides and predation (Gentry 1998).

Prior to the 1950s, the northern fur seal population on the Pribilof Islands was beginning to recover from a serious depletion largely due to hunting pressures. The population on the Pribilof Islands appeared to have stabilized at 35% to 45% of its peak population of 1.3 million animals between the 1980s and 1990s (Testa 2012). In 2010, the northeastern Pacific Ocean population had an estimated 664,000 animals, a decline of roughly 50% since the 1970s. The 2010 National Oceanic and Atmospheric Administration (NOAA) population assessment of northern fur seal pups showed a steady decline in the stock, and the Bering Sea population was classified as depleted by the NOAA Office of Protected Resources in 1988 (Testa 2012). The St. Paul Island population has declined approximately 6% per year since the 1980s (Trites 1992; Ream and York 2006; Sterling 2009; Testa 2012; Lee 2014; Rosen et al. 2014). The St. George Island population appeared to have stabilized at approximately 30% of its peak population in the early 2000's (Testa 2012). The Bogoslof Island population has been increasing at a rate of approximately 12% per year since it was discovered north of the Aleutian Islands in 1980 (Loughlin and Miller 1989; Perrin et al. 2009; Lee 2014).

The decline of northern fur seals on the Pribilof Islands is a serious concern (Fowler 1987; Trites and Larkin 1989; Trites 1992; Spraker and Lander 2010). A number of potential causes have been considered, including nutritional stress, disease, and trauma. Nutritional stress was found to be the most common cause of death among pups on St. Paul Island. Approximately 53% of pups found dead between 1986 and 2006 were emaciated and appeared to have died of starvation. Traumatic injuries (18%) were the second-most common cause of death, while mortality from disease was only found in 3% of dead pups. Among juvenile male seals, the leading cause of death was hyperthermia (Spraker and Lander 2010). Juvenile northern fur seals are known to experience high mortality in their first two years at sea and may have difficulties capturing their prey. This nutritional stress may be a hindrance to their ability to thermoregulate leading to hyperthermia (Rosen et al. 2014). Nutritional stress may be related to changes in the Bering Sea ecosystem. During El Niño events, analogous species of eared seals have suffered nutritional stress, leading to lower pup and juvenile survival (Rosen and Trites 2000; Trites and Donnelly 2003).

Northern fur seals stay at rookeries on the Pribilof and Bogoslof Islands from approximately June to November each year for breeding and pupping (Bartholomew and Hoel 1953; Sterling 2009; Nordstrom et al. 2013a). Female fur seals become sexually mature at three years of age and may live up to 18 years. Female seals produce 1 pup per year after they reach sexual maturity. Male fur seals typically reach sexual maturity at 8-9 years of age, thereby decreasing their breeding life (Gentry 1998; Perrin et al. 2009).

The foraging behavior of northern fur seals varies based on the rookery in which they return each year as the rookeries experience variability in oceanographic conditions depending on their proximity to the continental shelf edge. The Pribilof Islands are located near the shelf break of the Bering Sea continental shelf while Bogoslof Island is located in deeper waters just north of the central Aleutian Islands arc. Foraging behavior is indicative of proximity of the island to the continental shelf break. This proximity is related to whether the seals forage on or just off the shelf where different types of prey are available (Sterling 2009; Nordstrom et al. 2013a). The seals from the Bogoslof Island rookery had shallower dives that were centered around the island. Northern fur seals from St. Paul Island foraged for long periods (1-14 days) (Bartholomew and Hoel 1953; Sterling 2009; Benoit-Bird et al. 2013; Nordstrom et al. 2013a), returning to nurse their pups less frequently than the female seals from Bogoslof Island (Sterling 2009; Benoit-Bird et al. 2013; Nordstrom et al. 2013a). While many species of female pinnipeds fast when they are nursing their pups, northern fur seals do not. Female fur seals need to consume 9 to 20% of their body weight per day while nursing pups (Wickens and York 1997). Northern fur seals are weaned abruptly at approximately four months of age (Baker et al. 1995; Gentry 1998; Rosen et al. 2014).

Foraging patterns in northern fur seals is related but not always dependent on rookery location. Sterling and Ream (2004) satellite tagged 28 male northern fur seals, age three to six years old, and found foraging locations tended to be rookery-specific. Of the animals studied, 43% also traveled to other rookeries on St. Paul Island and 27% of the male fur seals visited St. George Island at some point during the studied period. The diets of juvenile males and adult females were found to be similar while they were on the Pribilof Island rookeries (Sterling 2009).

Female fur seals leave the rookeries from late October to early November (Kenyon and Wilke 1953; Sterling et al. 2014). The female fur seals have a longer migration than the male seals (Kenyon and Wilke 1953) and travel to lower latitudes

(Gentry 1998). From the Pribilof Islands the female seals leave the Bering Sea and travel south and east. Northern fur seal females have been frequently observed off the coastlines of southern Oregon and northern California during their migratory period (Kenyon and Wilke 1953; French and Reed 1989; Burton et al. 2000). Female seals are concentrated on the continental margins (Gentry 1998; Burton et al. 2000). A number of female seals were satellite tagged on St. Paul Island, which showed the animals travelling through Unimak Pass on their way toward the Gulf of Alaska and onward to the California Current (Sterling et al. 2014). Ten female seals from St. Paul Island were tracked from St. Paul Island heading southeast through the Aleutian Island passes. The female fur seals then traveled into the North Pacific Ocean and Gulf of Alaska. Seven traveled to the coastal areas of Washington and California and three traveled into the transition zone between the edges of the California Current and the North Pacific Ocean basin (Ream et al. 2005). The adult male seals show a wider variety of migratory behaviors. Adult male seals have been tracked migrating to higher latitudes than adult female seals (Kenyon and Wilke 1953; Gentry 1998; Burton et al. 2000; Kurle and Worthy 2002; Sterling and Ream 2004; Sterling et al. 2014). Satellite tagging data demonstrate that several fur seals stayed in the Bering Sea for months after most of the animals left the rookeries before heading south into the North Pacific Ocean. Some of the seals went south immediately after leaving the rookery and some traveled between the Bering Sea and North Pacific Ocean (Sterling et al. 2014). The male seals return to the rookeries before the females arrive (Kenyon and Wilke 1953).

After leaving the rookeries in November and December, northern fur seals forage throughout the Bering Sea and North Pacific Ocean and haul out for short periods at various land outcroppings. Data from historical sealing reveal that younger male fur seals tended to be in more southerly latitudes, similar to where the adult females have been found (Lander and Kajimura 1982; Ream et al. 2005). Juvenile fur seals make longer migrations than the adult animals (Dalton et al. 2014). Some juvenile male seals may remain in the North Pacific Ocean without returning to the rookeries for several years (Baker et al. 1970; Gentry 1998; Baker 2007). Juvenile fur seals are often found in proximity to the adult females during the winter migration (Gentry 1998; Burton et al.

2000). Data from historical sealing found that younger male fur seals tended to be in more southerly latitudes, similar to where the adult females have been found (Lander and Kajimura 1982; Ream et al. 2005), and make longer migrations than the adult animals (Dalton et al. 2014).

Northern fur seals feed primarily on demersal, pelagic, and mesopelagic fishes such as walleye pollock (*Theragra chalchogramma*), Pacific herring (*Clupea pallasii*), Pacific cod (*Gadus macrocephalus)*, and myctophids (Myctophidae) as well as gonatid squid (Riedman 1990; Trites 1992; Ream et al. 2005; Perrin et al. 2009; Sterling 2009, Zeppelin and Orr 2010; Kelleher 2016). Seals tend to be nocturnal hunters and their dive patterns are shallower at night. Juvenile pollock, a preferred prey item, are found in shallower waters at night, likely due to diel movement of prey species (Nordstrom et al. 2013a). Adult females and juvenile male fur seals typically prefer juvenile walleye pollock while at the rookeries in the summer months (Call and Ream 2011). Kurle and Worthy (2001) determined that adult fur seals foraged at a higher trophic level than juvenile fur seals. Female northern fur seals forage at different depths and for different periods of time depending on the rookery from which they are based.

Bering Sea and Pribilof Islands

The Bering Sea is a marginal, sub-polar sea separated from the North Pacific Ocean by the volcanic Aleutian Island arc. It is split into a large continental shelf on the eastern side along the Alaska coast and a deep, oceanic basin to the southwest (Okkonen et al, 2001; Sullivan et al. 2008). The shelf is divided into three domains which are characterized by their depths (Springer et al. 1996; Brodeur et al. 1999; Moore et al. 2002; Sullivan et al. 2008). The inner, or coastal, domain is shallow and well-mixed, primarily by tidal forces. The middle domain ranges in depth from 50-100 m and is distinguished by a sharp thermocline with a wind mixed upper layer and current mixed bottom layer. The outer domain extends to the edge of the shelf (100-200 m) and is the deepest of the three domains (Brodeur et al. 1999; Sullivan et al. 2008). The shelf slope is bounded by the Bering Sea Current (BSC) and separates the shelf from the basin. Water from the BSC extending onto the shelf has been linked to the primary productivity of the outer and middle domains. The current generates a strong eddy field, particularly in the warmer months, which is likely to increase the nutrient exchange onto the shelf (Okkonen 2001).

The formation of mesoscale eddies influences primary productivity by increasing upwelling and downwelling along the shelf edge. Cyclonic (counter-clockwise) eddies have been shown to have increased upwelling at their center which brings nutrients to the surface waters and boosts phytoplankton growth. Anticyclonic eddies are also found in the BSC and show increased downwelling at the center of these eddies, and increased upwelling along the edges (Mizubata et al. 2002; Mizubata et al 2004). The eddies are responsible for the increased *Chl a* distribution and high primary productivity in the so-called "Green Belt," the waters bordering the Bering Sea shelf break. Primary production in the Green Belt can be up to 60% higher than in the outer domain and up to 270% greater than in oceanic regions (Springer et al. 1996). Larval pollock and other prey species are found in higher densities near mesoscale eddies (Mizubata et al 2004). The Green Belt is used by many species as a foraging area, including northern fur seals (Springer et al. 1996; Mizubata et al. 2002; Mizubata et al. 2004; Okkonen et al. 2004; Sambrotto et al. 2008).

Primary productivity in the Bering Sea is linked to temperature and sea ice formation. Current water column temperature is partially determined by the previous year's sea ice coverage (Reed 1999). During years when sea ice coverage in the Bering Sea lasted through April (cold years), phytoplankton blooms occurred earlier than years when sea ice was lost during or before March. Cold years often have phytoplankton blooms under the ice while warm years have much later phytoplankton blooms (Stabeno et al. 2002; Stabeno et al 2012). Phytoplankton blooms also are influenced by upwelling events, lower salinity, and increased amounts of sunlight in the photic zone (Okkonen and Neibauer 1995). Phytoplankton blooms lead to increased zooplankton activity (Springer et al. 1996; Hunt et al. 2008). Calanoid copepods, such as *Calanus* sp., are more abundant in years with a later sea ice retreat (Coyle et al. 2008; Stabeno et al. 2012). The Bering Sea has seen an increase in gelatinous zooplankton which began in the early 1990s and has been correlated with an increase in sea surface temperatures (Brodeur et al. 1999, 2008; King 2005).

The high productivity in the Bering Sea supports a wide variety of life which includes several commercially important fishes and crustacean species, such as walleye pollock (the largest commercial fishery in the United States), herring, king crab (*Paralithodes* spp.), and numerous other species (Springer et al. 1996; Bailey et al. 1999; Grebmeier et al 2006; Jin et al. 2009; Haynie and Pfeiffer 2013). Due to the Bering Sea's high productivity, it also supports a wide variety of sea birds and marine mammals, including northern fur seals (Benson and Trites 2002). Several species of cetaceans are found in the Bering Sea and tend to be located in distinct areas on the shelf. Large whales can be used as bioindicators of abundant areas of zooplankton and other prey species. Increases in baleen whales can be indicative of robustness in the ecosystem (Moore et al. 2002, 2003).

The Pribilof Islands (St. Paul and St. George Island) are located between the middle and outer domain of the continental shelf in the Bering Sea (Sullivan et al. 2008; Perrin et al. 2009; Testa 2012). The islands are considered to be the Pribilof domain due to the unique hydrographic features centered on the islands. Tidal and wind-forced mixing causes the waters around the Pribilof Islands to be more mixed than the rest of the middle domain. The flows around the Pribilof Islands are in an anticyclonic direction (Hunt et al. 2008; Sambrotto et al. 2008; Sullivan et al. 2008). Primary productivity in the Pribilof domain is enhanced compared to the middle and outer domains and shows similarities to that found in the Green Belt (Hunt et al. 2008).

Environmental fluctuations

The Bering Sea is subject to a multitude of environmental changes which occur on time scales ranging from seasonal to decadal (Niebauer 1988, Jin et al. 2009). Regime shifts are long term shifts into steady states in an ecosystem, typically occurring every 20 to 30 years, and have been noted in the North Pacific Ocean and Bering Sea since 1925 (King 2005; Jin et al. 2009). The oscillations alter ambient air and sea surface temperatures and upwelling cycles. The environmental changes occurred with little warning and were rapid in their effect on the Bering Sea (Benson et al. 2002; King 2005). The exact causes of the regime shifts are unknown, although it seems to be a response to environmental changes within the various oceans throughout the world (Benson and Trites 2002).

The Pacific Inter-Decadal Oscillation (PDO) is an index for tracking long-term regime shifts in the North Pacific Ocean (King 2005). The PDO is tracked in a similar manner as the El Niño-Southern Oscillations. Anomalous SST are commonly used to track the positive and negative phases of the PDO. During the positive shifts, the northern waters show increased sea surface temperatures while the southern, lower latitude areas show a decrease in sea surface temperature and the reverse occurs during the negative phase (Mantua et al. 1997, King 2005). Regime shifts can shift between a negative and positive phase or shift to a completely new pattern (King 2005). The positive phase that began in 1977 was associated with warm anomalies in the coastal areas and cooling in the Pacific Ocean. Prior to 1977, cooler waters were observed on the northeastern coastal areas of North America with warm anomalies in the Pacific Ocean. (King 2005). Ocean temperatures vary vertically in the water column, and sea surface temperature appears to be a response to surface winds, though there is a one-month lag between the air temperature shift and the sea surface temperature change. The strongest variability occurs during the months of May and June (Mantua et al. 1997; Wang et al. 2012). A number of potential mechanisms for the PDO have been identified, including atmospheric forcing or by the (ENSO tropically, mid-latitude coupling of ocean-atmosphere systems, deep-ocean mixed layer re-emergence, and variability in the Kuroshio Current and the Aleutian lowpressure system (Wang et al. 2012).

The PDO affects temperatures in the Bering Sea which controls when sea ice retreats. Early retreats of sea ice happen in warmer waters when the temperatures are between 3 and 5° C. During the colder phase of the regime shift, phytoplankton grows more rapidly due to mixing of nutrients into the ocean’s photic zone. Phytoplankton are the base of the oceanic food web, supporting higher trophic levels (Mantua et al. 1997; Hunt et al 2008; Jin et al. 2009; Coyle et al. 2011). During the most recent cold shift, from 1947-1976, seasonal productivity was higher than that from 1976 to the1990’s when the Bering Sea entered a warmer phase. In the warm phase, primary productivity declined roughly 30%, with the maximum amount of primary productivity in the Green Belt on the shelf break (Schell 2000). Seasonally, the Bering Sea shows variations in sea surface temperature (SST) and sea ice cover (Niebauer 1988, Jin et al. 2009). Temperatures around the Pribilof Islands range from 1˚ C in April up to 9˚ C in August (Niebauer 1988). Sea ice may cover 1000 km in the winter but will be completely gone by during the summer months (Niebauer 1999). Seasonal variations in temperature and sea ice cover are important to fisheries as they affect the phytoplankton blooms at the base of the food web.

El Niño-Southern Oscillations are observed primarily at tropical latitudes, altering the thermocline and coastal upwelling which affects productivity and local fisheries. ENSO events have also been shown to affect the Bering Sea climate and ecosystem. Warming events in sea surface temperature (SST) have been correlated to ENSO events and decreases in sea ice cover, with a lag of several months up to a year. The El Niño in 1997 was correlated negatively with sea ice cover in the Bering Sea (Neibauer 1988, 1999). Since 1979, seasonal variability increased in the region which affected the abundance of all the species in the area, including fishes like walleye pollock and Pacific cod, squid, marine mammals, and seabirds (Benson and Trites 2002; Trites et al. 2005). Temperature shifts can cause changes in ocean current patterns and have been shown to affect the recruitment of juvenile walleye pollock, one of the primary prey items of northern fur seals (Walther et al. 2002).

Stable isotope ratios

Stable isotopes are naturally occurring forms of an element that have one or two extra neutrons in their nucleus, which increases their atomic mass. Stable isotopes do not decay and are transferred from one organism to another by digestion and assimilation (DeNiro and Epstein 1978, 1981; Peterson and Fry 1987). Stable isotope studies are a valuable tool for studying the life history, diet, and habitat use in marine mammals. Stable isotope ratios can be used to study trophic transfer, dietary changes, salinity, and sea surface temperature (DeNiro and Epstein 1978, 1981; Peterson and Fry 1987; Rozanski et al. 1992; Borrell et al. 2013). Variations in $^{13}C/^{12}C$ show shifts in primary productivity and geography while changes in the ratio of $^{15}N/^{14}N$ reveal trophic level changes in food sources (Fry 1988; Hobson et al. 1997). The use of $\delta^{13}C$ and $\delta^{15}N$ in conjunction are valuable tools for researchers to elucidate the local food web of an ecosystem (DeNiro and Epstein 1978, 1981; Post 2002; Nino-Torres et al. 2006; Mendes et al. 2007). The $^{18}O/^{16}O$ has been used to measure environmental shifts in conjunction with $\delta^{13}C$. The information gathered can be used to track environment fluctuations and the impacts those fluctuations have on the local ecosystem (Hansen et al. 2009). Fractionation of $\delta^{13}C$ from diet to enamel is generally thought to be between 9‰ and 10‰ for carnivores, though fractionation of pinnipeds has not been tested (Clementz and Koch 2001; Clementz et al. 2006; Clementz et al. 2012).

The isotopic ratios are compared to an accepted standard; $\delta^{15}N$ is compared to atmospheric nitrogen and the $\delta^{13}C$ standard is the Pee Dee Belemnite (PDB) limestone formation in South Carolina. The $\delta^{18}O$ is compared to Vienna Standard Mean Ocean Water (V-SMOW) (Peterson and Fry 1987; Koch et al. 1989). The differences in mass can be detected using a mass spectrometer and the ratio of heavy to light isotopes.

Trophic dynamics

Trophic dynamics can be tracked using $\delta^{15}N$ and $\delta^{13}C$ found in fur seal tissues. Enrichment in $\delta^{15}N$ is caused by biomagnification of isotopes ratios through the food web, and there is an increase of 3-5‰ per trophic levels (DeNiro and Epstein 1978, 1981; Peterson and Fry 1987; Cabana and Rasmussen 1996; France and Peters 1997; Hirons 2001; Post 2002; Dehn et al. 2007; Matthews and Ferguson 2014 (a); Beltran et al. 2016; Wright et al. 2016). The $\delta^{13}C$ is enriched by approximately 0.5-1‰ per trophic level and is indicative of the carbon source at the base of the food web. This fractionation can be used to identify sources of the primary production in an area and allows an understanding of spatial habitat use (DeNiro and Epstein 1978, 1981; Schell et al. 1989; Hirons et al. 2001; Post 2002; Dehn et al. 2007; Matthews and Ferguson 2014 (a); France and Owsley 2015; Beltran et al. 2016). Changes in $\delta^{13}C$ are correlated to upwelling events that bring older waters to the surface, that are enriched with $\delta^{13}C$. Younger surface waters are more depleted in $\delta^{13}C$ due to the "Suess effect" (Schell et al. 1989). The Suess effect is an ongoing depletion in atmospheric $\delta^{13}C$, a change from -6.4‰ to ~ -8.0‰ since the industrial revolution in the mid-1800s, which increased the amount of δ^{13}C-depleted CO_2 (Keeling 1979; Bauch et al. 1998). As surface waters absorb CO_2 from the atmosphere, they are more depleted in δ^{13}C than deeper waters that have little to no gas exchange with the atmosphere (Bauch et al. 1998).

Stable isotopes can be used to determine changes in trophic levels and predation strategies of northern fur seals by comparing the stable isotope values in northern fur seal tissue to the isotopic values found in common prey species in the Bering Sea (DeNiro and Epstein 1978, 1981; Post 2002). Prey species found nearshore have different isotopic composition than those in deeper water and these variations will be reflected in the isotopic compositions found in the fur seal tissues (Trites 1992; Sterling 2009). Nearshore waters are generally more productive than offshore waters that result in enriched stable carbon and nitrogen isotope ratios (France and Peters 1997). Nearshore, continental shelf potential prey species are more enriched in δ^{13}C and δ^{15}N than the prey caught in deeper waters, off the shelf (Hirons 2001; Nino-Torres et al. 2006; Dehn et al. 2007). Animals in a given trophic level that feed offshore are more depleted in δ^{13}C and δ^{15}N (France and Peters 1997; Walker 1999; Post 2002). Michener and Kaufman (2007) found benthic organisms in the Bering Sea were more enriched in δ^{13}C than those in pelagic waters. The enriched carbon is then incorporated into the seals' tissues and act as tracers of productivity and water masses in which they traveled and foraged.

Stable isotope ratios of carbon and nitrogen have been used in conjunction with stomach contents in pagophilic phocid seals and the rations have been found to correlate with stomach content analysis (Dehn et al. 2007). Research into the life history of common dolphins (*Delphinus capensis*) found that the stable isotope ratios vary between coastal and offshore feeding areas, as well as by the age of the animal, due to variations in prey types (France and Peters 1997; Nino-Torres et al. 2006; Dehn et al. 2007). Northern fur seals feed both in pelagic waters and on the continental shelf, depending on the time of year, so stable isotope changes in body tissues can be correlated to the months they are on the rookery (Trites 1992; Sterling 2009).

Environmental change

Studies using $\delta^{13}C$ and $\delta^{18}O$ have found that these stable isotope ratios can be indicative of changes in the environment when correlated with each other. Measurements of $\delta^{13}C$ in the bioapatite of marine mammal teeth were found to be negatively correlated to sea surface temperature (Hansen et al. 2009), while $\delta^{18}O$ has been used to indicate changes in ocean salinity, the overall temperature of water, and differences in water masses (Koch et al. 1989; Campana 1999). The $\delta^{18}O$ of ocean water is expected to be at 0‰ (Schaffer and Swart 1991). Precipitation has a higher proportion of ^{18}O to ^{16}O than found in seawater. Precipitation reduces sea surface salinity (SSS) temporarily. Increased SST is also reflected in heavier $\delta^{18}O$ (Koch et al. 1989; Rozanski 1992). Higher latitudes are more depleted in $\delta^{18}O$ than low latitudes due to the increased evaporation at lower latitudes (Schaffer and Swart 1991; Clementz et al. 2012; Borrell et al 2013; Clementz et al. 2014). $\delta^{18}O$ varies linearly with mean annual atmospheric temperature and is negatively correlated to SST. Inshore waters are often more depleted than offshore waters due to more depleted terrestrial water runoff (Clementz and Koch 2001).

Variations in $\delta^{18}O$ in animal tissues are related to the water ingested by drinking and water that is derived from prey animals (Straight et al. 2002; Newsome et al. 2010; Clementz et al. 2014). Mammals and other endotherms are good recorders of $\delta^{18}O$ because body temperature does not affect the $\delta^{18}O$ of body water (Straight et al 2004; Clementz et al. 2006; Clementz et al. 2012). A direct relationship exists between meteoric $\delta^{18}O$ and body water $\delta^{18}O$ (d'Angela and Longinelli 1990). In terrestrial mammals >50% of the $\delta^{18}O$ is from drinking water, 25% from atmospheric water, 15% from water vapor, and 10% is metabolic water. Aquatic mammals get 98% of the oxygen flux from the water in which they live (Kohn 1996; Clementz and Koch 2001; Clementz et al. 2006). Teeth and bone are commonly as target tissues in $\delta^{18}O$ research as these tissue preserve $\delta^{18}O$ for long periods of time. Permanent teeth are recommended for study to avoid enrichment related to nursing (Clementz et al. 2006). Studies utilizing $\delta^{18}O$ can be employed to differentiate between habitats, freshwater versus marine for example, or time-series of temperature. Marine animals typically are enriched in $\delta^{18}O$ compared to freshwater or terrestrial mammals (Clementz et al. 2006; Clementz and Koch 2001). For example, research on right whales (*Eubalaena australis*) found that variation in $\delta^{18}O$ within the population was linked to separate feeding grounds (Vighi et al. 2014).

Typically, there is low variability in $\delta^{18}O$ within a species, but high variability between taxa. High variability in $\delta^{18}O$ is typically found in species that travel from high to low latitudes. Animals that feed offshore are more depleted in $\delta^{18}O$ than nearshore feeders (Clementz et al. 2012). Pinnipeds tend to be 2‰ more depleted than cetaceans (Clemetz and Koch 2001). Fractionation in $\delta^{18}O$ through trophic levels has not been observed (Straight et al. 2004.)

Tissues

Vibrissae

This study used two types of tissues: vibrissae and canine teeth. Vibrissae are made of keratin, like fur or hair, but are much longer and stiffer. Vibrissae most commonly occur on the head (Murphy 2013). While vibrissae are found in many mammalian species, the largest are found on pinnipeds (Ling 1977, Ginter et al. 2012; Murphy 2013). Vibrissae are arranged in horizontal rows on both sides of pinnipeds' muzzle (Dehnhart 1994). Vibrissae in pinnipeds are either undulated or smooth. Undulated vibrissae are found in most species of phocids, while otariids have smooth vibrissae that are thicker at the base and taper to appoint to the tip (Hirons et al. 2001; Ginter et al. 2012; Murphy et al. 2013). In cross section, vibrissae are slightly flattened (Ginter 2012; Murphy et al. 2013). Vibrissae are tactile, sensory organs and as such are heavily innervated at the base and used in foraging and obstacle avoidance (Dehnhart 1994; Dehnhart et al. 1998; Schusterman et al. 2000; Murphy et al. 2013; Murphy 2013). Though phocids and otariids have not been observed to be able to move individual vibrissae, they are able to move the mystacial vibrissal array on the sides of their muzzle. When foraging, the vibrissae are swept forward and the seal uses a lateral movement of the head to locate prey and explore objects in close proximity to their bodies (Murphy 2013). California sea lions have been shown to use their vibrissae to determine differences in various sized discs with extreme accuracy (Dehnhart 1994). The vibrissae in otariids grow throughout the animal's lifetime unless damaged, while phocids tend toshed vibrissae with more frequency (Hirons et al. 2001; Ginter et al. 2012; Rea et al. 2015; Kelleher 2016, McHuron et al. 2016). The vibrissae follicle on pinnipeds has a subdermal capsule that can reach 2 cm under the surface of the skin and has up to 10× the number of nerves as terrestrial mammals (Schusterman et al. 2000; Murphy 2013). Vibrissae in younger animals have been shown to have an increased growth rate (Rea et al. 2015; Kelleher 2016). Northern fur seal vibrissae are smooth, sensory whiskers found on the snout. This study used mystacial vibrissae pulled whole from the seals' rostra.

Kelleher (2016) estimated the growth rate in northern fur seals using oscillations in $\delta^{13}C$. Young of year pups had a growth rate of 0.12 mm/day while juvenile (1-4 years of age) males had a growth rate of approximately 0.09 mm/day. This is similar to research done on Steller sea lion (*Eumetopias jubatus*) vibrissae, which found wild adults had vibrissae growth rates of 0.10 – 0.17 mm/day (Hirons et al. 2001). Biochemical examinations of vibrissae have shown oscillations in $\delta^{13}C$ and $\delta^{15}N$ that are linked to changes in foraging behavior and seasonal movements (Hirons et al 2001; Dalerum and Angerbjörn 2005; Rea et al. 2015; Kelleher 2016).

Vibrissae are metabolically inert and preserve stable isotopic ratios and, thus, reveal long-term information on the animal's diet (Hirons et al. 2001; Kernaléguen 2012; Rea et al. 2015; Kelleher 2016). Many pinniped species have seasonal variations in their diets (Hirons et al 2001; Dalerum and Angerbjörn 2005; Rea et al. 2015; Kelleher 2016). The trophic data found in vibrissae reveal information on a scale of days to months. The fine time scale in vibrissae allows for the incorporation of dietary changes during the year due to the seals' migration to the rookeries (Hirons et al. 2001; Kelleher 2016).

Teeth

Teeth of many marine mammals have been used for aging and stable isotope research. Growth layer groups (GLG) are repeating patterns of dentin and cementum found in teeth of marine mammals that correspond with the growth of the animal (Lockyer et al. 2010). Dentin and cementum are primarily composed of hydroxyapatite though cementum has higher proportions of carbon and is a lighter color compared to the dentin (Lockyer et al. 2010). Hydroxyapatite ($Ca_5(PO_4)_3(OH)$) is found in the bones and teeth of mammals and is analyzed for $\delta^{18}O$ and $\delta^{13}C$. Bioapatite typically has some structural carbonate replacing the -OH or phosphate groups (Clementz et al. 2014; Matthews and Ferguson 2014 (a); France and Owlsey 2015). Northern fur seal dentin was analyzed and found to have ≤ 5% carbonate (Staudigel, P. RSMAS pers. comm.). Fractionation of $\delta^{18}O$ between body water and carbonate has been estimated at 26.3 to27.0‰ (V-SMOW) in mammals though fractionation is species and climate dependent (Clementz and Koch 2001; France and Owlsey 2014). Precise fractionation of hydroxyapatite in northern fur seals or any other pinniped has not been calculated (Clementz and Koch 2001). Dentin, unlike skeletal bone, does not alter over time, preserving the isotopic record (Newsome et al. 2006; Matthews and Ferguson 2014 (a)).

Dental tissue does not turn over the way metabolically active tissues are, thus preserving the isotopic signatures. Dental tissue is laid down throughout the animal's lifetime, which keeps the stable isotopes in chronological order (Dalerum and Angerbjörn 2005). Studying the variations in the stable isotope ratios of oxygen in dental tissues allows a better understanding of seasonal movements, shifts in diet, temperature, and precipitation. Colder temperatures were correlated with depleted $\delta^{18}O$ found in dental tissue (Koch et al. 1989) and increased sea surface temperature was reflected in enriched $\delta^{18}O$ (Rozanski et al. 1992).

Dentin is formed by odontoblasts in the pulp cavity and grows out toward the outer edge of the tooth (Laws 1961; Klevezal et al 2006). Early layers are found toward the outer edge of the tooth and later annuli are closer to the pulp cavity (Laws 1961). Dentinal layers cease forming when the pulp cavity is filled or when death occurs (Laws 1961; Klevezal and Stewart 1994; Klevezal et al. 2006). As pinnipeds form primary teeth in the womb, fetal (pre-natal) dentin can be observed in longitudinal sections of teeth. Neonatal lines (NNL) are found in enamel and dentin (Schour 1936). The NNL has been observed in the dentin of many pinnipeds, which is caused by a discontinuity in the growth layers during birth (Laws 1961). When aging a pinniped using dentin, counting begins at the neonatal line and continues inward toward the pulp cavity (Stewart et al. 1996). Dentin is more useful in aging younger animals, however, as the growth layer groups tend to be indistinct once the pulp cavity is filled (Laws 1961). As dentin is laid down annually, it is a useful tissue to age (Matthews and Ferguson 2014 (a)). The dentin in canine teeth is primarily laid down after birth (Chiasson 1957). The pre-birth dentin has a lighter coloration than the post-birth dentin. The dental growth rates are faster in the spring, and slow in the summer and fall (Scheffer 1980).

Northern fur seals also have deciduous teeth that erupt while in the womb, beginning in the upper jaw. These teeth are shed before birth and the permanent teeth are in place before the pups are born. The permanent teeth grow rapidly once they have erupted (Kubota and Komura 1961). Enamel is present within 1 month after birth. Variations in canine size are related to gender and age of the animal. Canine teeth from male fur seals are larger than those from the female northern fur seals due to the high degree of sexual dimorphism this species exhibits (Newsome et al. 2006).

The use of GLG in teeth for the aging of marine mammals has a long history and commonly involves counting the GLGs within teeth. The accuracy of this method varies depending on the species in question. Hawaiian monk seals (*Neomonachus schauinslandi*) tend to have breaks in GLG as a result of fasting. Cementum was found to be useful for up to 11 years in Hawaiian monk seal females and up to 20 years in the males (Kenyon and Fiscus 1963). Mediterranean monk seal studies also used cementum counts as a reliable way to age the animals (Murphy et al. 2012). South American fur seals (*Arctocephalus australis*) canines are similar to northern fur seal canines. Occlusions form in the pulp cavity and the external rings on the root of the tooth are related to GLGs that are formed from dentin and cementum. Stained tooth sections with decalcification were shown to be the most effective method for use with South American fur seals (Molina-Schiller and Pinedo 2004). The upper canines in Cape fur seals (*Arctocephalus pusillus*) were preferred for GLG counts. Dentin was more effective than cementum for aging these animals (Oosthuizen 1997).

Materials and Methods

Permits

The marine mammal tissues were processed under NOAA permit number 764-1703-01. The vibrissae and canine teeth were collected in the Pribilof Islands with the cooperation and assistance the of the Aleut community during subsistence hunts from 1993 to 2013. A Memorandum of Agreement (MOA) exists between the Aleut community of St. Paul and Drs. Trites and Hirons for the collection of these tissues. The vibrissae were pulled whole from the mystacial region (snout) and the upper canine teeth were removed whole from the maxilla.

Laboratory analyses

Vibrissae

Vibrissae (whiskers) were scrubbed with a new, coarse, plastic sponge and deionized water to remove surface contaminants, and dried at 60° C for at least 24 hours. Each vibrissa was cut into 0.25 cm sections from base to tip and weighed. Every other vibrissa section, including base and tip, was placed in individual tin capsules. All samples analyzed at the Smithsonian Institution's Museum Support Center in Suitland, Maryland for δ^{13}C and δ^{15}N. The differences in mass were detected using a Europa 20/20 continuous-flow isotope-ratio mass spectrometer. Results are reported in the standard δ^{13}C and δ^{15}N notation:

$$\delta\ (‰) = [(R_{sample} * R_{standard})-1] * 1000.$$

The δ^{13}C were reported relative to a Vienna Pee Dee Belemnite (VPDB) standard and δ^{15}N was reported relative to atmospheric nitrogen (air).

Approximate vibrissae growth rate was calculated based on maximum and minima in the δ^{13}C and δ^{15}N. The distance between each oscillating, covarying peak (maxima) was calculated and the average determined. The average growth rate was calculated to be 0.09 mm/day. the death date of each seal was known, it was readily determined that the maximum, or most enriched isotope, values for δ^{13}C and δ^{15}N, occurred during the summer months when the fur seals were most likely to be in the highly productive Bering Sea.

Prey muscle isotopic data were acquired from Dunton et al. 1989, Sydeman et al. 1997, Hirons 2001, Kurle and Worthy 2001, Miller et al. 2010, Carlisle et al. 2012, Choy et al 2015, Naman et al. 2016, Witteveen et al. 2016, and Wright et al. 2016. All prey samples were collected from animals in the Bering Sea and northeastern Pacific Ocean.

Muscle was corrected for fractionation to keratin by subtracting 1.56 ‰ from $\delta^{13}C$ and adding 0.63 ‰ to $\delta^{15}N$ in keratin (Hirons 2001). Stable isotope data from prey were sorted into northern (Bering Sea), southern (northeastern Pacific Ocean), and intermediate (Aleutian Islands, Gulf of Alaska, Kodiak Island) regions based upon the locations where the prey were caught. Stable isotope values for potential prey items were compared to corrected vibrissae isotope values in an effort to determine what regions the seals were foraging throughout the year.

Teeth

Each canine tooth was washed with deionized water and scrubbed with steel wool to remove surface contaminants and then placed in a 50:50 solution of bleach/deionized water for 1 hour. The teeth were rinsed in deionized water and dried at 60° C for one to two hours. The outer ridges on the tooth root were rubbed with powdered graphite to enhance visibility of external growth layers and counted. The counts of internal and external GLG's were compared to the known age of each individual animal, which was determined by an independent researcher and found to be within ±1 year (B. Volpov, University of British Columbia). The teeth were then sectioned longitudinally using an Isomet saw with diamond embedded blades. An approximately 2 mm thick section was removed from the center of each tooth and mounted on a glass slide with clear epoxy. Growth layer groups (GLG) were examined using a dissecting microscope with diffuse light and the GLGs counted a minimum of three times by at least two people to ensure accuracy (Figure 2).

Each growth layer was ground using a micromill at a depth of 300 µm and 50 % speed (10,000 rpm). At least 0.6 mg of powdered dentin was required for analysis. The powdered dentin was transferred to labeled Eppendorf vials and $\delta^{13}C$ and $\delta^{18}O$ were measured using a Kiel III interfaced with a Thermo-Finnigan Delta Plus Mass Spectrometer. These analyses were performed at the Stable Isotope Laboratory at the Rosenstiel School of Marine and Atmospheric Science, University of Miami. All data were corrected for the usual isobaric inferences at mass 45 and 46 and were reported relative to Vienna Pee Dee Belemnite (VPDB). The precision of the $\delta^{13}C$ and $\delta^{18}O$ values was less than 0.1 ‰ determined by repeated measurement of a standard.

In order to determine the fractionation of $\delta^{13}C$ between keratin and dentin, a comparison of both a canine tooth and vibrissa was conducted for 10 fur seals and the difference between $\delta^{13}C$ from each animal's keratin and dentin was calculated. Care was taken to only compare keratin and dentin from the same animal. Yearly means of $\delta^{13}C$ from keratin in vibrissae were compared to $\delta^{18}O$ from the same year. Ten canine teeth with three plus sequential GLGs were compared to vibrissa from the same animal in an attempt to find correlation between the annual $\delta^{13}C$ in GLGs and monthly $\delta^{13}C$ in vibrissae over time. Linear regression was calculated for GLGs of canine teeth $\delta^{13}C$ from years 1-3 and for $\delta^{13}C$ of vibrissae from base to tip.

Environmental data on sea surface temperature (SST) and chlorophyll (*Chl a*) were taken from the National Oceanographic and Atmospheric Administration's (NOAA) Bering Sea Climate and Ecosystem website (http://www.beringclimate.noaa.gov/). Sea surface temperature is correlated with $\delta^{18}O$, while chlorophyll is being used as a proxy for primary productivity. Data were collected from National Aeronautics and Space Administration, Goddard Institute for Space Studies http://www.giss.nasa.gov/tools/panoply/ and from the National Oceanographic and Atmospheric Administration, the National Centers for Environmental Information Extended Reconstructed Sea Surface Temperature (https://www.ncdc.noaa.gov/data-access/marineocean-data/extended-reconstructed-sea-surface-temperature-ersst-v3b). The SST data were gathered from the AVHRR Pathfinder satellite and compared with SST calculated from the canine $\delta^{18}O$ using the equation $SST = 16.9 - 4.3 * \delta^{18}O$ (Epstein et al. 1953). The $\delta^{18}O$ data of ocean water were collected from https://data.giss.nasa.gov/o18data/ (Ostlund et al. 1987; Grebmeier et al. 1990; Cooper et al. 1997; Ostlund and Grall 1993; Munchow et al. 1999). Outlying $\delta^{18}O$ data points of ocean water were determined based on abnormal values for salinity and were removed. Abnormally high or low salinity in surface water can indicate unusual localized precipitation, ice melt or increased river run off which would also alter surface $\delta^{18}O$ temporarily. A linear regression was run to determine the rate of change in $\delta^{18}O$ by 10° latitude. Chlorophyll data were acquired from the SeaWIFS satellite from 1997 to 2010. Chlorophyll (Chl *a*) data for eight locations in the Bering Sea and northeastern Pacific

Ocean were used as a proxy of primary production in waters off the northern Bering Sea rookeries and the southern Pacific Ocean wintering grounds.

Statistical analyses were conducted using Microsoft Excel (2013) and Primer-E 7 (Clark and Gorley 2015) software. Covariance and correlation was calculated between $\delta^{13}C$ and $\delta^{15}N$ in each vibrissa using the statistical software package R. One-way Analysis of Variance (ANOVA) was used to assess if any differences between age classes existed in $\delta^{13}C$ and $\delta^{15}N$ in vibrissae. Multivariate analysis of minimum and maximum values was conducted to test for significance between age classes. Prey data were analyzed for multivariate differences in $\delta^{13}C$ and $\delta^{15}N$ between the northern, southern and intermediate areas. One-way ANOVA tested for significant differences in canine teeth $\delta^{13}C$ and $\delta^{18}O$ between years and between individual GLGs and ages. Multivariate analysis of $\delta^{13}C$ and $\delta^{18}O$ in canine teeth was conducted to test for variations between each year and between individual GLGs. The significance level was established at $\alpha = 0.05$.

Results

Vibrissae

Vibrissae were collected from 30 northern fur seals selected based on year of death, island and length. All vibrissae were obtained from the St. Paul Island subsistence harvest between 1993 and 2013. All but one of the vibrissae were either male or of unknown gender. If age class of the seal was not known, it was based on estimated age via calculated growth rate of the vibrissa. Growth rate was calculated based upon the regular oscillations indicative of a migration and found to be 0.09 mm/day based on repeated oscillating patterns found in both the $\delta^{13}C$ and $\delta^{15}N$ of vibrissae as well as known growth rates from similar species and recently published research on juvenile male northern fur seals (Hirons 2001; Rea et al. 2015; Kelleher 2016). Of the 30 vibrissae, 56% were juvenile or presumed juvenile, 23% were subadults (or presumed as such), and 20% were adults.

Vibrissae showed three common patterns. The first pattern primarily showed covarying, oscillating peaks, likely reflecting a migratory pattern often interspersed with areas that have no change in $\delta^{13}C$ and $\delta^{15}N$ (Figure 3). The second pattern showed the aforementioned migratory pattern or had a stable pattern at the base of the vibrissa followed by a U-shaped pattern that covered a one to two-year time period toward the tip. The third pattern showed negative covariance, at the tip of the vibrissa, indicating at least 6‰ depletion in $\delta^{15}N$ and enrichment of at least 1‰. The $\delta^{15}N$ was enriched at the tip, or oldest growth, of the whisker and declined sharply toward the base; conversely, carbon was depleted at the tip and more enriched toward the base of the whisker (Figure 4). This negatively, covarying pattern was found in multiple vibrissae in varying years. The largest inverse relationships were found in three animals harvested in 1992 and 1993. A smaller, negative covarying pattern was found in four other northern seals harvested in 1990 and 1991.

A one-way ANOVA was run to determine variation between age classes. Mean $\delta^{15}N$ indicated no significant differences between age classes. Mean $\delta^{13}C$ showed significant variability between adults, subadults and juveniles (df = 29, F = 15.6, p value = 3.13E- 05). Multivariate analysis was conducted because $\delta^{13}C$ and $\delta^{15}N$ often covary together and this covariance may be indicative of changes in foraging location rather than dietary changes. Minima and maximum $\delta^{13}C$ and $\delta^{15}N$ in vibrissae showed significant variability between age classes based on multivariate analysis of similarity (ANOSIM). Adults' $\delta^{13}C$ and $\delta^{15}N$ varied significantly from juveniles (r: 0.301 and $p < 0.015$), subadults' $\delta^{13}C$ and $\delta^{15}N$ differed from juveniles (r: 0.283 and $p < 0.007\%$). Adults' $\delta^{13}C$ and $\delta^{15}N$ significantly differed from subadults with (r: 0.227 and $p < .0001\%$). Strong correlations between $\delta^{13}C$ and $\delta^{15}N$ appeared in 57% vibrissae. Covariance between $\delta^{13}C$ and $\delta^{15}N$ was shown in 53% vibrissae. The $\delta^{13}C$ ranged from -19.62 ‰ to -14.45 ‰ with a mean of -17.1 ‰. The $\delta^{15}N$ ranged from 10.69‰ to 19.72‰ with a mean of 14.8 ‰ (Table 1). Linear trendlines in 53% of vibrissae showed no change in $\delta^{13}C$ and 56% of $\delta^{15}N$ trendlines showed no significant change $\delta^{15}N$. Linear trendlines in 39% of vibrissae had no significant changes in $\delta^{13}C$ and $\delta^{15}N$ together. The trendlines show that that there is often very little overall change in $\delta^{13}C$ and $\delta^{15}N$, often in conjunction over a number of years.

Table 1. Minimum, maximum, range and mean of $\delta^{13}C$ and $\delta^{15}N$ (‰) in northern fur seal (*Callorhinus ursinus*) vibrissae, St. Paul Island, Alaska, 1993-2013.

Individual	**$\delta^{13}C$ Min**	**$\delta^{13}C$ Max**	**$\delta^{13}C$ Range**	**$\delta^{13}C$ $\bar{x}$**	**$\delta^{15}N$ Min**	**$\delta^{15}N$ Max**	**$\delta^{15}N$ Range**	**$\delta^{15}N$ $\bar{x}$**
NFSA-001	-17.70	-16.14	1.56	-16.90	13.49	16.28	2.79	14.90
NFSA 057	-17.55	-15.77	1.78	-16.90	13.11	16.69	3.58	15.10
NFSA 175	-18.65	-16.75	1.90	-17.50	10.69	17.36	6.67	13.60
NFSA 206	-18.61	-16.49	2.12	-17.40	10.94	17.61	6.67	13.60
NFSB 001	-18.10	-16.78	1.32	-17.40	11.14	15.08	3.94	13.30
NFSB 054	-19.40	-16.61	2.79	-17.60	11.55	18.60	7.05	14.30
NFSB 091	-18.06	-14.45	3.61	-16.60	11.82	17.89	6.07	15.10
NFSB 115	-19.62	-16.20	3.42	-17.70	10.93	18.96	8.03	14.40
NFSB 142	-18.16	-16.08	2.08	-17.20	12.84	18.06	5.22	15.50
NFSB 207	-18.07	-16.57	1.50	-17.20	11.44	15.25	3.81	13.10
SP-13-94-CU	-18.02	-16.86	1.16	-17.40	11.07	15.95	4.88	13.70
SP-95-11-CU	-18.26	-15.98	2.29	-17.00	12.44	18.97	6.53	16.10
SP-11-97-CU	-18.09	-16.30	1.79	-17.00	12.92	17.15	4.23	14.80
SP-06-97-CU	-18.13	-15.58	2.55	-17.00	12.77	17.50	4.73	15.80
SP-17-98-CU	-18.30	-16.16	2.14	-17.00	12.46	20.21	7.75	16.20
SP-09-98-CU	-18.76	-16.25	2.51	-17.20	10.88	19.71	8.83	15.10
SP-05-99-CU	-18.27	-16.30	1.97	-17.30	10.99	19.72	8.73	15.20

04-CU-A10	-17.24	-15.65	1.58	-16.50	15.14	17.00	1.86	16.20
CU-Z4-13	-18.33	-16.11	2.22	-17.10	11.66	18.22	6.55	15.00
CU-Z8-13	-18.99	-17.33	1.66	-17.97	12.68	18.87	6.19	15.84
CU-Z2-13	-18.41	-16.76	1.65	-17.69	13.82	18.34	4.52	15.46
CU-Z1-13	-18.87	-17.86	1.01	-18.38	12.21	17.47	5.25	14.95
CU-L2-13	-18.35	-16.18	2.17	-17.45	13.34	18.13	4.79	16.08
CU-L13-13	-18.76	-16.97	1.79	-17.77	11.35	18.18	6.83	14.50
CU-R2-13	-18.93	-17.23	1.71	-17.84	11.92	17.39	5.47	14.87
CU-R3-13	-19.18	-16.71	2.47	-17.77	12.28	19.35	7.06	15.35
CU-R5-13	-18.40	-16.69	1.71	-17.63	12.71	17.21	4.50	15.03
CU-R9-13	-18.45	-16.41	2.04	-17.41	13.83	18.66	4.82	15.89
CU-R10-13	-18.85	-16.86	1.99	-17.90	11.90	17.20	5.30	14.83
CU-R11-13	-18.69	-16.85	1.84	-17.94	10.21	18.80	8.59	13.80

Prey

Prey data were collected from Dunton et al. (1989), Sydeman et al. (1997), Hirons (2001), Kurle and Worthy (2001), Miller et al. (2010), Carlisle et al. (2012), Choy et al. (2015), Naman et al. (2016), Witteveen et al. (2016), and Wright et al. (2016). Prey data were only taken from regions along northern fur seal migratory routes from the Bering Sea to the northeastern Pacific Ocean. The $\delta^{13}C$ and $\delta^{15}N$ from the potential prey were plotted against $\delta^{13}C$ and $\delta^{15}N$ collected from fur seal vibrissae. A one-way ANOVA showed significant differences in $\delta^{13}C$ between regions (df= 84, F= 10.7, p-value = 7.22-05). A one-way ANOVA of $\delta^{15}N$ of prey showed no significant differences between regions (p-value = 0.39). ANOSIM showed no significant differences between the intermediate zone (Aleutian Islands, Alaskan Peninsula, British Columbia, and Kodiak Island) and the northern regions ($p < .15$), significant differences between the northern (Bering Sea domains) and southern areas (the California Current, from Washington to the Gulf of California, and the northeastern Pacific Ocean) (r: 0.191, $p < 0.1$), and significant differences between the southern and intermediate areas (r: 0.056, $p < 0.046$). Prey data were plotted for the northern and southern parts of the migratory range alongside maximum and minimum $\delta^{13}C$ and $\delta^{15}N$ found in the vibrissae.

Chlorophyll data from eight locations in the Bering Sea and North Pacific Ocean (1997-2010) (Table 2) was used as a proxy for phytoplankton biomass. Of the eight locations, the annual mean of the Bering Sea was more productive than the northeastern Pacific Ocean with the exception of San Miguel Island, CA, which had a mean Chl*a* equivalent to St. Paul Island and the inner Domain. St. Paul Island had a mean Chl*a* of 1.81 mg m^{-3} day$^{-1\,(}$0.34 mg m^{-3} day^{-1} - 10.5 mg m^{-3} day^{-1}). St. George Island was less productive than St. Paul Island and mean of 1.43 mg m^{-3} day^{-1} (0.2 - 21.0 mg m^{-3} day^{-1}). Of the inner, middle and outer domains of the Bering Sea, the middle domain had the highest productivity (mean of 2.09 mg m^{-3} day^{-1}; range 0.30 - 21.4 mg m^{-3} day^{-1}) followed by the inner domain (mean 1.70 mg m^{-3} day^{-1}; range 0.52 - 5.80 mg m^{-3} day^{-1}). The outer domain had the lowest productivity of the three domains with a mean of 1.23 mg m^{-3} day^{-1} (0.26 mg m^{-3} day^{-1} - 12.0 mg m^{-3} day^{-1}. San Miguel Island, CA had the highest productivity of the areas analyzed in the northeastern Pacific Ocean, with a mean of 1.80 mg m^{-3} day^{-1} and range from 0.30 mg m^{-3} day^{-1} - 6.30 mg m^{-3} day^{-1}. The northeastern Pacific Ocean basin had a mean of 0.39 mg m^{-3} day^{-1} and range of 0.20 - 1.10 mg m^{-3} day^{-1}.while the Oregon Coast had a mean of 0.37 mg m^{-3} day^{-1} and range of 0.10 - 1.40 mg m^{-3} day^{-1}.

Table 2. Minimum and maximum chlorophyll (Chlα) in mg m^{-3} day^{-1} at locations in the Bering Sea (BS) and northeastern Pacific Ocean, 1997-2010. St. Paul Island (57.5^{0}N, 170.5^{0}E), St. George Island (56.5^{0}N, 169.5^{0}E), Inner Domain (BS) (59.5^{0}N, 168.5^{0}E), Middle Domain (BS) (57.5^{0}N, 168.5^{0}E), Outer Domain (BS) (57.5^{0}N, 172.5^{0}E), Oregon coast (43.5^{0}N, 127.5^{0}N), northeastern Pacific Ocean basin (48.5^{0}N, 158.5^{0}E), San Miguel Island, CA (34.5^{0}N, 120.5^{0}E). SeaWiFS Project. 2003. SeaWiFS Global Monthly Mapped 9 km Chlorophyll a. Ver. 1. PO.DAAC, CA, USA. n represent number of data points.

Location	St. Paul Island	St. George Island	Inner Domain	Middle Domain	Outer Domain	Oregon Coast	Northeastern Pacific Ocean Basin	San Miguel Island, CA
n	95	101	70	95	103	147	119	150
Max	10.5	21.0	5.80	21.4	12.0	1.40	1.10	6.30
Min	0.34	0.2	0.52	0.30	0.26	0.10	0.20	0.30
Range	10.2	20.8	4.28	21.1	11.7	1.3	0.96	6.0
$\bar{x}$	1.81	1.43	1.70	2.09	1.23	0.37	0.39	1.80
SD	2.01	2.32	0.98	3.0	1.85	0.18	0.17	1.10

Teeth

Thirty-one canine teeth were selected based on rookery and visibility of growth layer groups. All the teeth were from male fur seals on St. Paul Island, AK. Teeth ranged from three to five years of age with 55% of teeth from 4 year old, 42% from three year olds and 3% from five year old seals. The GLGs covered the years from 1992 to 2013. All teeth were aged externally and internally by a minimum of two people, three times each. If teeth were from known-age animals, the internal and external counts were compared to the known age. Age of the teeth was used to identify the years to which each growth layer group corresponded. Two fur seals had teeth extracted in 1995, four fur seals had teeth extracted in 1996, three fur seals had teeth extracted in 1997, and two fur seals had teeth extracted in 2005, 2007, 2008, and 2009. Forty-five percent of canine teeth were from animals harvested in 2013, with GLGs ranging from 2010 to 2013.

Eighty-eight growth layer groups were analyzed for $\delta^{13}C$ and $\delta^{18}O$ at the Rosenstiel School of Marine and Atmospheric Science at the University of Miami (Figure 2.) One GLG was removed from the data due to the inaccuracy of the cut, and two data points were removed after an interquartile range test indicated they were outliers. The $\delta^{13}C$ in the GLGs ranged from –15.42 to -10.99 ‰, with a mean of -13.86 ‰. The $\delta^{18}O$ ranged from 26.84 to 33.54 ‰, with a mean of 28.4 ±1.28 ‰ (range = 6.9 ‰ (n = 86) (Table 2). Twenty of the 30 teeth had three or more sequential GLGs analyzed. The $\delta^{13}C$ and $\delta^{18}O$ did not correlate to each other significantly. The change (Δ) between each GLG and between Year 1 to the last GLG milled on the micromill.was calculated. One-way ANOVA showed no significant differences in Δ between GLGs and between Δ year 0-1 and the year of death in the canine teeth ($p < 0.29$). One-way ANOVA of $\delta^{13}C$ showed no significant variation between years and between individual GLGs ($p < 0.24$), Analysis of $\delta^{18}O$ showed no significant differences between individual GLGs ($p < 0.56$). ANOSIM analysis of $\delta^{13}C$ and $\delta^{18}O$ by age showed no significant differences ($p < 0.54$). A multivariate analysis of $\delta^{13}C$ and $\delta^{18}O$ in conjunction showed no significant variability between each year analyzed ($p < 0.067$). Linear regression of the annual mean $\delta^{13}C$ showed a significant depletion in $\delta^{13}C$ from 1993 to 2013 ($R^2 = 0.43$, $y = -0.573x$

+101.07), while linear regression of $\delta^{18}O$ annual means showed a significant enrichment in $\delta^{18}O$ (R^2.=0.37, y =0.0776x – 158.03). Ten seals showed enrichment of $\delta^{18}O$ during the second year of their life, while the other ten seals showed depletion in their second year.

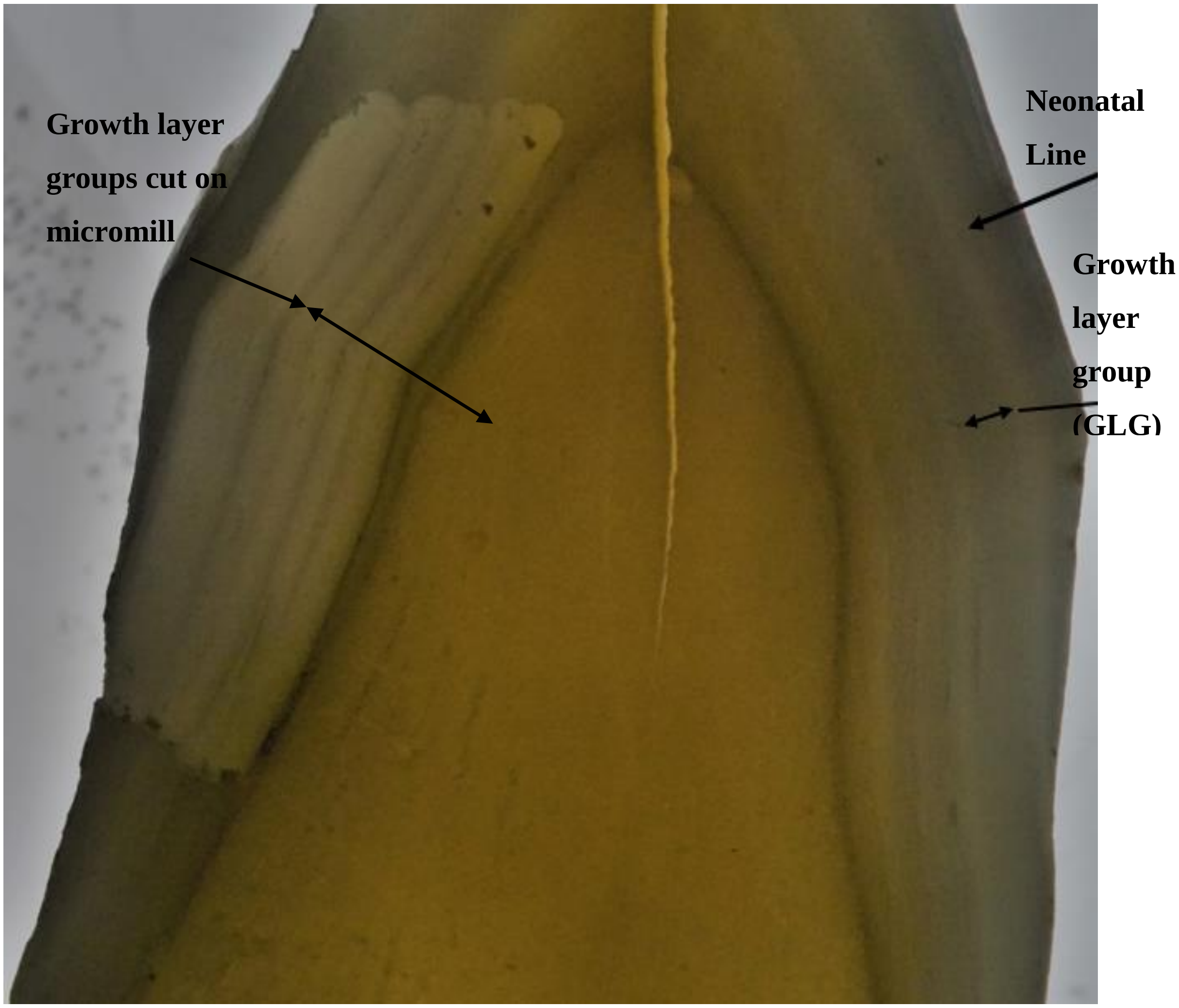

Figure 2. Sectioned northern fur seal tooth under dissecting microscope.

Table 3. Minimum, maximum, range and mean of $\delta^{13}C$ and $\delta^{18}O$ (‰) in northern fur seal (*Callorhinus ursinus*) canine teeth growth layer groups, St. Paul Island, Alaska, 1992-2013.

Dent code	**GLGs**	**$\delta^{13}C$ Min**	**$\delta^{13}C$ Max**	**$\delta^{13}C$ Range**	**$\delta^{13}C$ $\bar{x}$**	**$\delta^{18}O$ Min**	**$\delta^{18}O$ Max**	**$\delta^{18}O$ Range**	**$\delta^{18}O$ $\bar{x}$**
211	3	-14.11	-13.28	0.83	-13.70	-3.88	-1.90	1.98	-2.89
212	4	-14.04	-12.38	1.66	-13.37	-4.22	-3.02	1.20	-3.72
214	3	-19.04	-11.97	7.07	-15.51	-4.11	0.32	4.43	-1.89
215	4	-14.56	-12.73	1.83	-13.73	-5.89	-4.60	1.29	-5.16
217	4	-10.99	-8.21	2.78	-9.59	-3.91	-0.60	3.31	-2.09
219	3	-13.66	-13.12	0.54	-13.38	-4.49	-3.81	0.68	-4.05
220	4	-14.48	-13.28	1.20	-13.96	-5.01	-2.41	2.60	-3.80
221	3	-13.63	-13.19	0.44	-13.48	-3.37	-2.23	1.14	-2.87
222	3	-14.76	-13.15	1.61	-13.79	-3.54	-2.70	0.84	-3.17
223	3	-13.70	-13.06	0.64	-13.36	-1.85	-0.90	0.95	-1.81
226	5	-13.57	-13.39	0.26	-13.48	-3.70	-1.31	2.39	-2.37
228	3	-14.26	-12.55	1.70	-13.22	-3.67	-2.26	1.41	-2.95
230	4	-14.59	-14.26	0.33	-14.40	-2.95	-2.22	0.73	-2.52
231	3	-14.68	-13.34	1.34	-14.14	-3.25	-0.96	2.29	-2.25
234	4	-13.66	-13.38	0.28	-13.52	-3.03	-0.84	2.19	-2.27
235	3	-14.75	-13.73	1.02	-14.16	-3.93	-1.34	2.59	-2.77

238	4	-13.39	-12.60	0.79	-13.13	-2.62	1.69	4.31	-0.79
239	4	-14.40	-13.53	0.87	-14.09	-2.90	-1.42	1.48	-2.21
248	4	-14.32	-13.50	0.82	-13.99	-4.29	-2.81	1.48	-3.65
255	3	-14.52	-14.29	0.23	-14.40	-2.99	-2.44	0.55	-2.71
260	3	-14.63	-14.00	0.63	-14.31	-1.97	-0.74	1.23	-1.39
263	4	-14.57	-13.53	1.04	-13.94	-2.87	-1.72	1.15	-2.35
266	3	-15.42	-13.49	1.93	-14.45	-3.13	-0.93	2.20	-2.03
269	3	-14.26	-13.20	1.06	-13.89	-2.90	-0.34	2.56	-1.42
271	3	-14.69	-13.18	1.51	-13.92	-3.46	-1.70	1.76	-2.51
277	3	-14.69	-13.51	1.18	-14.10	-3.13	-1.00	2.13	-2.22
278	3	-14.95	-14.14	0.81	-14.60	-2.04	-0.40	1.64	-1.17
279	3	-13.93	-13.32	0.61	-13.67	-1.39	-0.94	0.45	-1.17

Sea surface temperature was calculated for nine locations in the Bering Sea and northeastern Pacific Ocean. The mean SST from the five locations in the Bering Sea was 4.5 C˚; the mean from San Miguel Island waters was 15.0 C˚; the California Current had a mean SST of 7.9 C˚ and the northeastern Pacific Ocean was 13.1 C˚. Data were collected from NASA's GISS $\delta^{18}O$ database. A linear regression of longitude by $\delta^{18}O$ showed a very slight downward trend of approximately 0.2‰ by 50˚ longitude. Linear regression showed a distinct downward trend in $\delta^{18}O$ as latitude decreases (approximately 0.2 ‰ by 10˚ latitude). One-way ANOVA showed this trend was significant (df = 92, F = 32.7, p-value = 1.36E-07). Sea surface temperature was calculated using equation $16.9 - 4.3 * \delta^{18}O = T$ (C˚) (Epstein et al. 1953). SST was calculated from the ranged from 38.36 – 15.53 ± 5.0 C˚ with a range of 22.9˚ and a mean of 27.79˚ (Table 4).

Table 4. Bering Sea Sea Surface Temperature (SST) locations in the Bering Sea (BS) and northeastern Pacific Ocean, 1970-2014. St. Paul Island (58^{0}N, 170^{0}E), St. George Island (56^{0}N, 170^{0}E), Inner Domain (BS) (60^{0}N, 168^{0}E), Middle Domain (BS) (58^{0}N, 168^{0}E), Outer Domain (BS) (58^{0}N, 172^{0}E), Bering Sea basin (58^{0}N 180^{0}E), Oregon coast (44^{0}N, 128^{0}E), northeastern Pacific Ocean basin (48^{0}N, 158^{0}E), San Miguel Island, California (34^{0}N, 120 ^{0}E). n represent number of data points.

These data were provided by GHRSST and the US National Oceanographic Data Center. This project was supported in part by a grant from the NOAA Climate Data Record (CDR) Program for satellites. Casey et al. 2010.

Location	St. Paul	St. George	Inner Domain	Middle Domain	Outer Domain	Bering Sea Basin	Oregon Coast	Northeastern Pacific Ocean	San Miguel Island, CA
n	544	544	544	544	544	544	544	544	544
Maximum	6.3	6.3	6.1	4.2	5.8	6.1	14.1	8.9	16.5
Minimum	3.8	3.9	4.2	2	2.8	3.6	12.2	7.3	14.1
Range	2.5	2.4	1.9	2.2	3	2.5	1.9	1.6	2.4
$\bar{x}$	4.9	5.2	4.9	3.1	4.3	4.9	13.1	8	15
SD	3.1	2.6	3.6	3.1	2.9	2.7	2.6	2.7	1.7

Fractionation of $\delta^{13}C$ between keratin (vibrissa) and dentin (teeth) was calculated to have mean Δ of 3.69‰ ± 0.65, the maximum fractionation was 4.98‰, and the minimum fractionation was calculated at 2.67‰, with a range of 2.31‰. Covariance between $\delta^{13}C$ in vibrissae and dentin was low at 0.09. This shows that yearly means in keratin and years in dentin are not varying together. Correlation between $\delta^{13}C$ in vibrissae and dentin was moderate at 0.36. Linear regression was calculated for GLGs of canine teeth for $\delta^{13}C$ from years 1-3 and for $\delta^{13}C$ of vibrissae from base to tip. The slope of the linear regression in teeth had a maximum of 0.5117 and a minimum of -0.974, while the vibrissae showed a maximum slope of 0.084 and a minimum of -0.0538. A total of 50% of the GLGs showed no significant change in $\delta^{13}C$ overall. The slope of the linear trendline of these teeth was less than 0.2.

Discussion

Vibrissae

Northern fur seals migrating from the highly productive Bering Sea ecosystem to the less productive northeastern Pacific Ocean throughout the winter would be expected to exhibit a covarying decrease in $\delta^{13}C$ and $\delta^{15}N$. A dietary change without a corresponding migration would show only a change in $\delta^{15}N$ (Schell et al. 1989; Hirons 2001; Hirons et al. 2001). When the seals travel back to the rookeries during the summer, then there should be a covarying increase in $\delta^{13}C$ and $\delta^{15}N$ as they return to the Bering Sea. This pattern appeared in a number of the vibrissae over multiple years and was estimated at 0.09 mm/day (3.25 cm /year). A recent study (Kelleher 2016) using known age fur seals found a similar growth rate in juvenile males. Using $\delta^{13}C$ as a proxy to estimate growth rate from known age seals, the growth rate for juvenile males was estimated at 3.6 cm/year. Kelleher (2016) noted a more rapid growth in young of year northern fur seals, approximately 4.3 cm/year. This is similar to the results of growth rate studies done on Steller sea lions (*Eumetopias jubatus*) (Hirons et al. 2001; Rea et al. 2015). As most of the vibrissae used in this study were of unknown aged seals, the increased vibrissa growth in the first year of life was not taken into account. In the two known-seals, the vibrissae appeared too short to include the entire first year of life.

Stable isotopes values for carbon and nitrogen showed a great deal of variation both within individual vibrissa and among the vibrissae sampled. Several repeated patterns were found among the seals' vibrissae. The most common patterns included the annual, covarying oscillations indicating large movements or migration (Figure 3) and the U-shaped pattern and large negative covariance at the tip of the vibrissae (Figure 4) were used to interpret the life history, migratory pattern and fluctuations in the environment. The annual oscillations were likely more pronounced in $\delta^{15}N$ than $\delta^{13}C$ because fractionation of $\delta^{15}N$ is 3-5 times larger than fractionation of $\delta^{13}C$. Changes in regional productivity of different water masses would be reflected as either increases or decreases in both isotopes simultaneously (DeNiro and Epstein 1978, 1981; Schell et al. 1989; Hirons et al. 2001; Post 2002; Dehn et al. 2007). In vibrissae that showed annual oscillations, most also showed periods where carbon and nitrogen showed little to no change. Stable periods (9+ months) were invariably areas of depleted $\delta^{13}C$ and $\delta^{15}N$ indicating these periods were when the animal was not in the Bering Sea but in the less productive, open waters of the northeastern Pacific Ocean. The longest vibrissae used in this study (38 cm) showed four periods of suspected non-migratory behavior that lasted at least one year (3.25 cm).

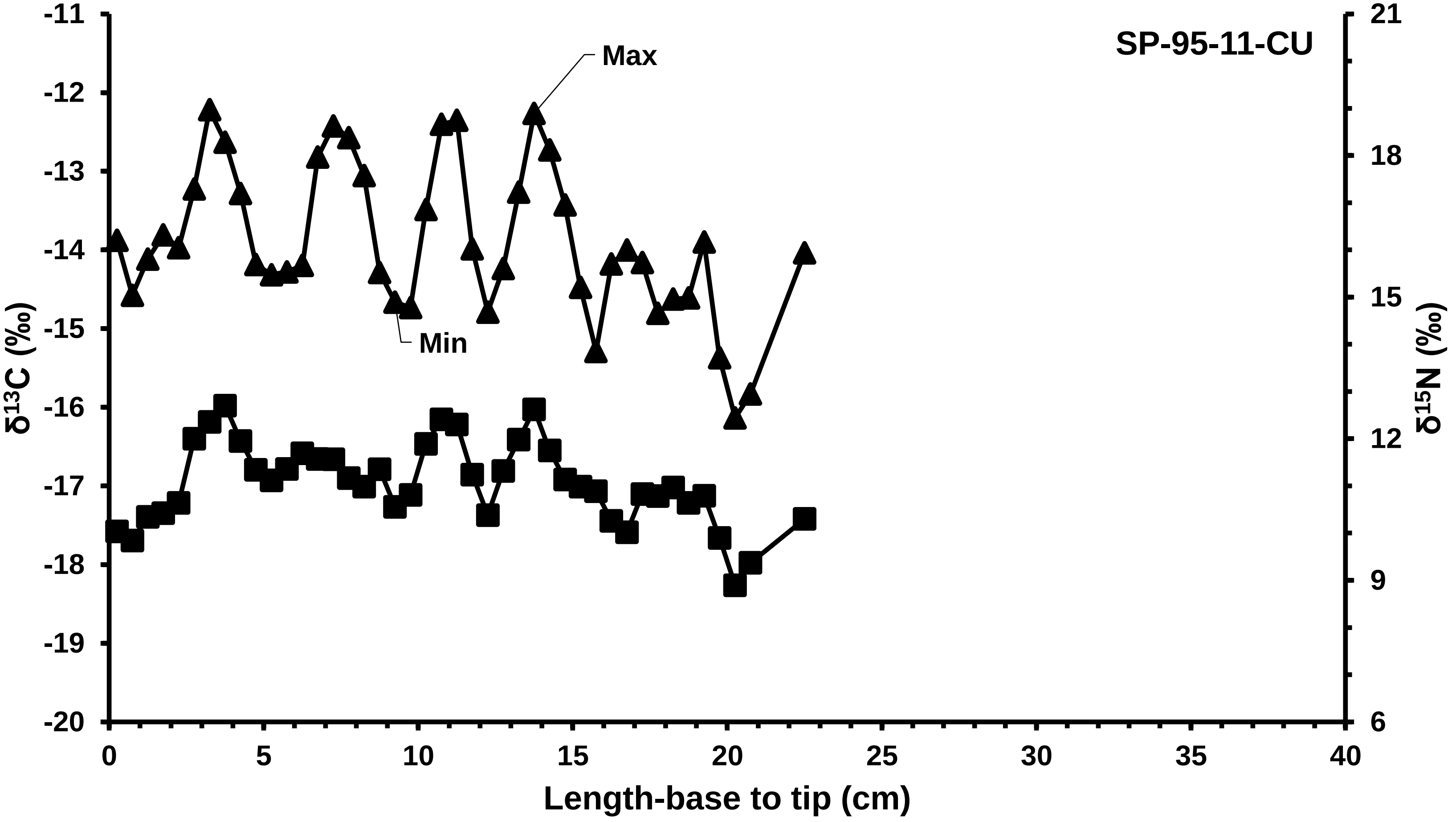

Figure 3. Northern fur seal vibrissa showing regular oscillating pattern, representing approximately six years migration. Max = summer, Min = winter. Triangle = δ^{15}N, square = δ^{13}C.

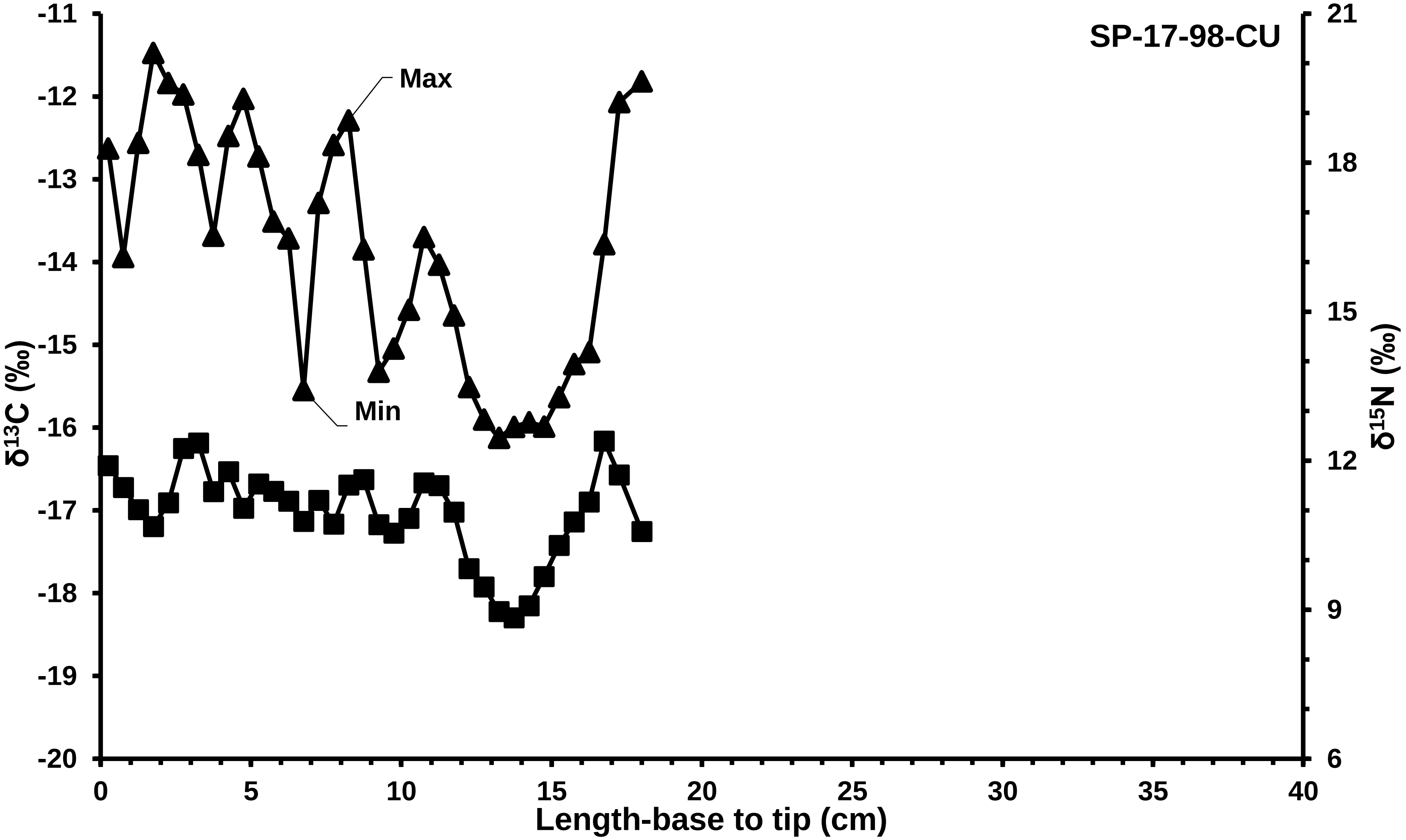

Figure 4. Northern fur seal vibrissa. Inverse isotopic pattern at tip of vibrissa (16.25-18 cm) represent transition from nursing to foraging. U-shape (11.25-16.75 cm) indicates residency (non-migration). Oscillatory pattern represents migration. Max = summer, Min = winter. Triangle = δ^{15}N, square = δ^{13}C.

The U-shaped pattern was most commonly found toward the tip of the vibrissae and covered between 1 and 2 years. The pattern showed a steep depletion in δ^{13}C and δ^{15}N, followed by a stable period at the most depleted point, and then an enrichment in δ^{13}C and δ^{15}N, though δ^{15}N was not as enriched as when the pattern began (Figure 4). When mammals nurse, their δ^{15}N are a trophic level above their mother while δ^{13}C is a trophic level lower (Hobson and Sease 1998; Polischuk et al. 2001; Aurioles et al. 2006; York et al. 2008; Aurioles-Gamboa et al. 2009; Cherel et al. 2015; Lowther and Goldsworthy 2016). Northern fur seals are weaned in four months (Gentry 1998) and must learn to hunt immediately upon leaving the rookery. Naïve seals would not be able to catch higher trophic level prey than subadults and adult seals due to their smaller size and lack of practice. This period of time while the seals are small and less able to hunt/ could be reflected the stable, depleted time (1-2 years) that appears in the vibrissae that show the U-shape pattern. This pattern was only found in the shorter (8-12 cm) vibrissae of the youngest seals, likely because the tip of the vibrissa wears with age. Older animals are unlikely to retain the portion of the vibrissa that reflects the first months' to-one-year of growth. Because this pattern is exhibited close to the tip of the vibrissae and begins with a depletion, this point is likely the beginning of the post-weaning period. The enrichment of both stable isotopes after the U-shape would indicate foraging in more productive waters at a higher trophic level, likely in the Bering Sea.

Juvenile northern fur seals are thought to follow the females on their migrations into the California Current off the coasts of Oregon and California, and they may not return to the Bering Sea for two years (Baker 1970; Gentry 1998; Baker et al. 2007). If the U-shaped pattern indicates the northern fur seals' first foray into the northeastern Pacific Ocean, the growth rate would be approximately 0.12 mm/day for the first year (Kelleher 2016), which is similar to the shortest U shape, representing approximately one years' growth. The longest of the U-shape patterns covers approximately 7 cm, which would represent almost two years' vibrissae growth based on Kelleher (2016), which reported the first two years of growth at ~ 0.1 mm/day.

The large, negative covariances were revealed in multiple vibrissae. This pattern of large negative covariance showed a large enrichment in $\delta^{15}N$ (5-6 ‰) and a corresponding depletion in $\delta^{13}C$ (1-2 ‰) and was always located near the tip of the vibrissae. As the negative covariance began toward the tip of the vibrissae, this is likely to be related to the end of weaning, with the immediate drop in trophic level indicative of the seals' first efforts to hunt for themselves.

Forty-two percent the juvenile northern fur seals killed in 2013showed a covarying depletion ~ 3.75 cm from the base. Assuming an estimated growth rate of 0.09mm/day, this depletion would have occurred in summer of 2012. Eighty percent of the aforementioned vibrissae were found in 3-year-old animals. As the Pacific Interdecadal oscillation was in its cool phase and ENSO was neutral that year, environmental fluctuations would not explain this change. The ocean waters off California in 2012 had the lowest pelagic fisheries landings in three years and had declined 36% relative to the fisheries landings from 2000 (Wells et al. 2013). If, as has been postulated above, some of the 1- and 2-year-old northern fur seals in the cohort were remaining in the northeastern Pacific Ocean during this time, the decrease of available prey could explain this depletion in $\delta^{13}C$ and $\delta^{15}N$.

Potential prey items were identified as being captured in the northern or southern regions to compare their isotopic values to the maximum and minimum $\delta^{13}C$ and $\delta^{15}N$ found in the vibrissae. Potential prey included a variety of teleosts, gelatinous zooplankton (Brodeur 1999), and cephalopods. Prey were included in the southern region if they were caught in the northeastern Pacific Ocean and California Current. These prey had the most depleted values compared to the northern region including the western Gulf of Alaska and Bering Sea. Northern fur seals appeared to primarily forage in the northeastern Pacific Ocean (the winter migratory region) on fatty fishes and cephalopods. Maximum $\delta^{13}C$ and $\delta^{15}N$ showed the seals foraging on prey on the Bering Sea shelf and break, and within the area of the Alaska Current along the south side of the Alaska Peninsula. The fur seals in the higher latitudes (the summer migratory region) were potentially feeding on lean fishes, fatty fishes, cephalopods, and gelatinous zooplankton (Figure 5).

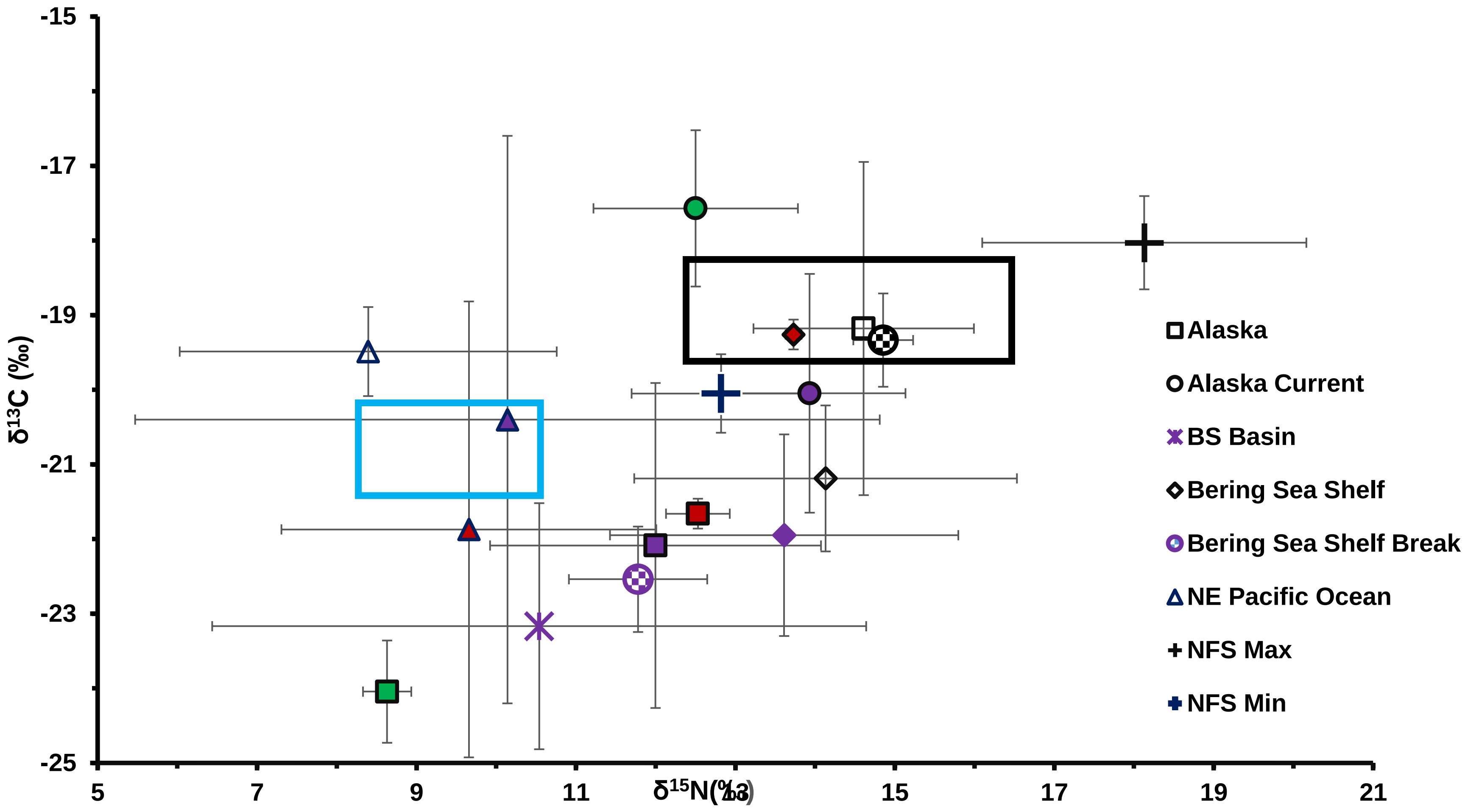

Figure 5. δ^{13}C and δ^{15}N of potential prey items collected from the northern (Bering Sea) and southern (northeastern Pacific Ocean) regions of the northern fur seal migration. Red: cephalopods, green: gelatinous zooplankton, purple: fatty fishes, black and white: lean fishes. Black box indicates regions seals are likely foraging during summer. Blue box indicates regions seals are likely foraging in the winter.

Teeth

Counts of GLGs in teeth have been shown to be an effective method of aging marine mammals (Kenyon and Fiscus 1963; Scheffer 1980; Lockyer et al. 2010). The $\delta^{18}O$ in bioapatite of northern fur seal teeth during this study was much more enriched than expected based on previous studies. Clementz et al. (2001) found northern fur seal dentin $\delta^{18}O$ had a mean of 25.8 ±0.5 ‰ with a range of 0.9 ‰ (n = 3). Fractionation of body water to carbonate has been estimated at 26.3-27.0 ‰ for terrestrial carnivores (Clementz and Koch; France and Owlsey 2015). The mean from the GLGs used in this study was 28.4 ±1.28 ‰ while the range was 6.9 ‰ (n = 86). The high variation may be related to the large number of seals sampled (n = 30). Northern fur seals are solitary animals away from the rookeries, so a diverse range of $\delta^{18}O$ (i.e., water masses) can be recorded in their tissues. Clementz and Koch (2001) studied three seals and they did not sample individual growth layers. They noted that $\delta^{18}O$ may vary by age and it is likely that the long migration of these animals alters $\delta^{18}O$. Ocean water $\delta^{18}O$ is depleted in higher latitudes due to changes in evaporation, precipitation, and sea surface temperature and varies in nearshore environments due to runoff (Clementz and Koch 2001; Trueman et al. 2012). Yearly averages of $\delta^{18}O$ between 1992-2013 showed an enrichment over time, which could indicate that the animals are spending less time offshore, or more time in the more southerly portion of their range (Figure 6).

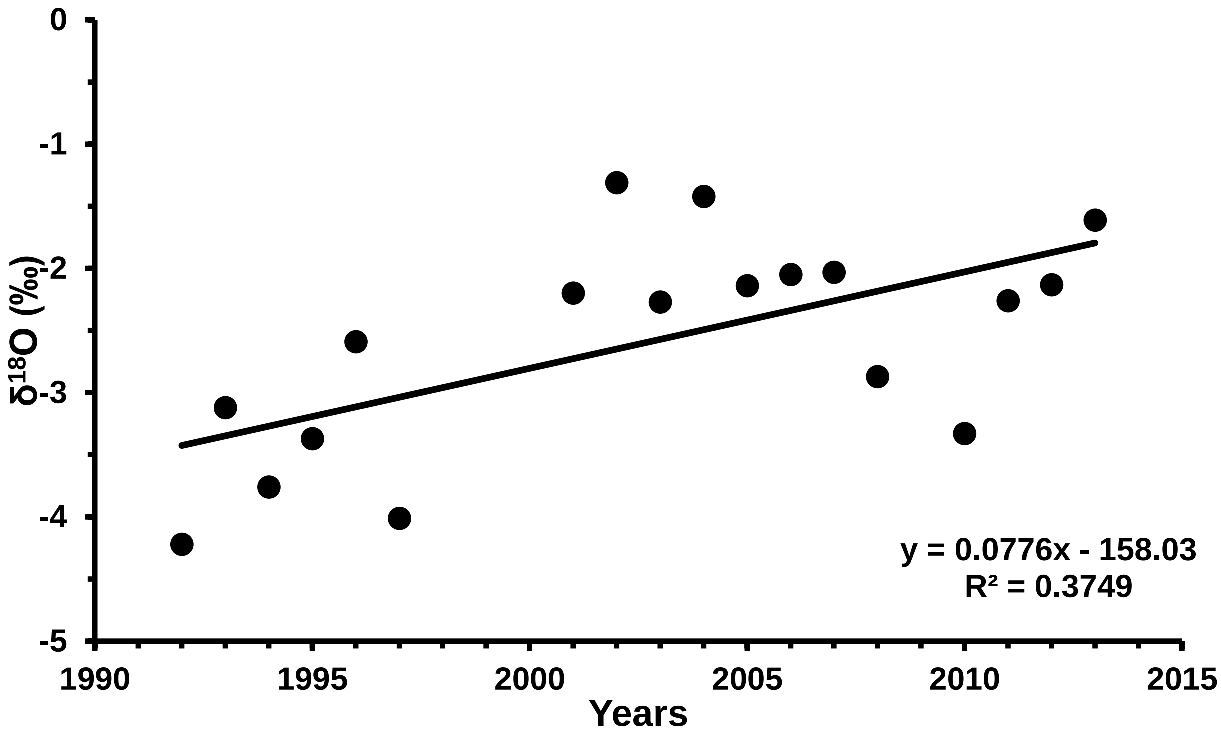

Figure 6. Annual mean δ^{18}O in northern fur seal canine teeth showing significant enrichment, 1993-2013. Each dot represents n = 1–13.

Sea surface temperatures calculated using Epstein et al. (1953) from actual δ^{18}O in the fur seals' teeth for years 1992-2013 showed temperatures far above recorded temperatures for the Bering Sea and the Northeastern Pacific Ocean. The lowest temperature recorded in the Bering Sea was 3.8˚ C while the highest temperature recorded was at San Miguel Island at 16.1˚ C (Table 4). The range of differences between calculated and actual SST is likely due to the animal's migrations between the cool waters of the Bering Sea and the warmer northeastern Pacific Ocean (Clementz et al. 2012). Calculated SST was highly variable among all individual animals and among different animals from the same year. The annual average SST calculated from δ^{18}O showed a decline from 1992-2013. The PDO in this time period was entering a short warm phase (less than a decade, then shifting to a three year cool phase, followed by a five-year warm phase. In the late 2000's, the PDO entered a cool phase that lasted until 2013 (http://www.beringclimate.noaa.gov/data/index.php). This instability in the PDO is unlikely to be the cause of the enrichment in δ^{18}O as seen in the data gathered from the fur seal teeth, but rather may be an effect of foraging in nearshore vs offshore environments. Offshore environments are more enriched in $\delta^{18}O$ than nearshore environs (Ciner et al. 2016), and this enrichment would show up in the calculations as a decrease in SST. A change in migratory behavior thus could influence $\delta^{18}O$. These data indicate that $\delta^{18}O$ found in GLGs of northern fur seals is not an accurate recorder of SST alone.

The GLGs' $\delta^{18}O$ revealed two main patterns. Ten of 20 tooth samples showed enrichment in GLG 2, which covers the time between ages 1-2. It has been speculated that some northern fur seal juveniles do not return to the rookeries during this time span and may remain in the southerly latitudes of the North Pacific Ocean (Baker et al. 1970; Gentry 1998; Baker 2007). Enrichment covering this period suggests that these animals are remaining in the warmer, $\delta^{18}O$ enriched waters of Northern Pacific Ocean. Juveniles of this age class have also been observed spending only a few weeks in the Bering Sea (Baker et al. 1970). Juvenile seals spending less time in the Bering Sea could also explain the enriched $\delta^{18}O$ found in canine teeth during this time period. If the younger juveniles (1-2 year olds) are spending less time in the Bering Sea than older juveniles (3-4 year olds), they would show enrichment of $\delta^{18}O$ for that period of time. The single 5-year-old tooth sampled upholds this pattern; it shows $\delta^{18}O$ enrichment at age 1-2, depletion at years 2-3, no change between years 3-4, and depletion between years 4-5. This tooth indicated the animal spent less time in cooler waters during years 1-2, increased the time spent in cooler waters in years 2-3, maintained this pattern in years 3-4 and increased the time in the Bering Sea between years 4-5.

The GLGs exhibited several patterns in $\delta^{13}C$: 30% showed no change over the course of the animals' lives, 25% of the seals were enriched in $\delta^{13}C$ 0.5-1‰ between at least two GLGs, 35% were enriched more than 1‰ between two GLGs, and 10% were depleted by at least 1 ‰. The majority of the teeth showed significant enrichment in $\delta^{13}C$ over time and only a small proportion were depleted. This indicated that the majority of the animals fed in areas with varying primary production over the course of their lives and this change may indicate that the seals were feeding at higher or lower trophic levels as they aged.

Northern fur seal reach sexual maturity at 6-7 years of age (Gentry 1989) and 5-year-old animals arrive at the Pribilof Islands sooner than the younger animals (Baker et al. 1970). Half of the twenty seals sampled had depleted $\delta^{18}O$ at GLG 2 compared to the other 10 GLGs at year two which were enriched. The variability of $\delta^{18}O$ among the seals shows that juvenile northern fur seals do not all follow the same migratory pattern early in their lives and also do not necessarily stay in the same water masses. Because $\delta^{18}O$ is more strongly affected by latitudinal changes than longitudinal changes in the North Pacific Ocean, it is likely that these changes in $\delta^{18}O$ in the seals' GLGs are related to latitudinal movement through the water. Latitudinal changes in $\delta^{18}O$ were found to account for approximately 0.20 ‰ by 10° latitude (Figure 7). Latitude alone cannot account for the high variability in the fur seals $\delta^{18}O$ which has a mean of 1.16 ± 0.79 ‰ and a range of 3.41 ‰. The only other factor that strongly affects $\delta^{18}O$ is SST and given that the seals make long migrations from very cold surface waters (the Bering Sea) to warmer surface waters (the northeastern Pacific Ocean), SST is likely to be the secondary factor. Sperm whales (*Physeter macrocephalus*) have been shown to have high variability in $\delta^{18}O$ that was thought to be caused by either migration from high to low latitudes and/or from changes related to shallow to deep-water foraging (Borrell et al. 2014). While northern fur seals are not deep divers, they do feed on vertically migrating lanternfishes (Myctophidae) (Zeppelin and Orr 2010). Juvenile northern fur seals are much shallower divers in the early years of life so depleted $\delta^{18}O$ may be related to changes in foraging over time as well.

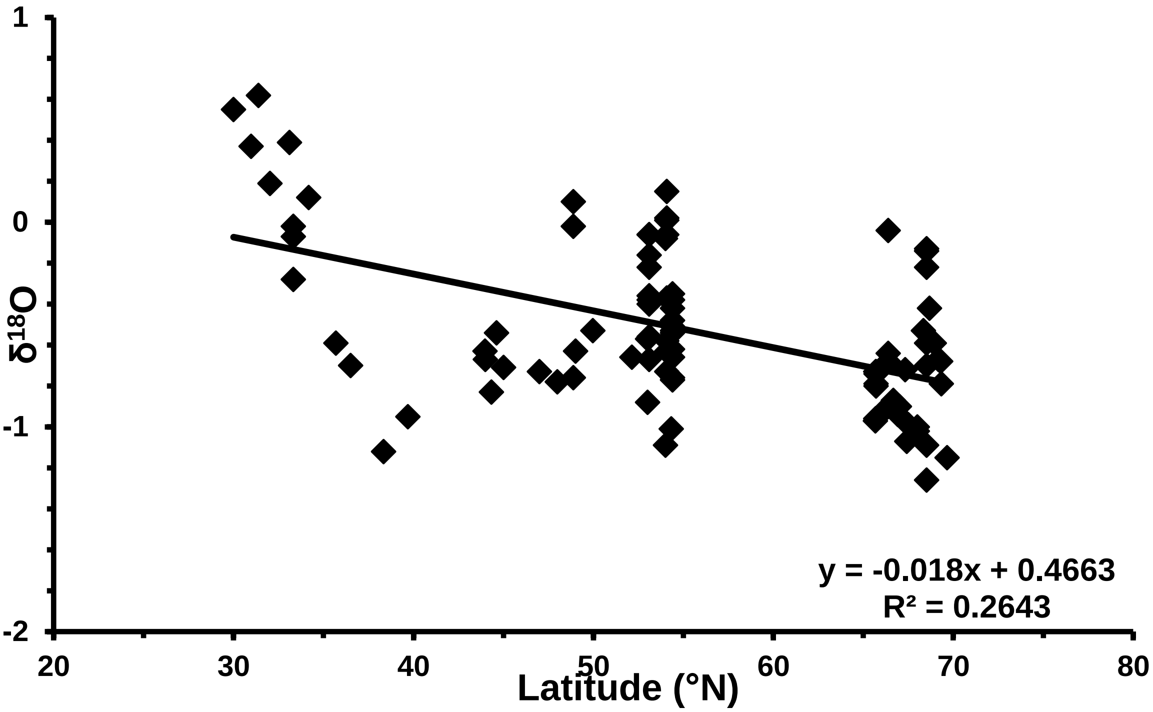

Figure 7. Change in δ^{18}O by latitude (ºN). (Data collected from https://data.giss.nasa.gov/o18data/)

The dentin indicated a slight but significant downward trend in δ^{13}C (Figure 8), which matches previous studies showing declining primary productivity in the Bering Sea (Schell et al. 2000; Hirons et al. 2001; Moore et al. 2003). The δ^{13}C is negatively correlated to SST (Hansen et al. 2009) and latitude, and the slight depletion in connection with the δ^{18}O enrichment could be indicative of a shift in the seals' range. As annual primary productivity is typically higher in areas of lower SST, this is what we would expect. The exception being ice covered waters, which the northern fur seals avoid as they spend the winter months in the warmer, southerly latitudes.

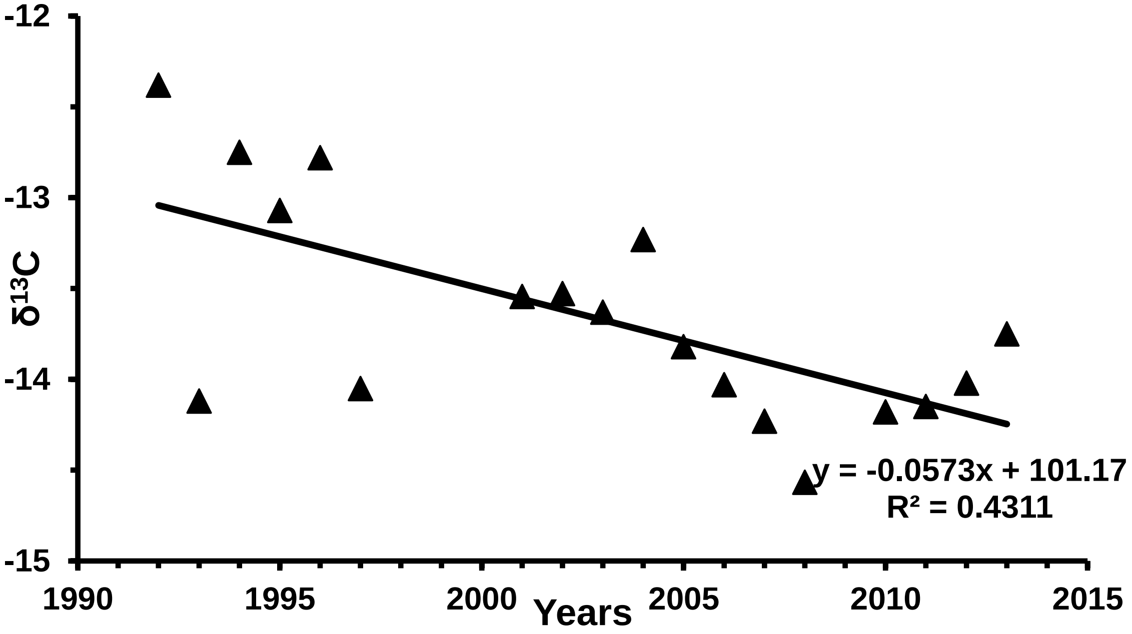

Figure 8. Annual mean δ^{13}C in northern fur seal canine teeth showing significant depletion in δ^{13}C, 1992-2013. Each dot represents n = 1-13 animals.

Vibrissae have been used in this study to gather data on primary production and trophic level changes on a timescale of days to months, while canine tooth dentin shows annual data on primary production and water masses. These separate timelines are difficult to resolve even within the same animal. Fractionation δ^{13}C of between the dentin and vibrissae was estimated at approximately 3.7‰ using concomitant teeth and vibrissa.

Several vibrissae showed long periods of depleted δ^{13}C and δ^{15}N that were estimated to occur over a minimum of one year. In one vibrissa, this pattern appeared at least twice. This year-long stable depletion indicates residency (non-migration) periods over the course of several non-consecutive years throughout the animals' life. Residency in northern fur seals is not expected. Northern fur seals between 2-3-year-olds have been reported to arrive much later to the Bering Sea than older animals (Baker 1970; Gentry 1989; Baker 2007).

The U-shaped pattern that appeared toward the tip of a number of vibrissae, typically lasting for at least one year, shows a depletion in $\delta^{13}C$ and $\delta^{15}N$ that corresponds with $\delta^{13}C$ and $\delta^{18}O$ patterns in the dentin. While it is difficult to get isotope data from the first year of life in the vibrissae, dentin has no such limitation. Once the neonatal line has been located, the first year, especially in a juvenile animal, is readily apparent. Of the animals that had at least three sequential years analyzed, 50% of them showed a significant enrichment in $\delta^{18}O$ between ages 1-2. This enrichment likely indicates increased time spent in lower latitudes over this period.

Sixteen of the 30 vibrissae sampled showed no change in $\delta^{13}C$ over the length of the vibrissae. This stable pattern in the vibrissae corresponded with the pattern in the10 canine teeth that showed no significant change in $\delta^{13}C$ throughout the GLGs.Linear trend lines in the juvenile northern fur seal vibrissae harvested in 2013 ($R^2 > 0.09$) from base to tip indicated very slight changes in $\delta^{13}C$ overall, while $\delta^{13}C$ in dentin of the seals showed no changes in slope of the trend line in 50% of cases. This variation between the individual animals $\delta^{13}C$ may be caused by two factors. One, while the teeth and vibrissae are from the same animal, they do not necessarily cover the same time period. Vibrissae were analyzed from the base, representing the date of death, to the tip. Due to mechanical wear and possible molting (Hirons 2001), it is highly unlikely the tip of a vibrissa represents the first year of the animal's life. Vibrissae are sensory organs and are used for foraging and during dives. Therefore, the tips wear down and in all but the youngest animals do not preserve a record of the earliest part of their lives. Dentin, on the other hand, records isotopic information in utero, but may not have a complete record of the most contemporary data. The amount of dentin required for stable isotope analysis is not always obtainable as the youngest layer of dentin is the thinnest in the tooth. Thus, when comparing the isotopic record in dentin and vibrissae, especially in an animal more than one year old, one is unlikely to have a complete record from birth to death in both tissues. The second potential issue is the growth rate. Vibrissae in northern fur seals have an estimated growth rate of 0.09 mm/day (Kelleher 2016) based on the isotopic oscillations in $\delta^{13}C$ and $\delta^{15}N$; growth rate in other otariids has been found to be variable depending on age (Hirons 2001; Rea et al. 2015; Kelleher 2016. This variability is certainly an issue when determining concomitant years between dentin and vibrissae.

Limitations

Stable isotopes of oxygen have been used as proxies for the paleoclimate for a long time. Invertebrates, dinosaurs, and other fossils have provided a wealth of information on the past climatic changes (Schaffer and Swart 1991; Straight et al. 2002 Clementz et al. 2012). There is far less research available for modern marine mammals, especially in pinnipeds, on calculating SST from δ^{18}O. This study provides preliminary information on the use of δ^{18}O in pinniped but further research is needed. Determining precisely why migratory species show larger ranges of δ^{18}O than can be explained by latitude would be a first step.

A further issue with this study involves the ages of the animals in question. When interpreting time scale data, the age of the animal is important. Estimates of time the vibrissae represent are possible based on the annual oscillations of δ^{13}C and δ^{15}N, having a known age is helpful and eliminates guess work when attempting to assign known years to vibrissa sections.

Another limitation of this study is the structure of the teeth. Because all of the fur seals whose teeth were used in this study were five years old or less patterns in the teeth could be difficult to ascertain. The thickness of the GLG varies along the length of a canine, particularly the final year, so the layer may often be too thin to be cut with the micromill. On a three-year-old animal this means only two years were likely to provide enough material for analysis. As these animals can reach 20+ years of age (Gentry 1998) and internal GLGs are discernable until age 15, after which the pulp cavity is filled and the GLGs become indistinct (Laws 1961; Klevezal and Stewart 1994; Klevezal et al. 2006), teeth from older animals would give a better overall picture of the animals' movements and allow a stronger understanding of their migratory patterns as they mature.

Conclusions

Vibrissae and canine teeth are valuable sources of information on environmental and behavioral changes in animals. Changes in the environment can play a crucial part in affecting the behavior of marine animals. SST affects prey availability and survivability, especially in smaller and younger animals. Areas such as the Bering Sea, which are subject to regime shifts and affected by PDO and ENSO events, are especially vulnerable. This study used three stable isotopes in two separate tissues to look at environmental fluctuations in the Bering Sea and North Pacific Ocean. Previous studies have used $\delta^{13}C$ and $\delta^{15}N$ in conjunction to look at environmental, dietary and productivity changes. Adding $\delta^{18}O$ to $\delta^{13}C$ and $\delta^{15}N$ augments our understanding of how environmental fluctuations can be monitored using the animals that dwell in that ecosystem. However, this study highlights how behavior must be taken into account. The evidence in this study showed that northern fur seals do not appear to follow the same migratory routes every year. A number of these animals established residency in less productive areas for 1+ years, and while this appears to be partially age dependent more often observed in younger animals between 0-2 years, several adults were seen to display this behavior repeatedly as well. Determining the causes of these residency periods will help to tease out whether a shift in $\delta^{18}O$, $\delta^{13}C$ and $\delta^{15}N$ is related to environmental fluctuations, foraging success, age, or other factors yet unknown. The data found in the vibrissae also suggested that many northern fur seals had no change overall in their $\delta^{13}C$. These results could indicate that the animals are returning to the same areas during the winter migration to forage every year. Given that northern fur seals show strong site fidelity in the summer migration, they may be showing site fidelity in the winter as well.

Future Research

In this study, it was not possible to get seasonality from the teeth, as the instruments available were not sensitive enough to isolate seasons with the tissue available. As northern fur seals are migratory, getting seasonal GLGs could show the seasonal oscillations like those, which are seen in the vibrissae and possibly lessen the discontinuity between actual and calculated SST. Further research into site fidelity in northern fur seals during the winter migration would be beneficial. If the seals are returning to the same areas during the southerly, winter migration, this could present us with an increase understanding of how to improve protections of these seals both during the migration and while they are in the North Pacific Ocean.

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Appendix

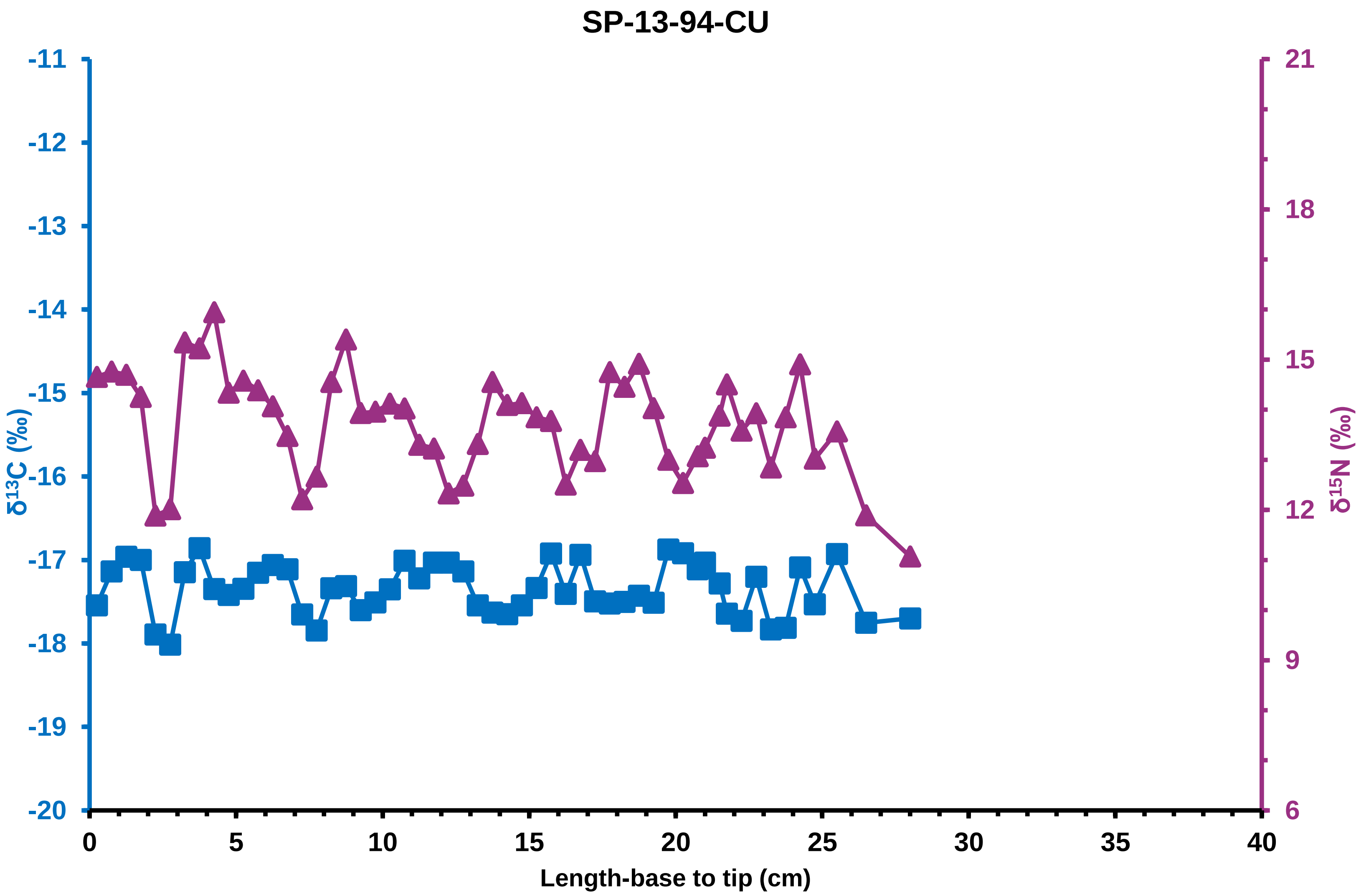


Figure A-1: Northern fur seal vibrissa showing regular oscillating pattern, representing approximately six years migration.

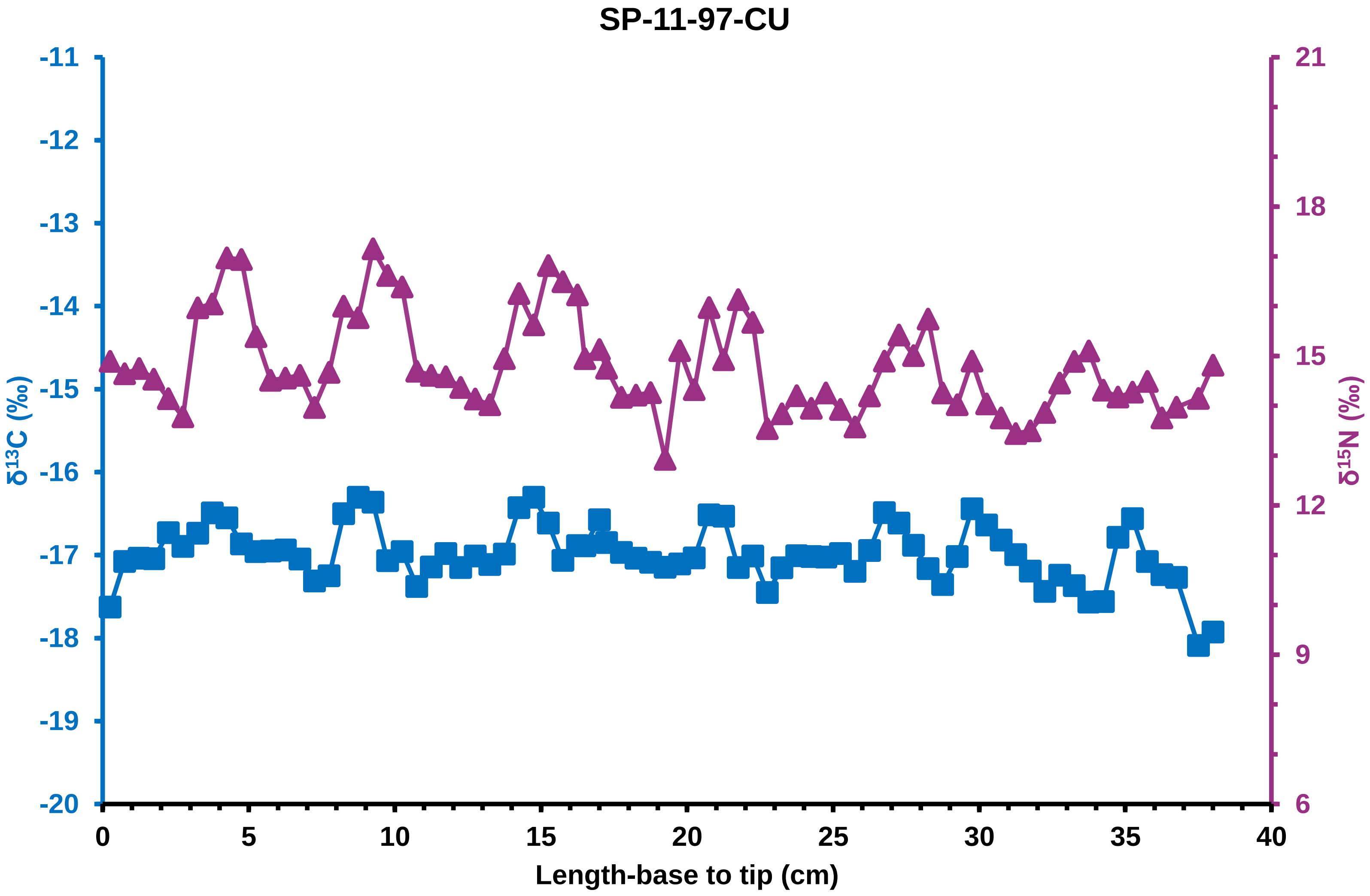


Figure A-2: Northern fur seal vibrissa showing regular oscillating pattern interspersed with year-long residency pattern, representing approximately eleven years migration.

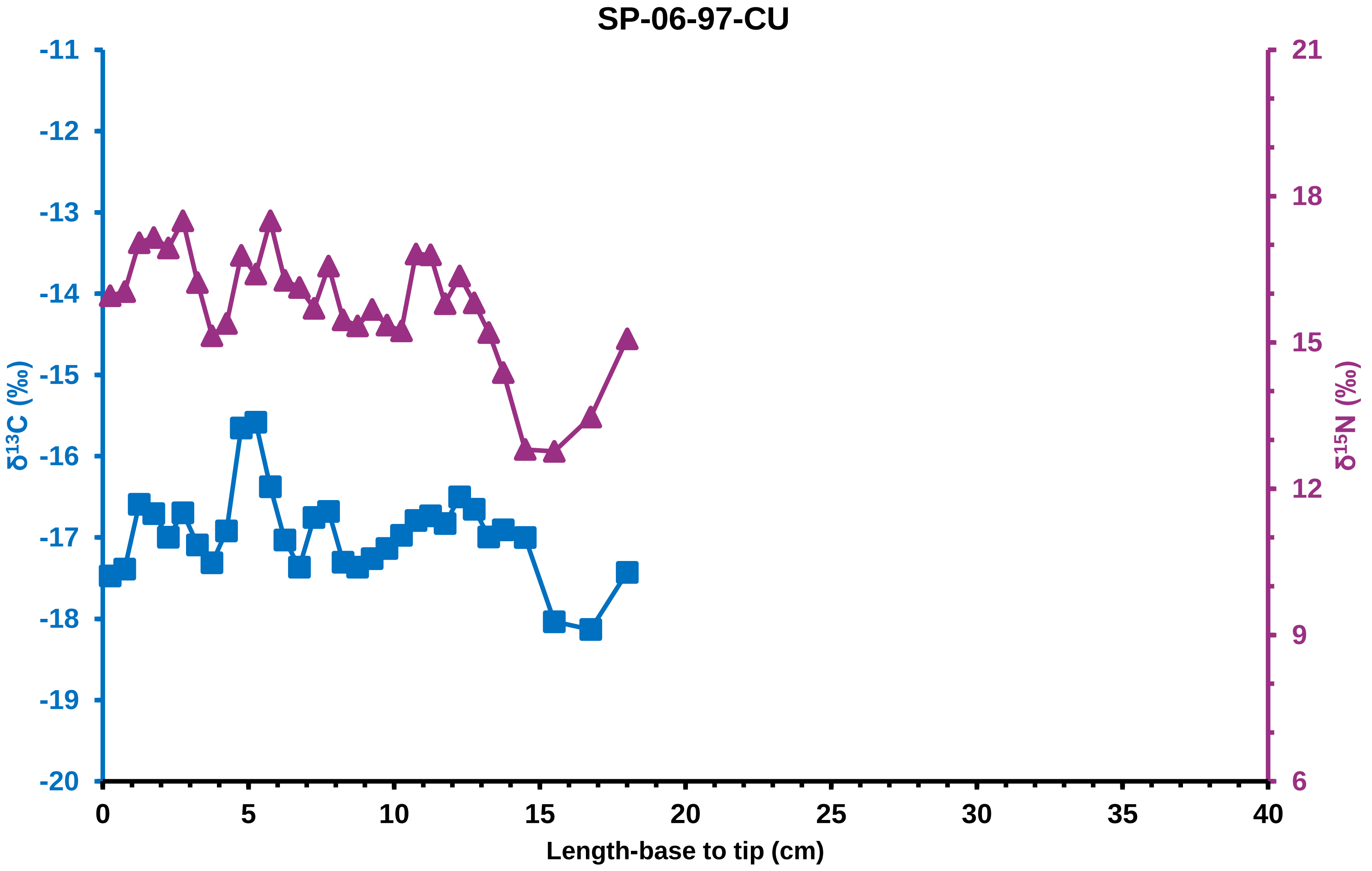


Figure A-3: Northern fur seal vibrissa showing abbreviated U-shape at tip.

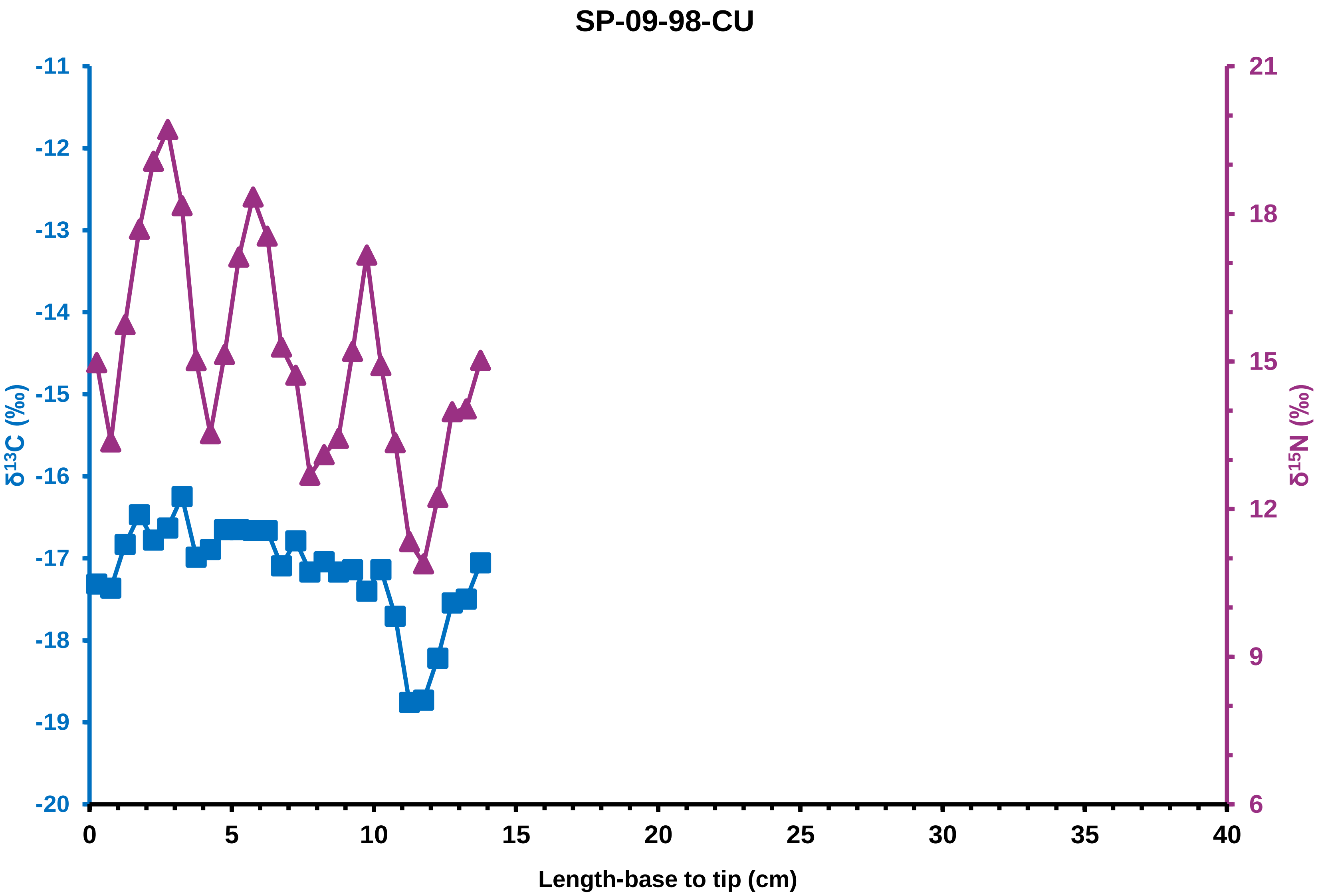


Figure A-4: Northern fur seal vibrissa showing regular oscillating pattern, representing approximately four years migration.

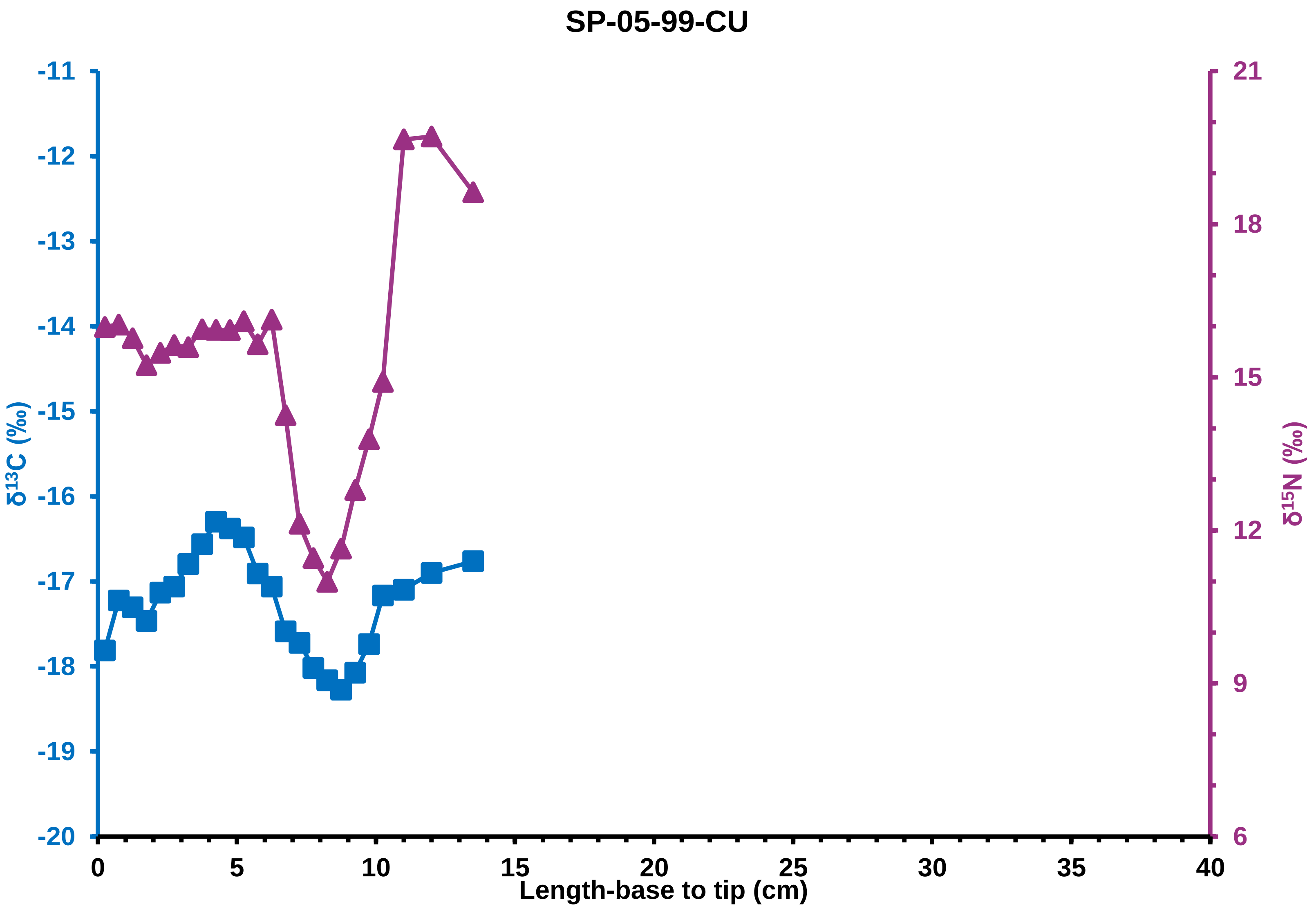


Figure A-5: Northern fur seal vibrissa showing abbreviated U-shape at tip

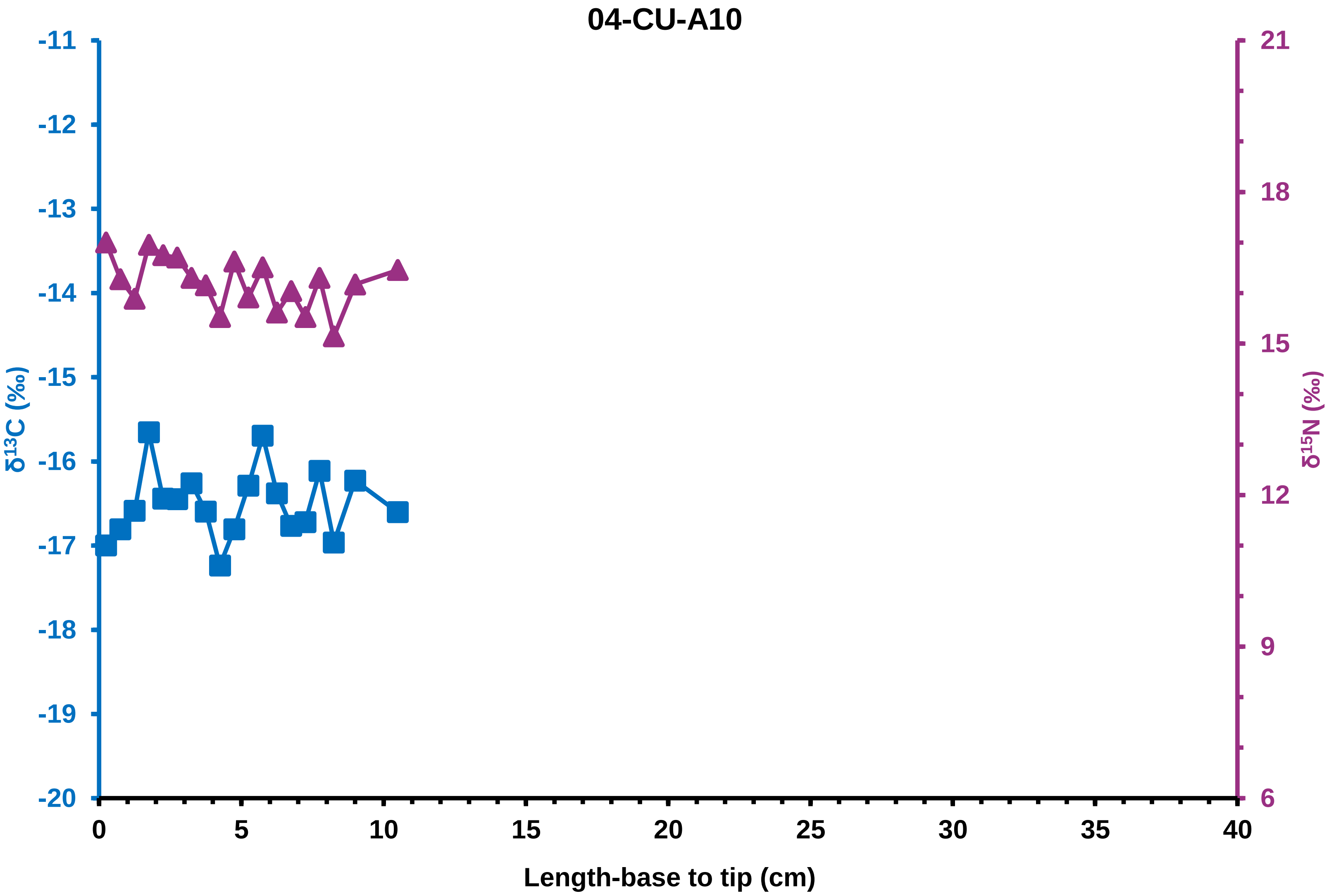


Figure A-6: Adult northern fur seal vibrissa showing three years growth.

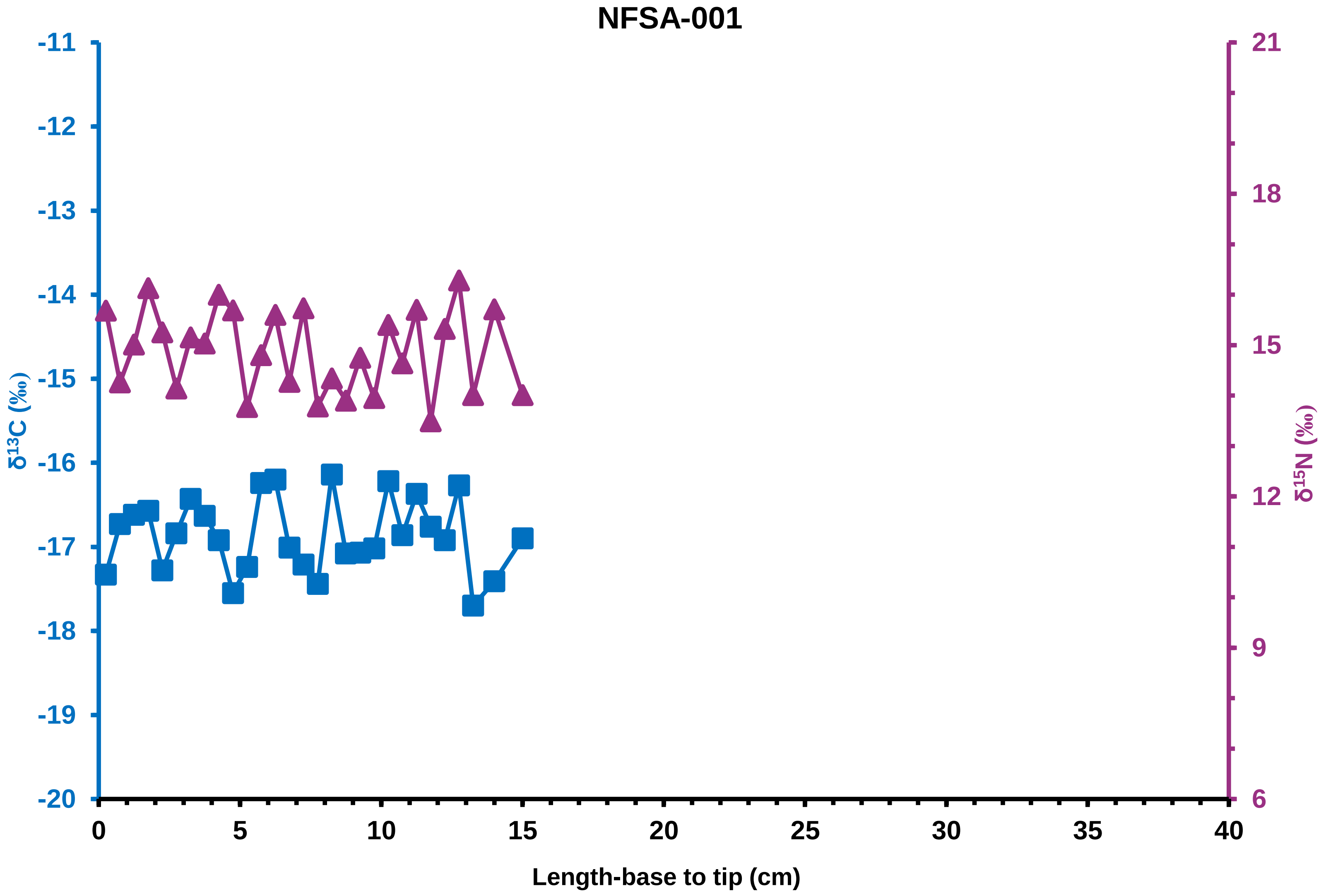


Figure A-7: Adult northern fur seal vibrissa showing four years growth.

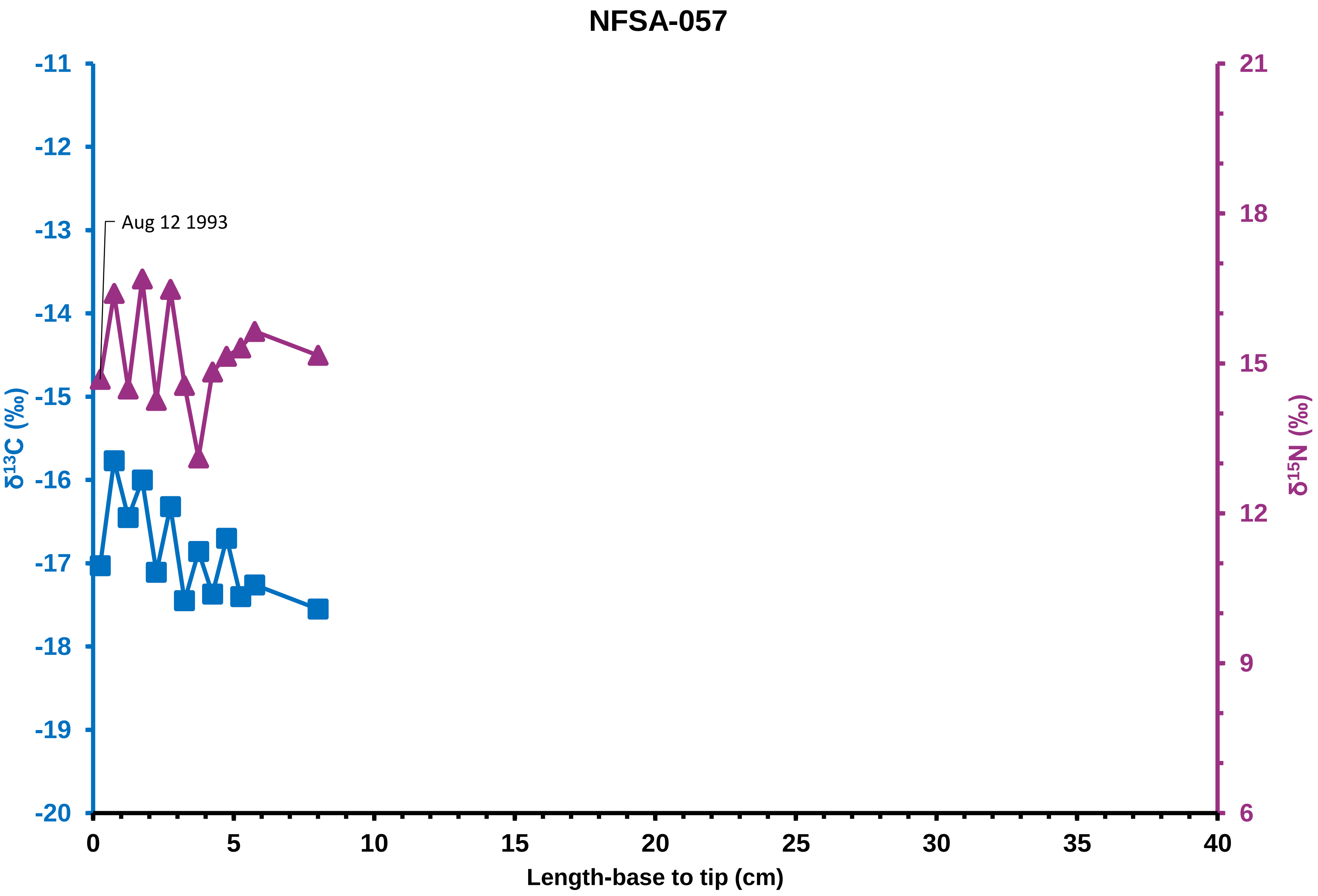


Figure A-8: Adult northern fur seal vibrissa showing two years growth.

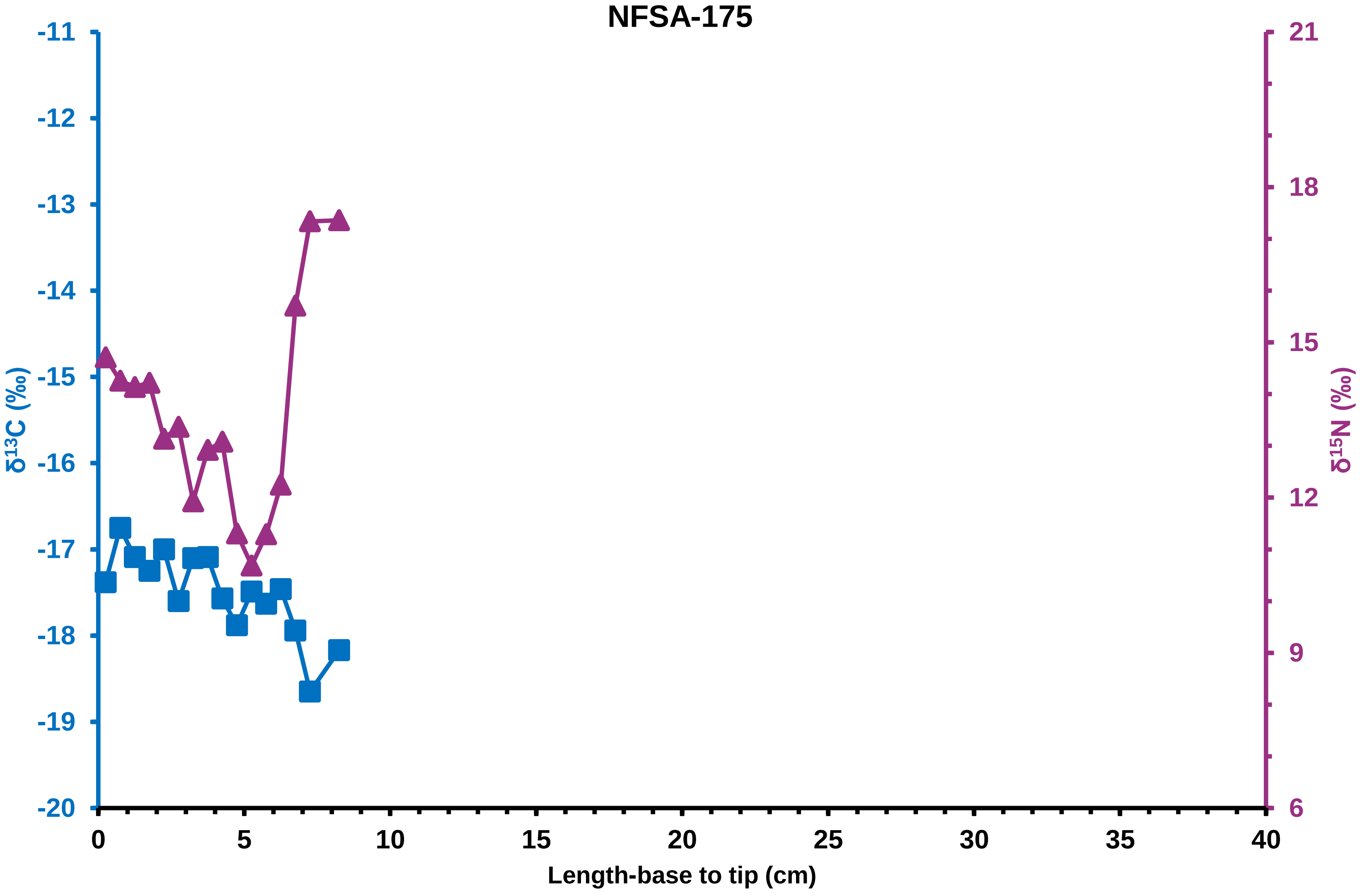


Figure A-9: Northern fur seal vibrissa showing post- weaning pattern and three years growth.

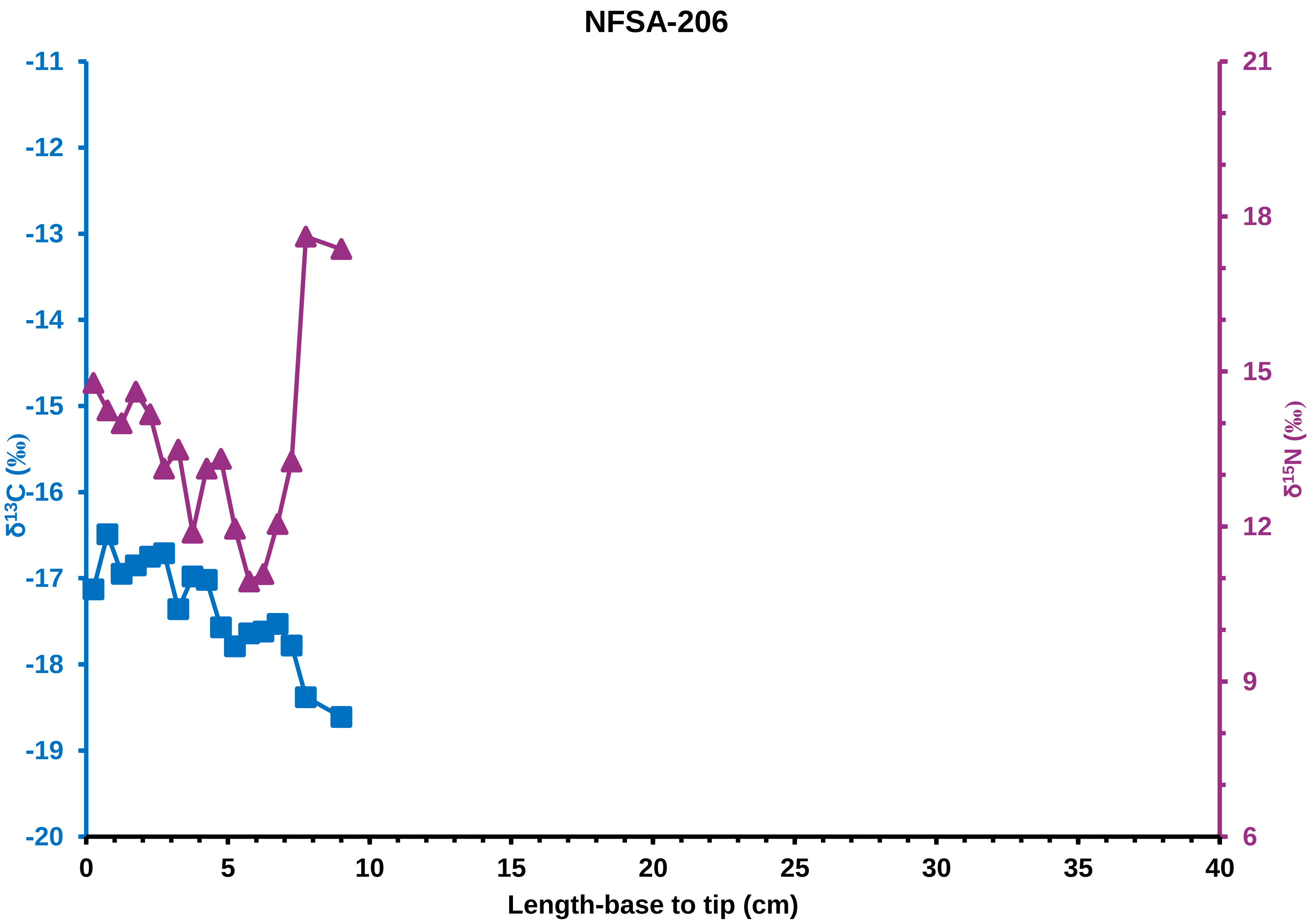


Figure A-10: Northern fur seal vibrissa showing post- weaning pattern and three years growth

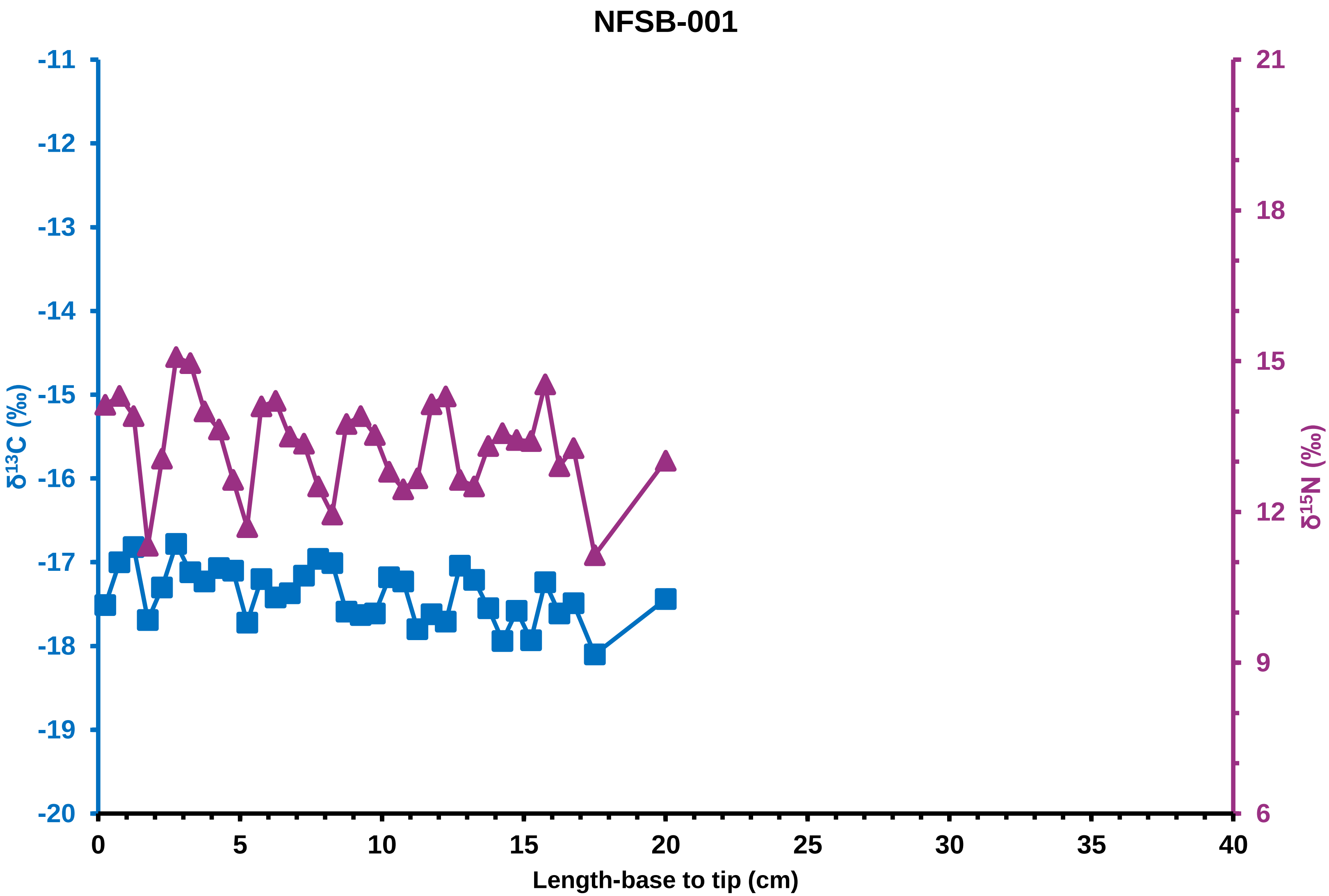


Figure A-11: Northern fur seal vibrissa showing regular oscillating pattern, representing approximately six years migration.

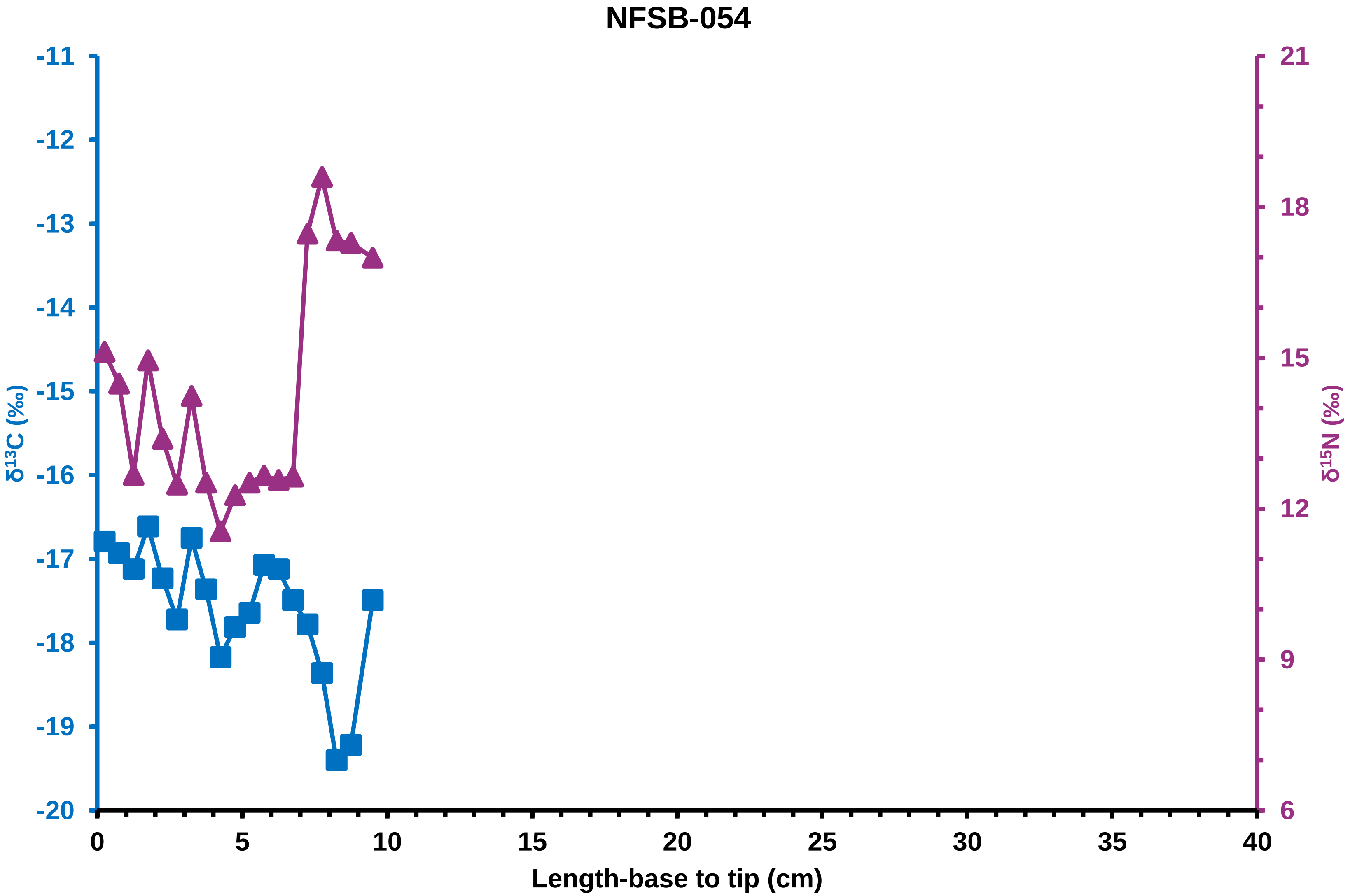


Figure A-12: Northern fur seal vibrissa showing post weaning pattern, representing approximately three years growth.

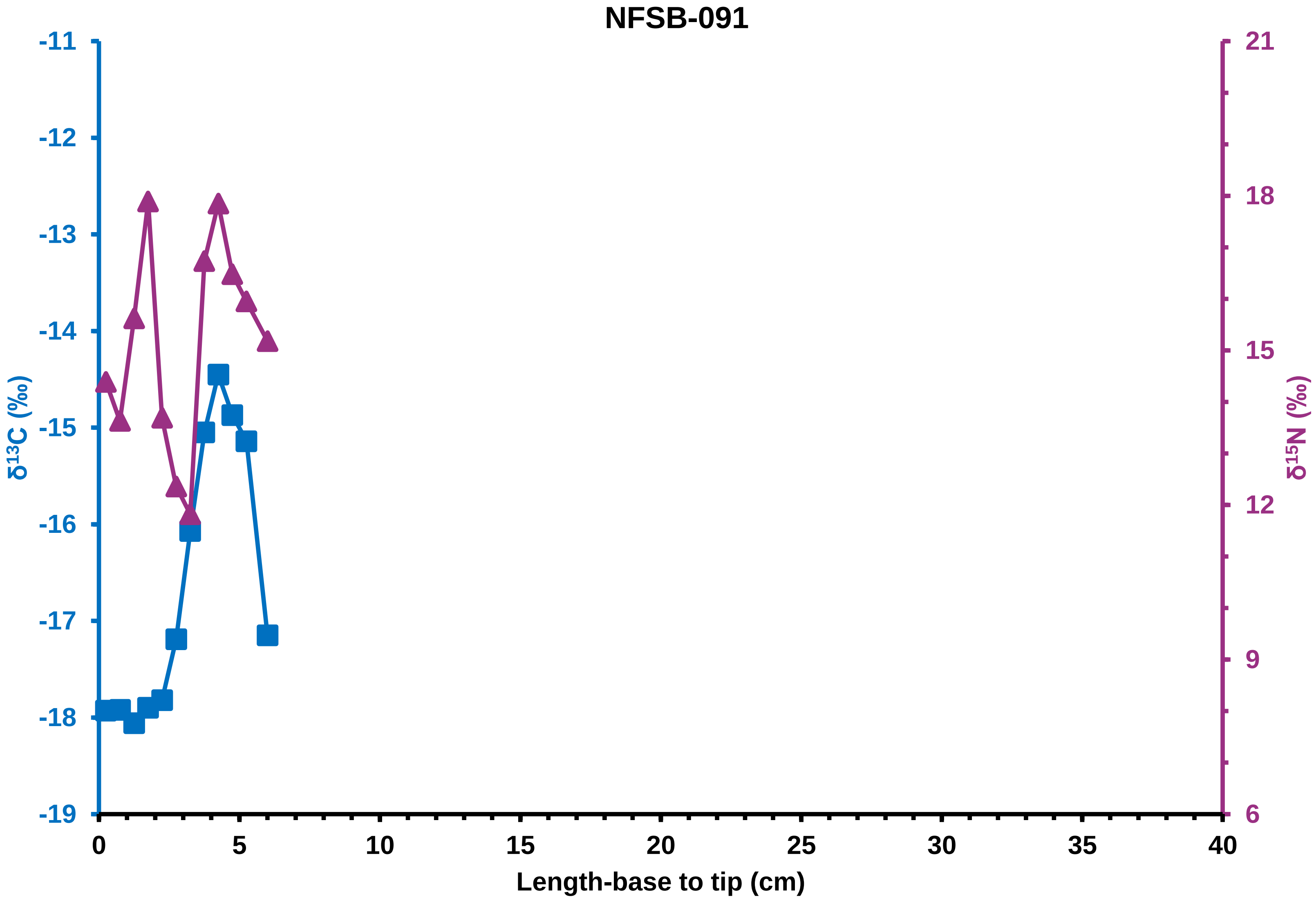


Figure A-13: Northern fur seal vibrissa representing approximately two years growth.

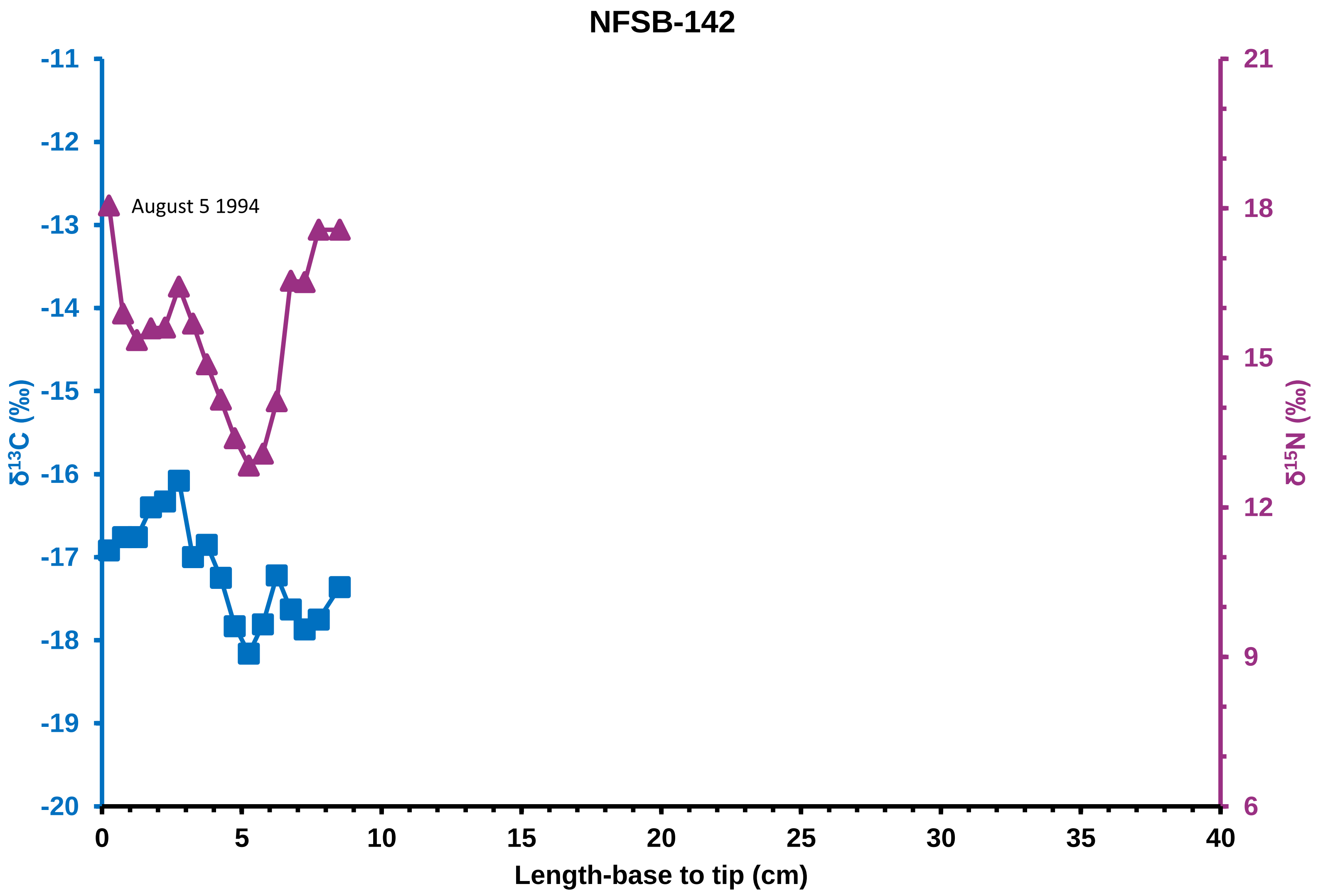


Figure A-14: Northern fur seal vibrissa showing post-weaning pattern followed by U-shape, representing approximately three years growth.

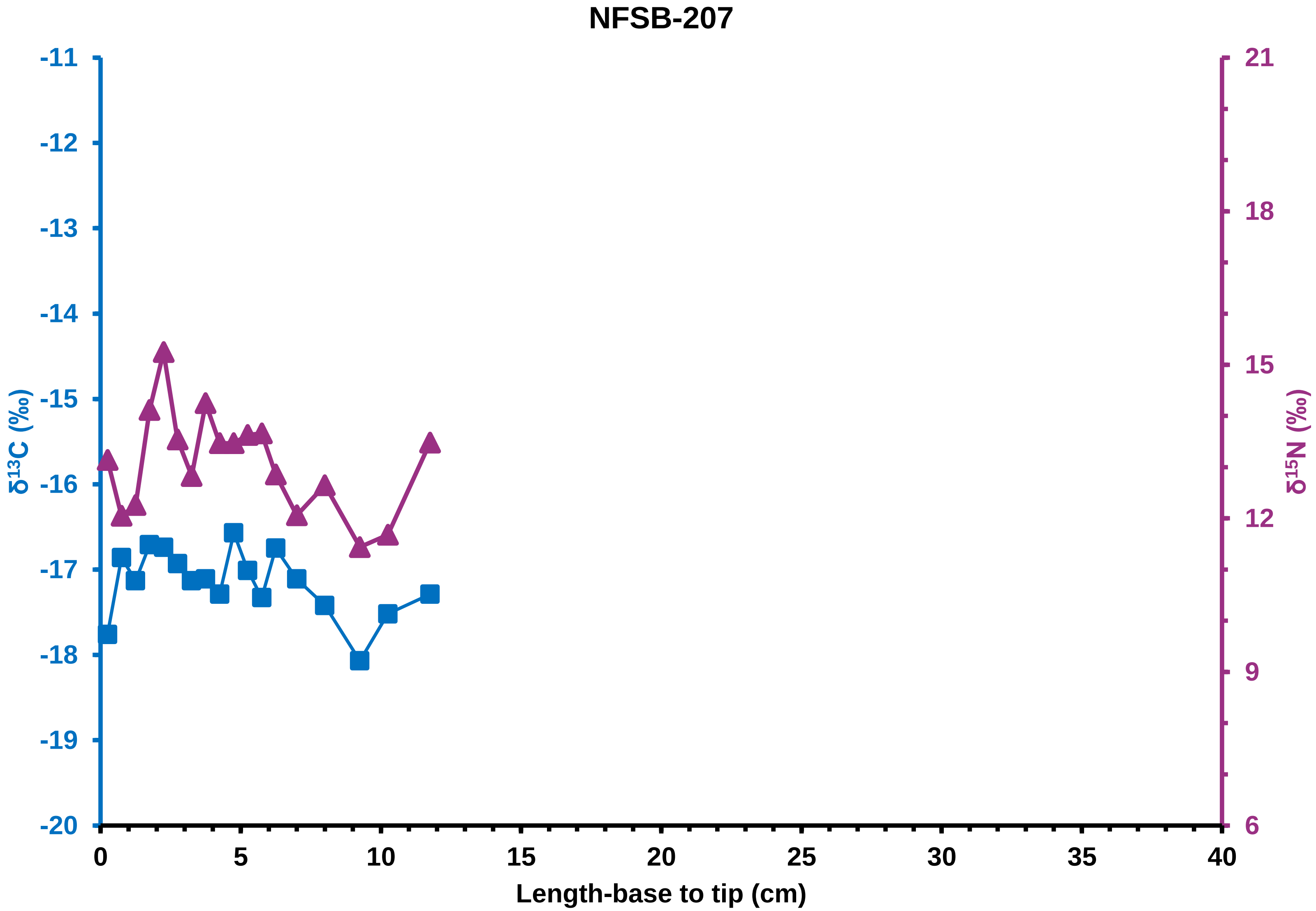


Figure A-15: Northern fur seal vibrissa representing approximately three years growth.

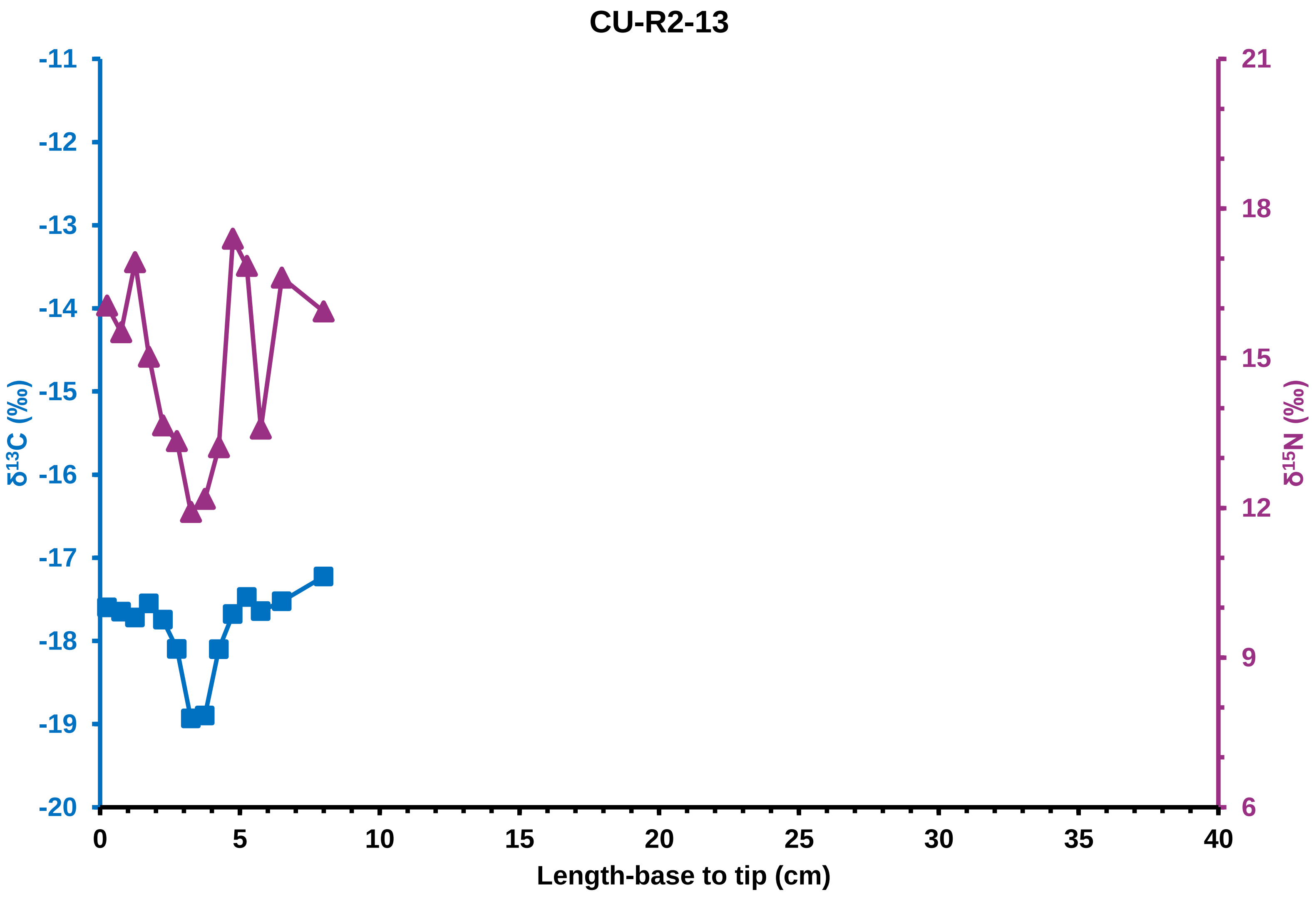


Figure A-16: Northern fur seal vibrissa representing approximately three years growth with covarying depletion one year from base.

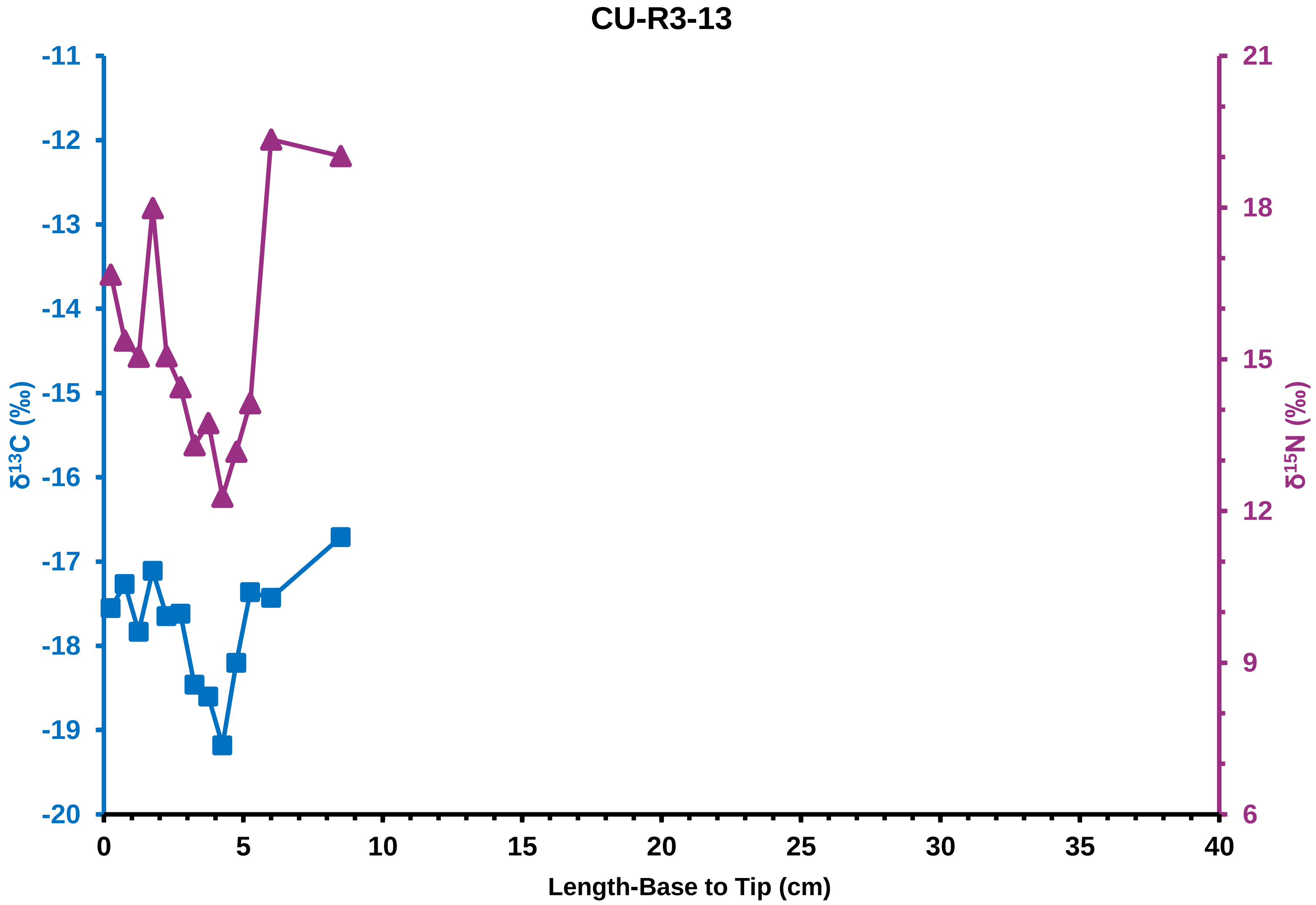


Figure A-17: Northern fur seal vibrissa representing approximately three years growth with covarying depletion one year from base.

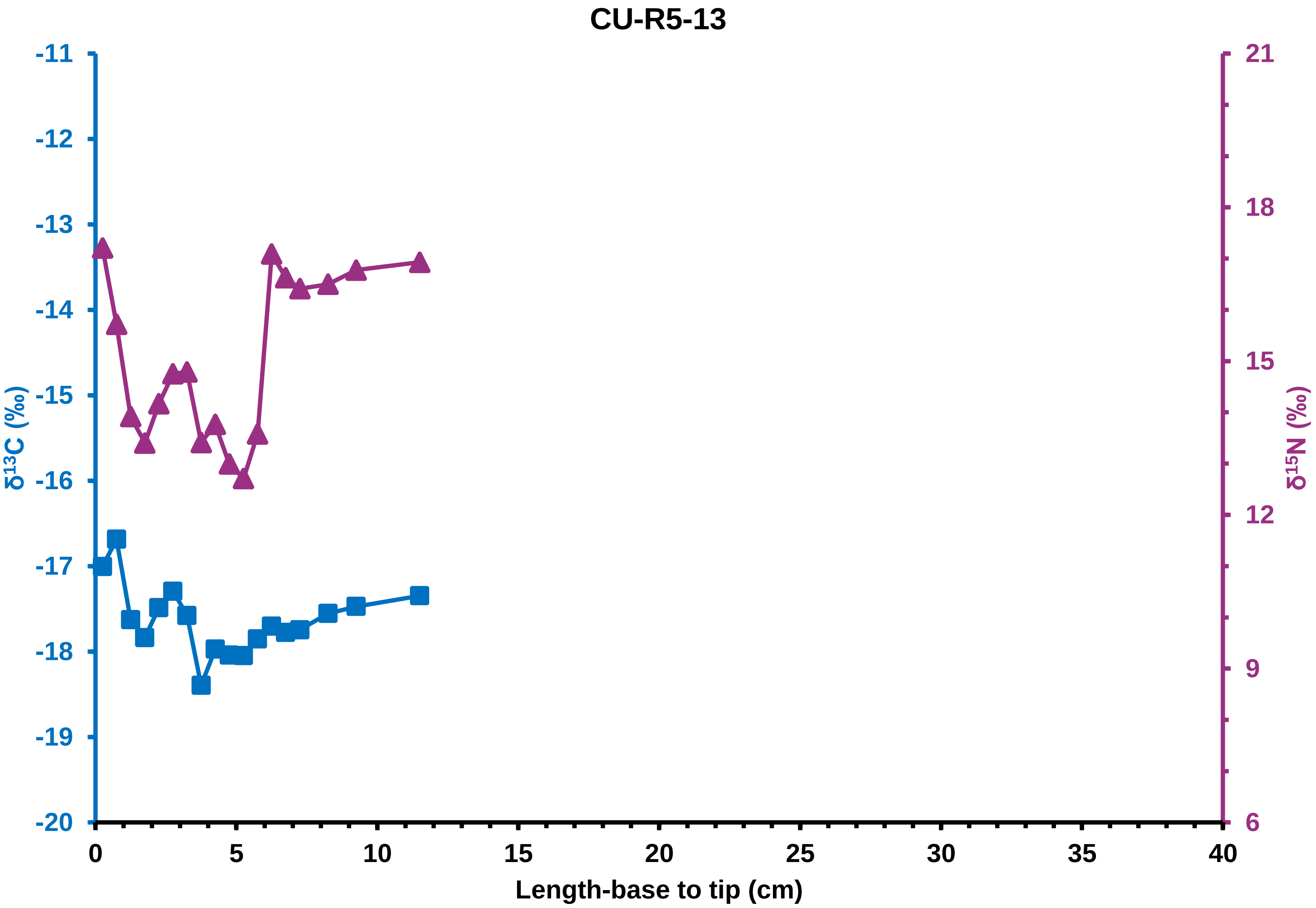


Figure A-18: Northern fur seal vibrissa representing approximately four years growth.

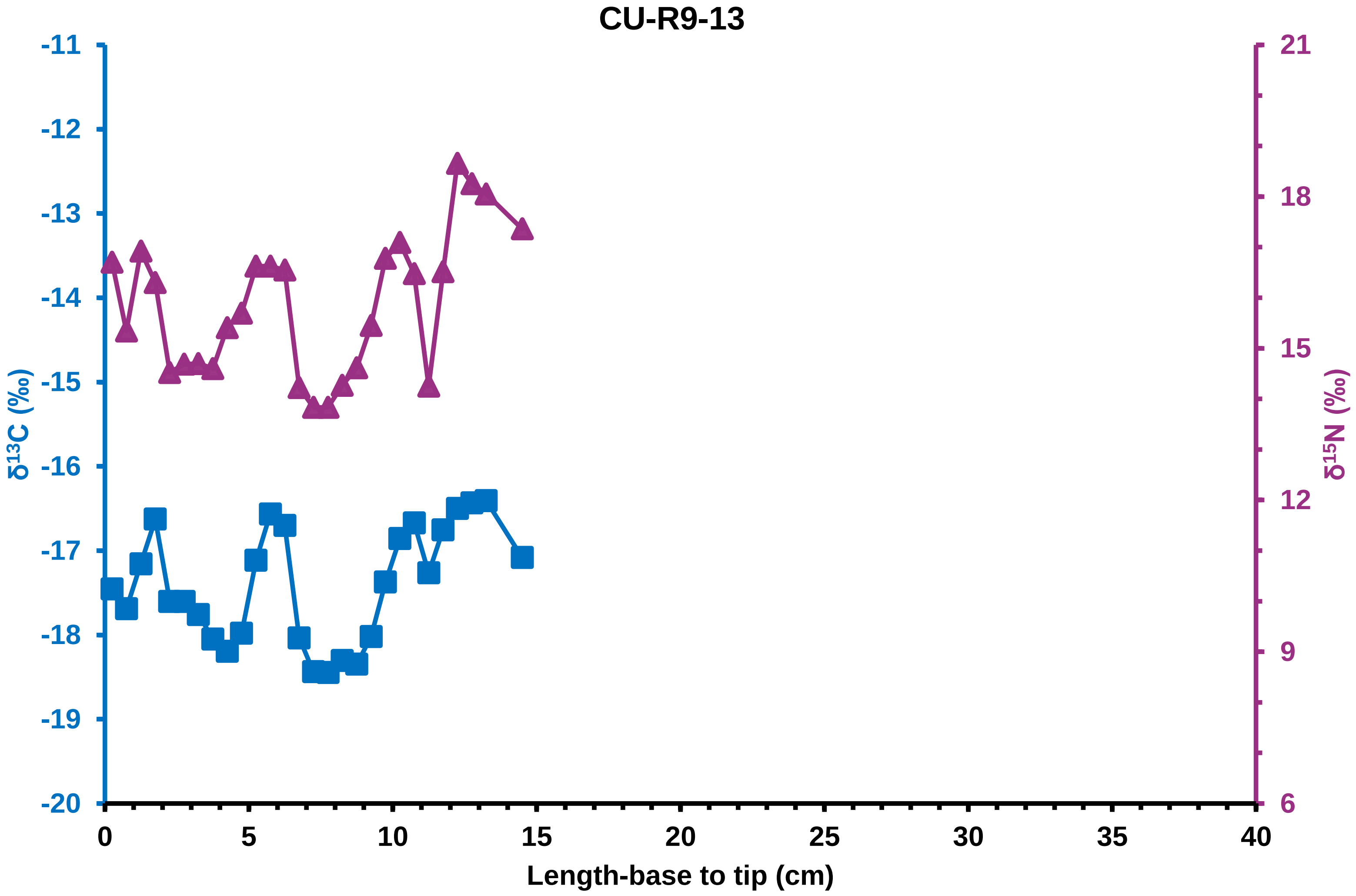


Figure A-19: Northern fur seal vibrissa representing approximately four years growth.

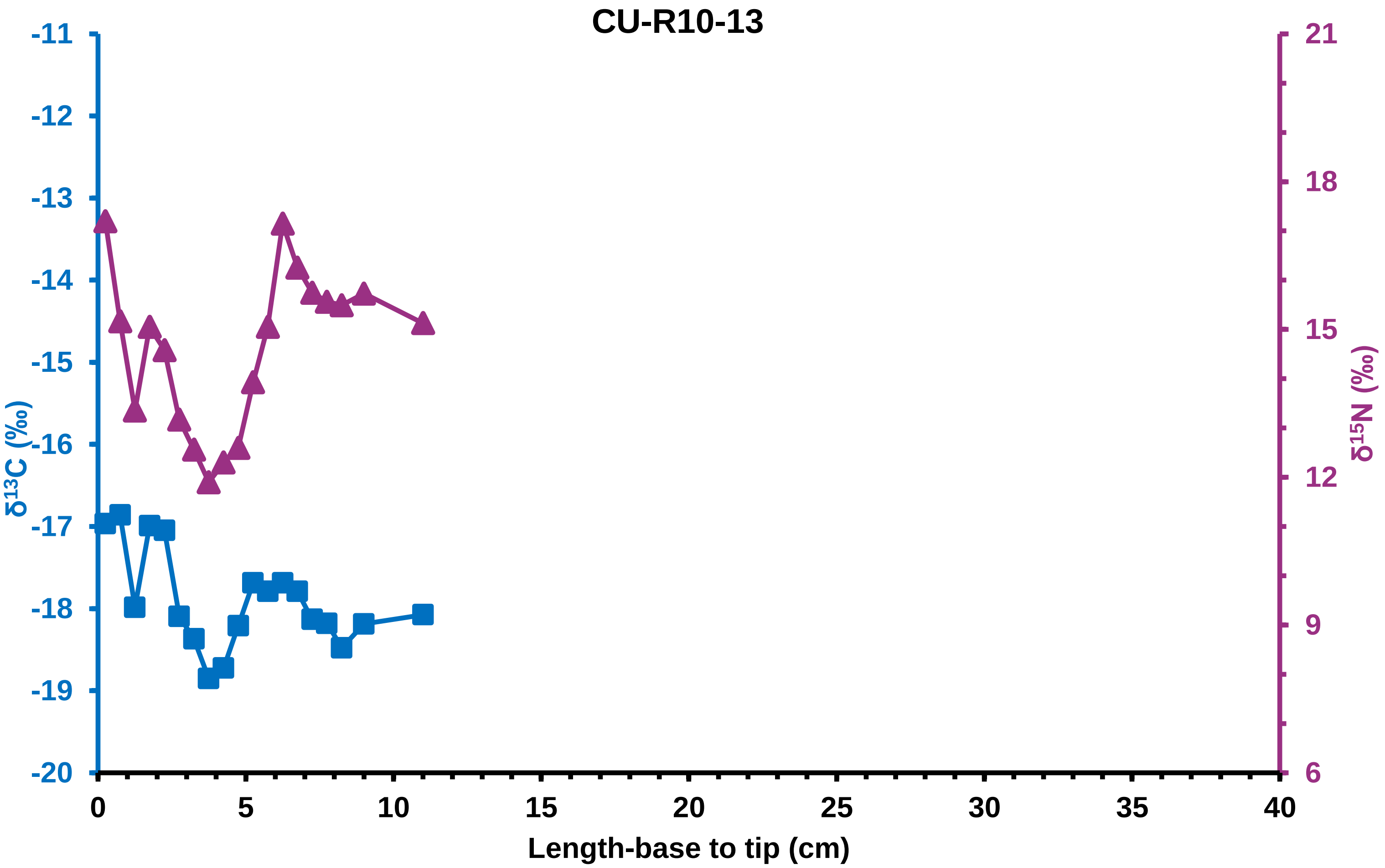


Figure A-20: Northern fur seal vibrissa representing approximately four years growth with covarying depletion one year from the base.

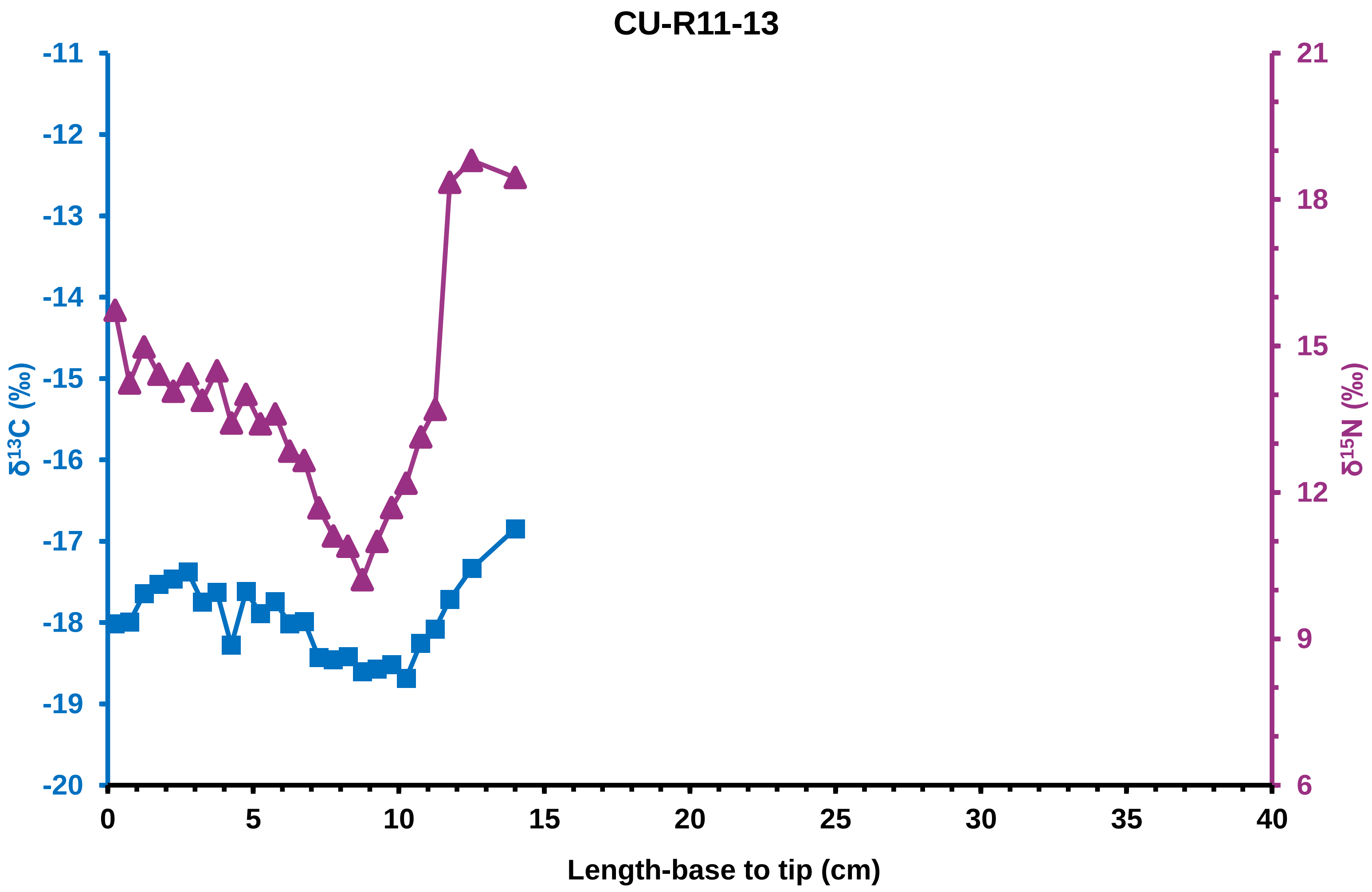


Figure A-21: Northern fur seal vibrissa representing approximately four years growth with U-shape at the tip.

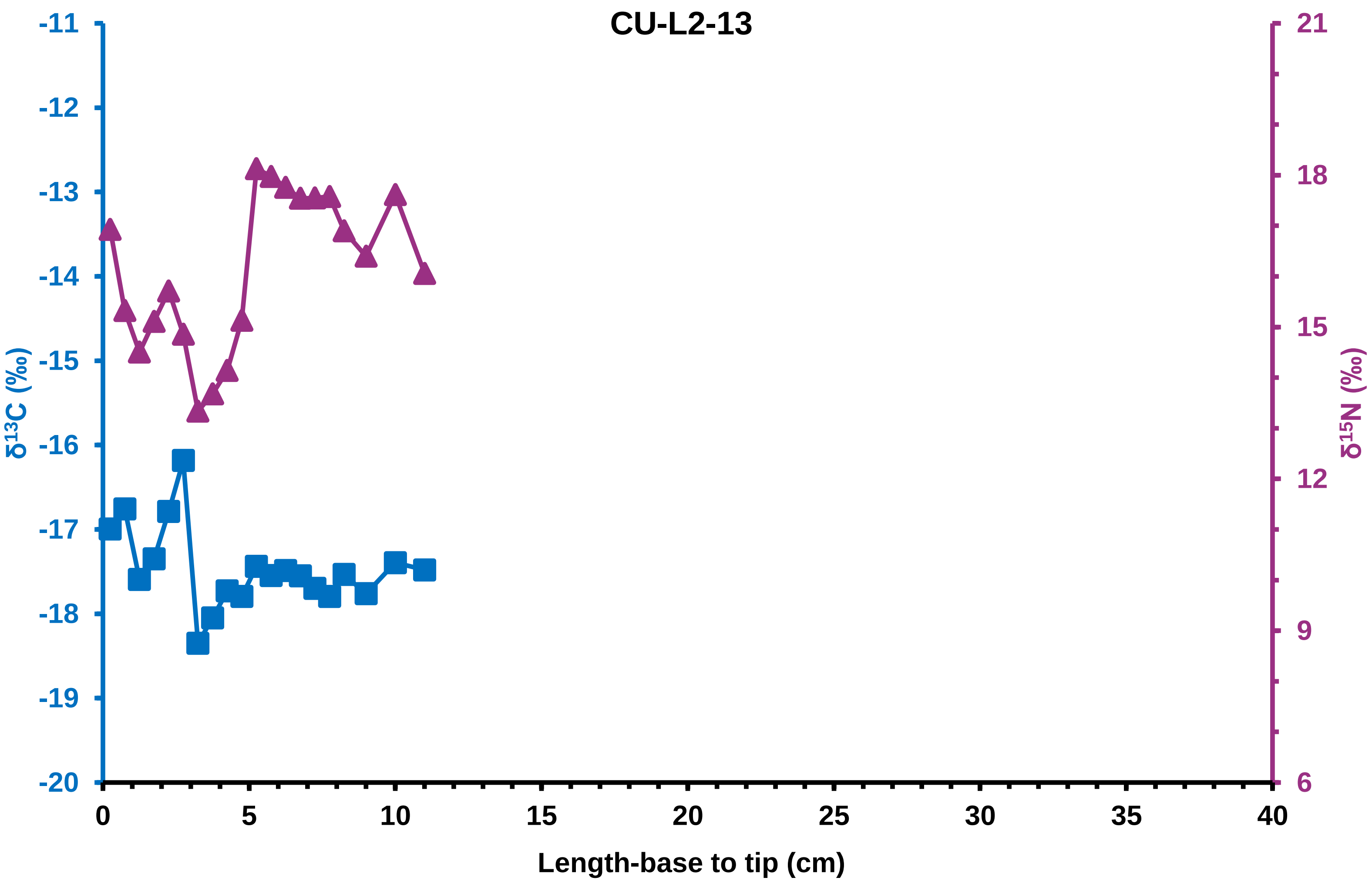


Figure A-22: Northern fur seal vibrissa representing approximately three years growth.

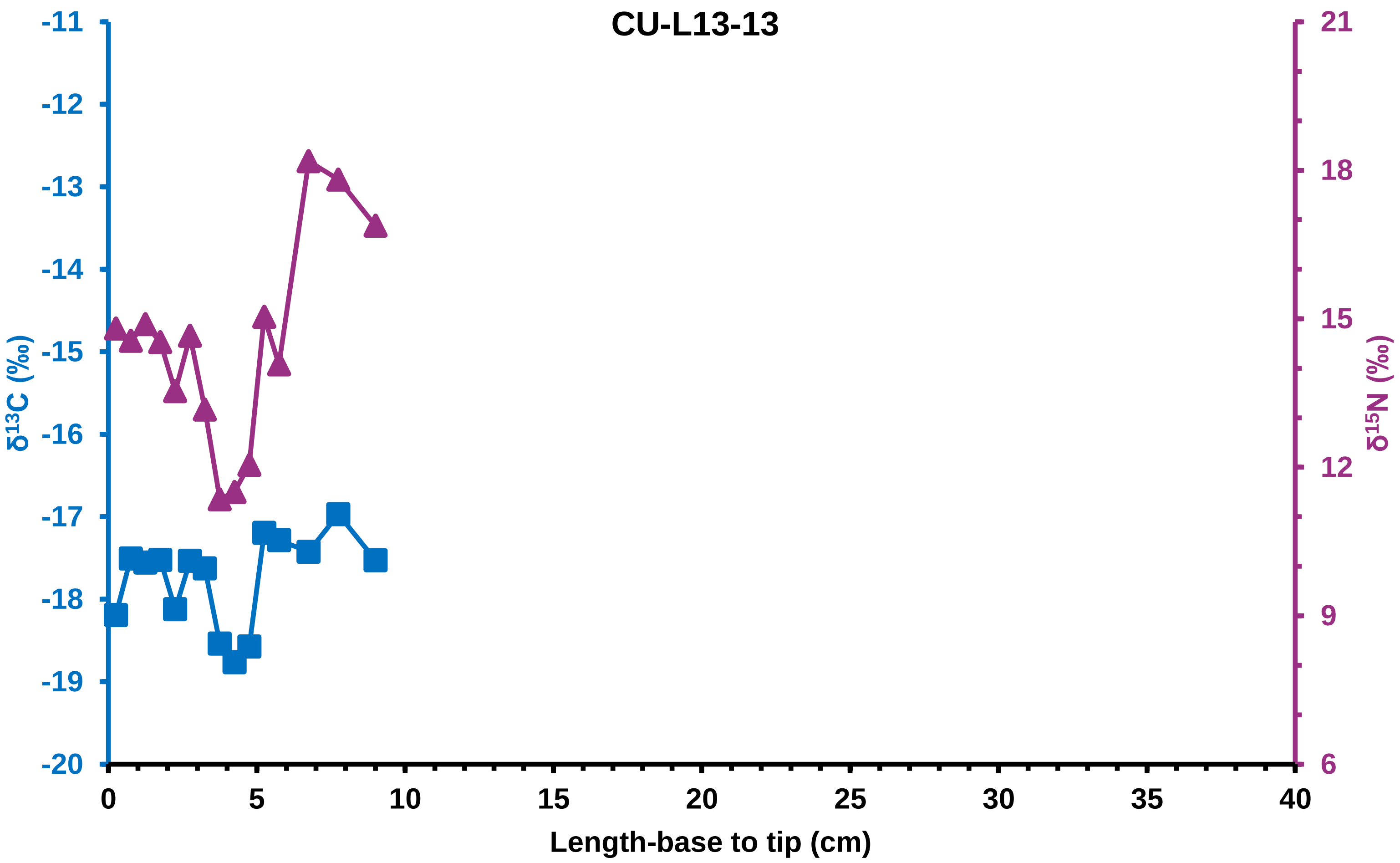


Figure A-23: Northern fur seal vibrissa representing approximately three years growth with covarying depletion approximately one year from the base.

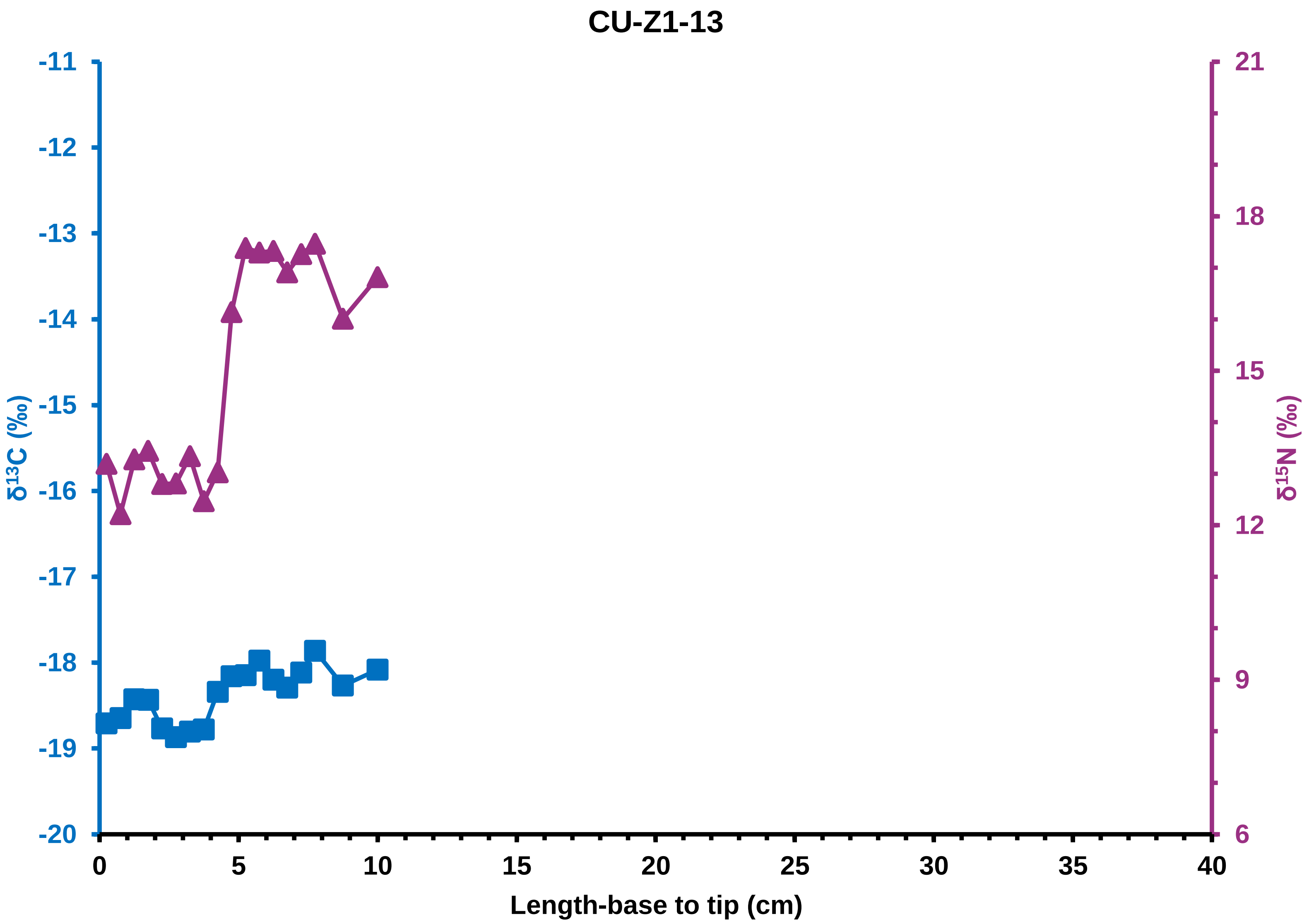


Figure A-24: Northern fur seal vibrissa representing approximately three years growth.

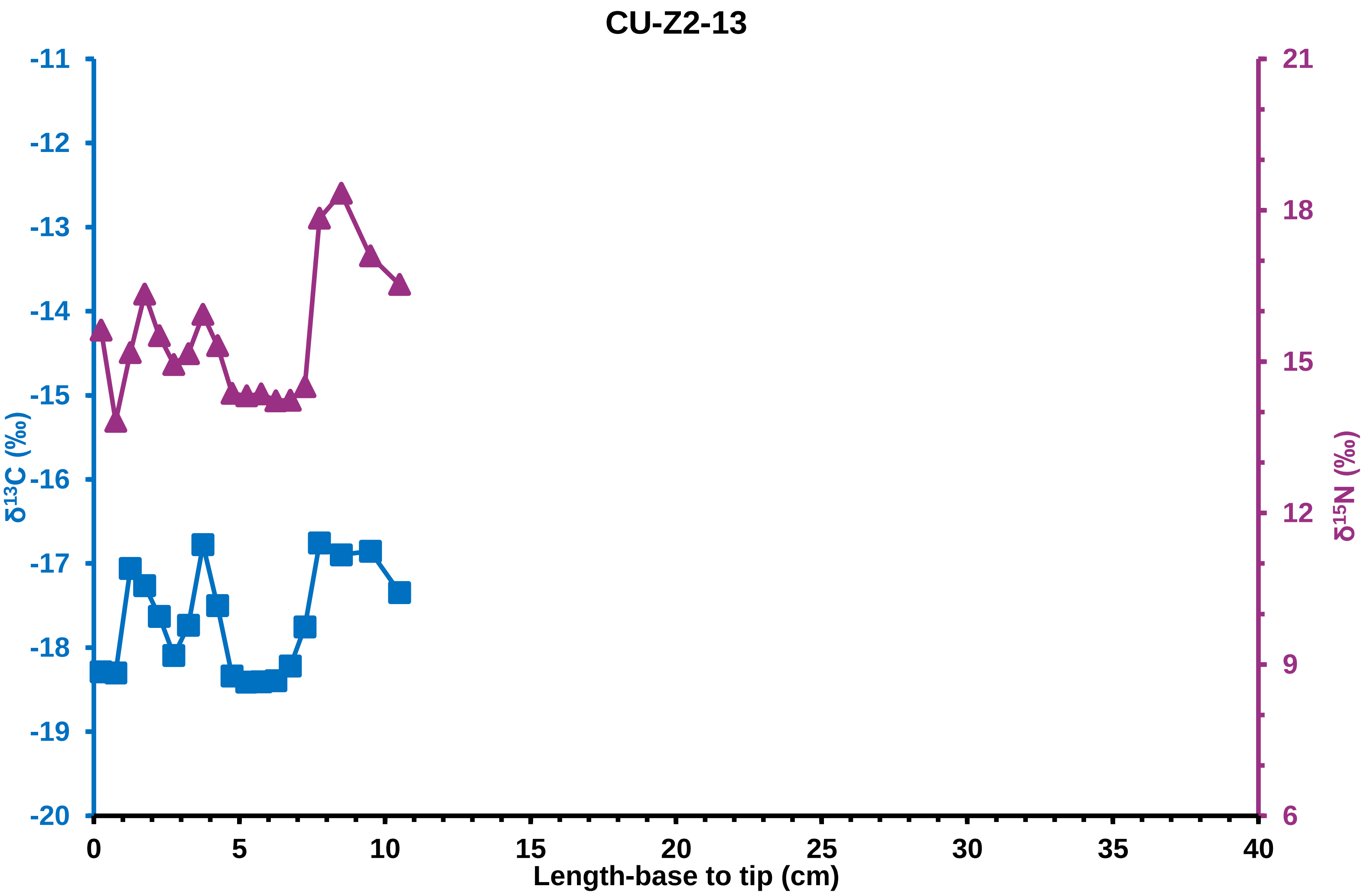


Figure A-25: Northern fur seal vibrissa representing approximately three years growth

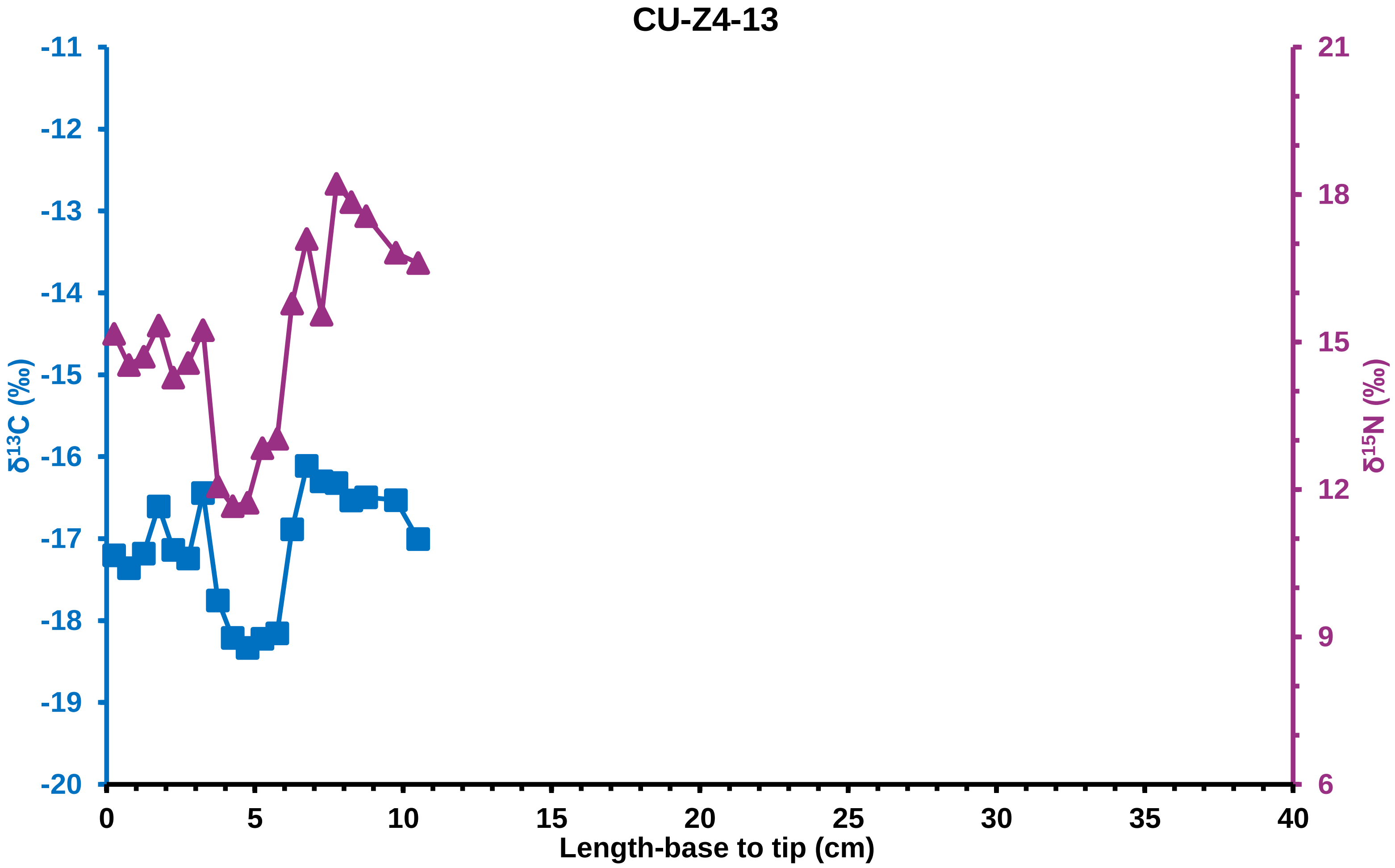


Figure A-26: Northern fur seal vibrissa representing approximately four years growth with covarying depletion one year from the base.

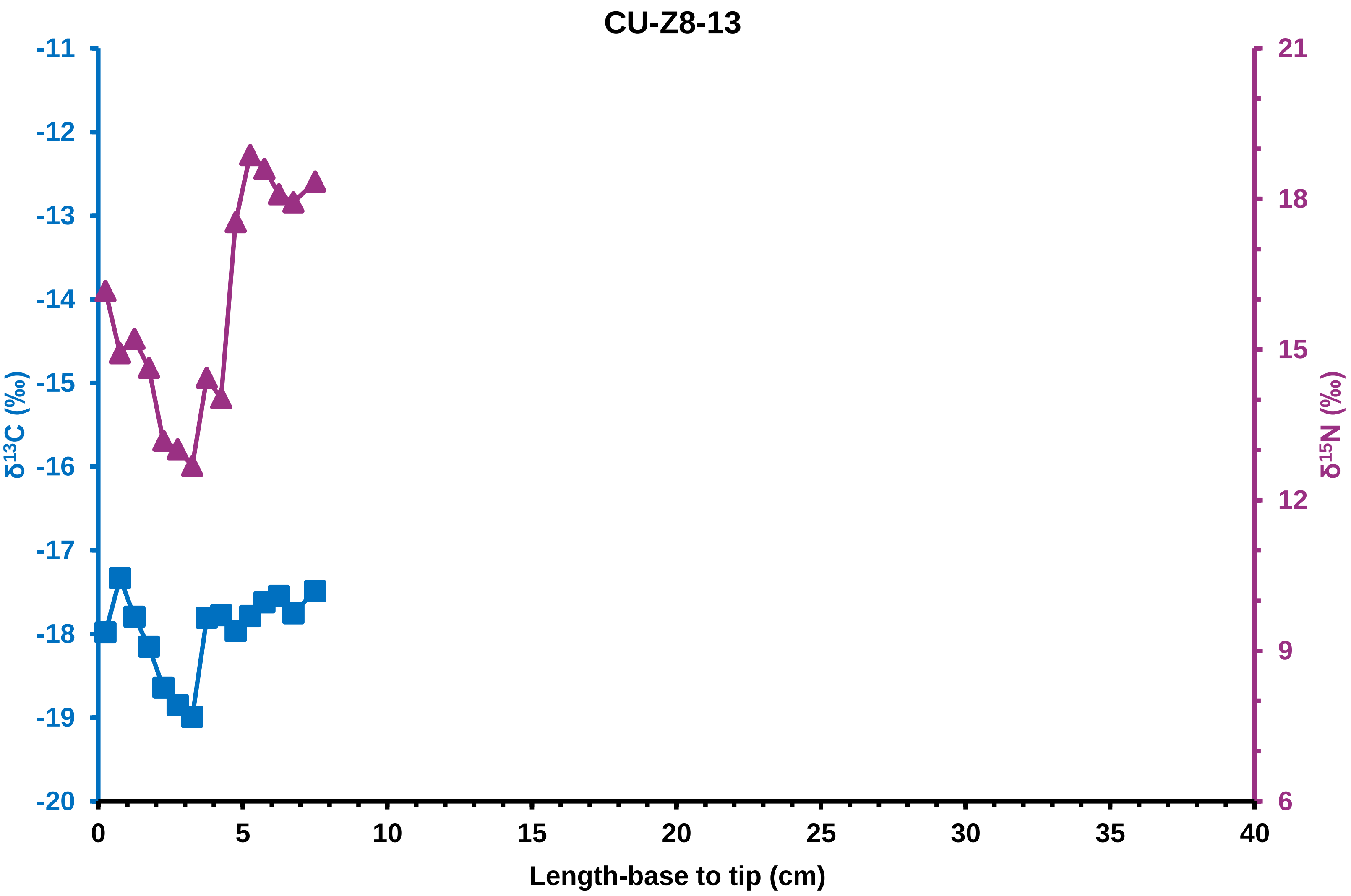


Figure A-27: Northern fur seal vibrissa representing approximately three years growth with covarying depletion one year from the base.

Appendix B

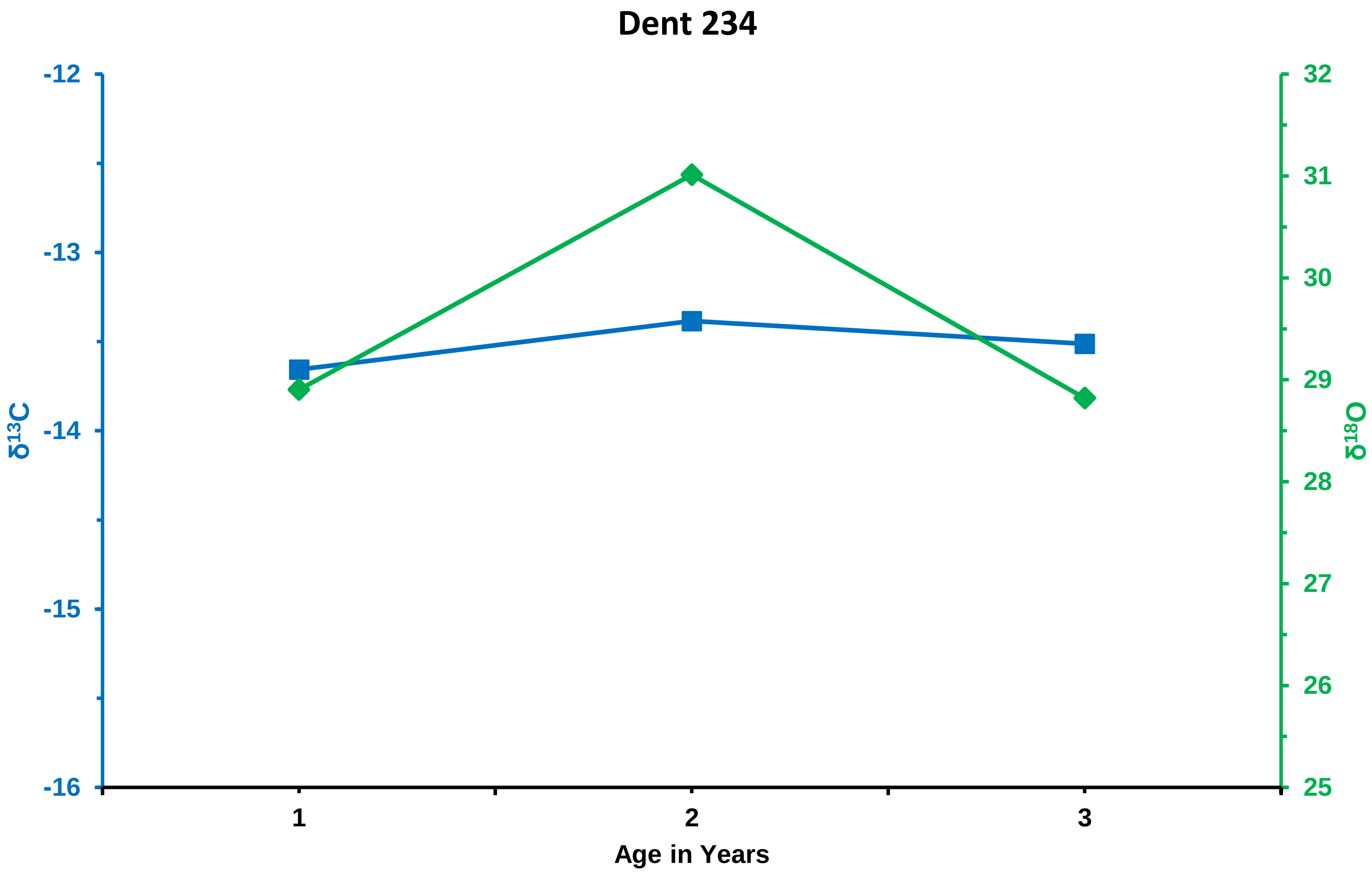


Figure B-1: Northern fur seal canine tooth showing enrichment of δ^{18}O at year two.

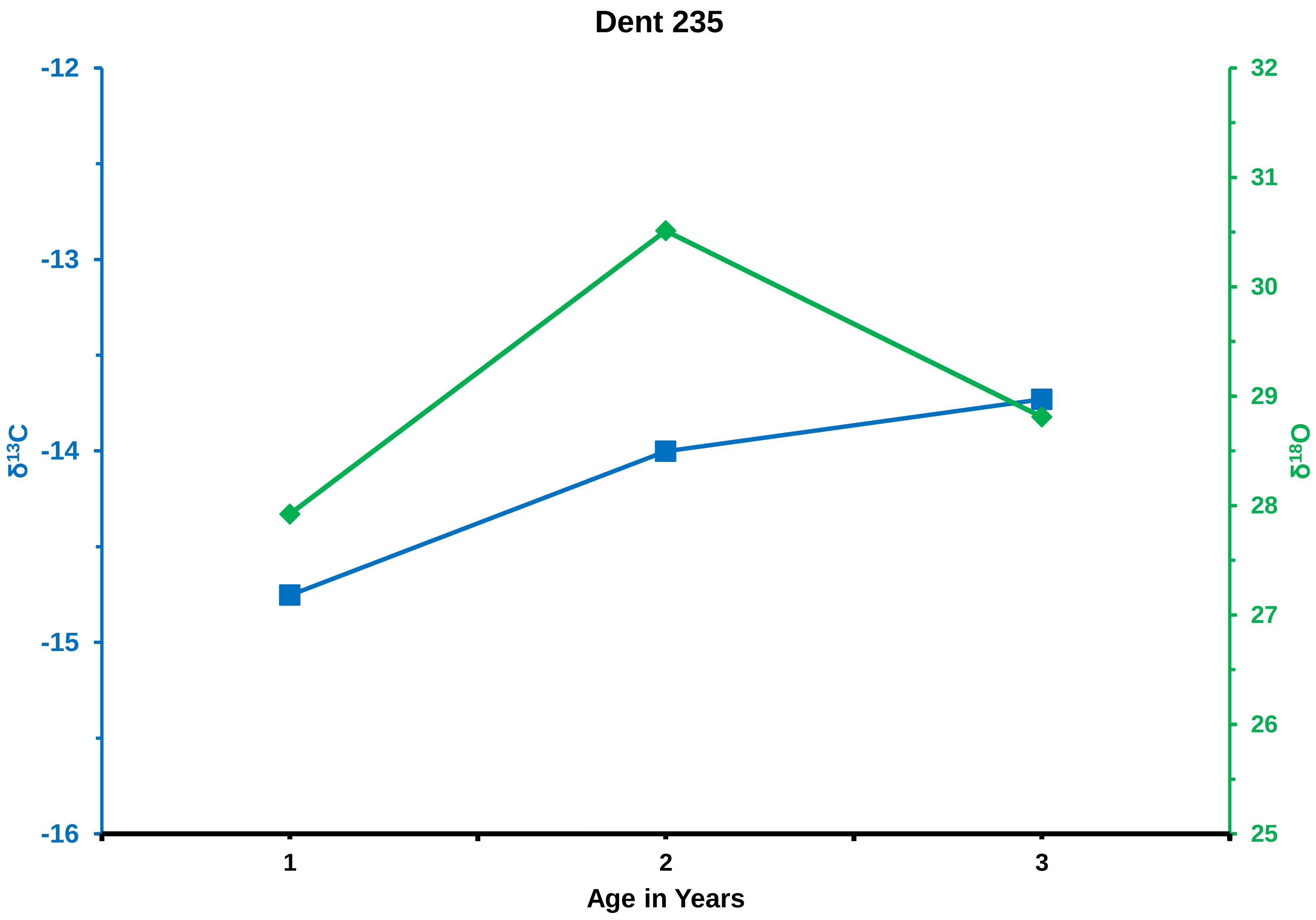


Figure B-2: Northern fur seal canine tooth showing enrichment of $\delta^{18}O$ at year two.

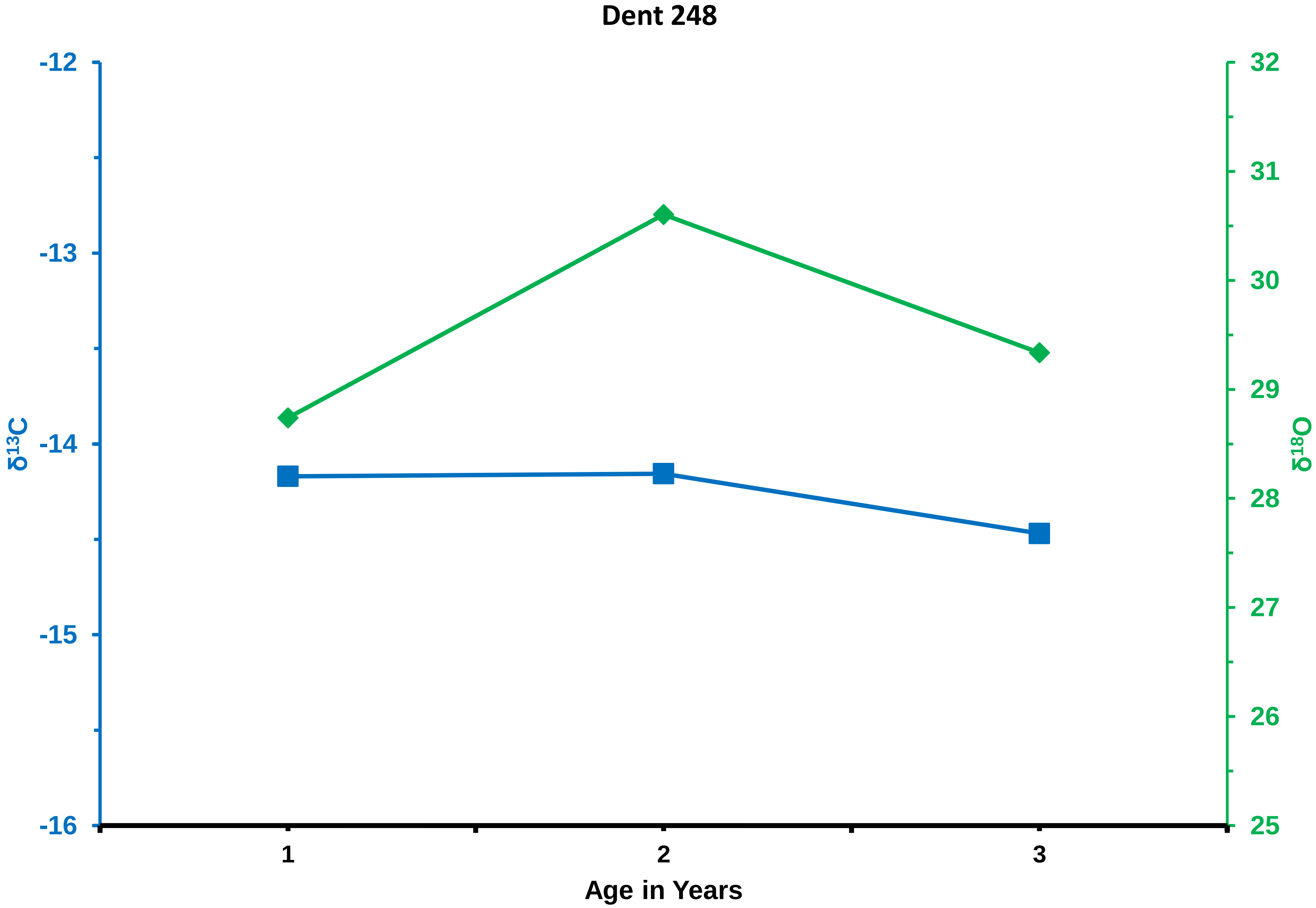
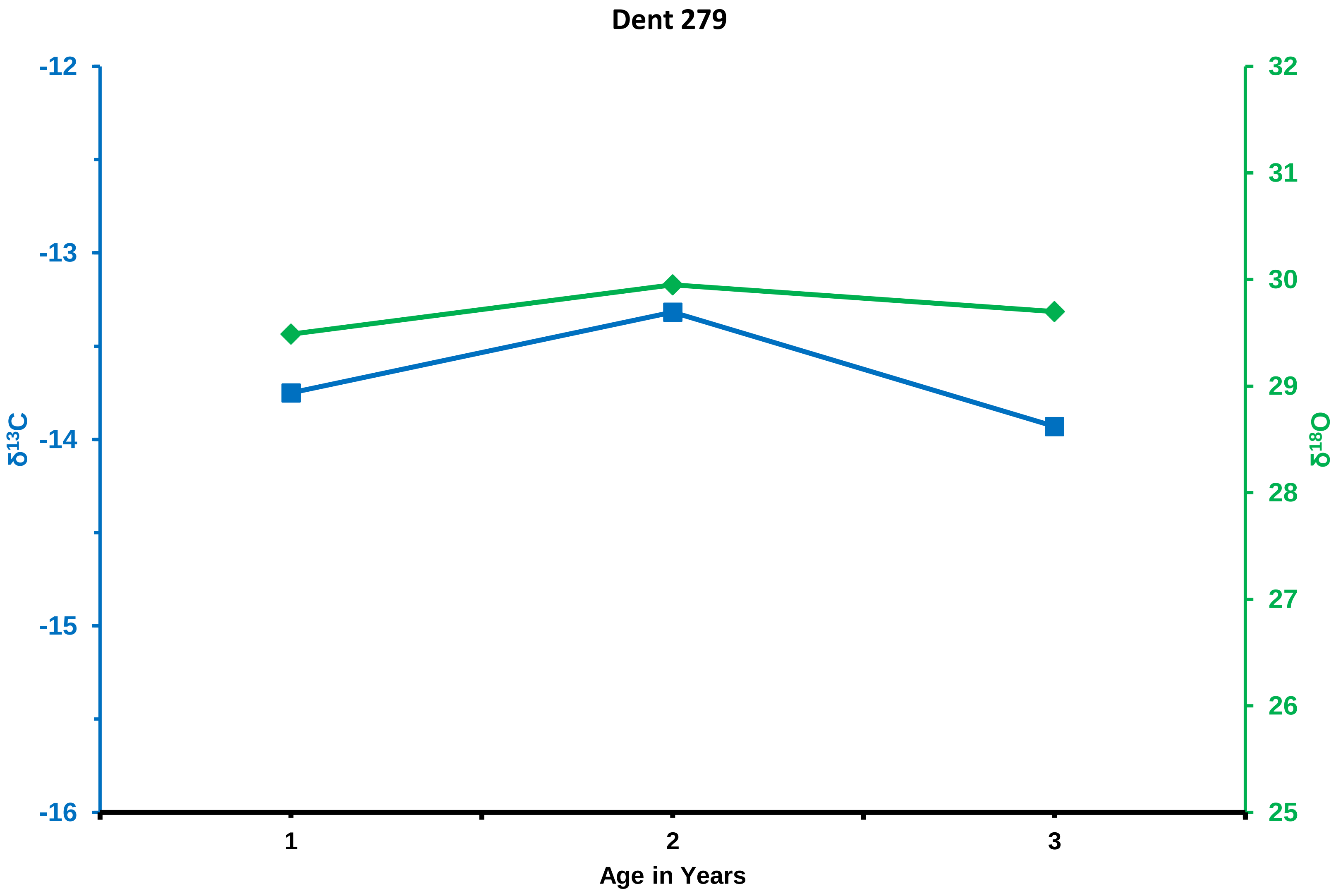


Figure B-3: Northern fur seal canine tooth showing enrichment of $\delta^{18}O$ at year two.



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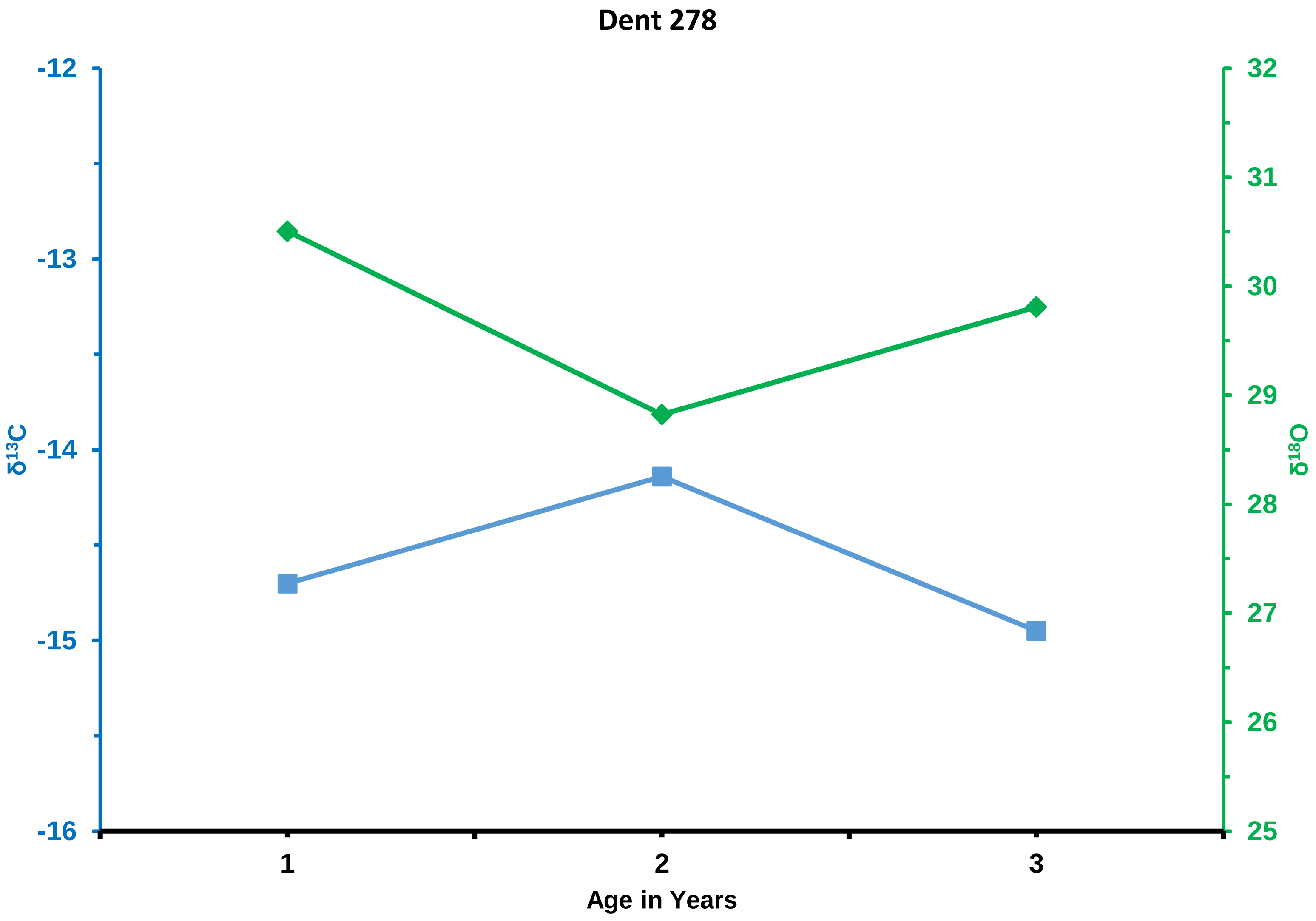

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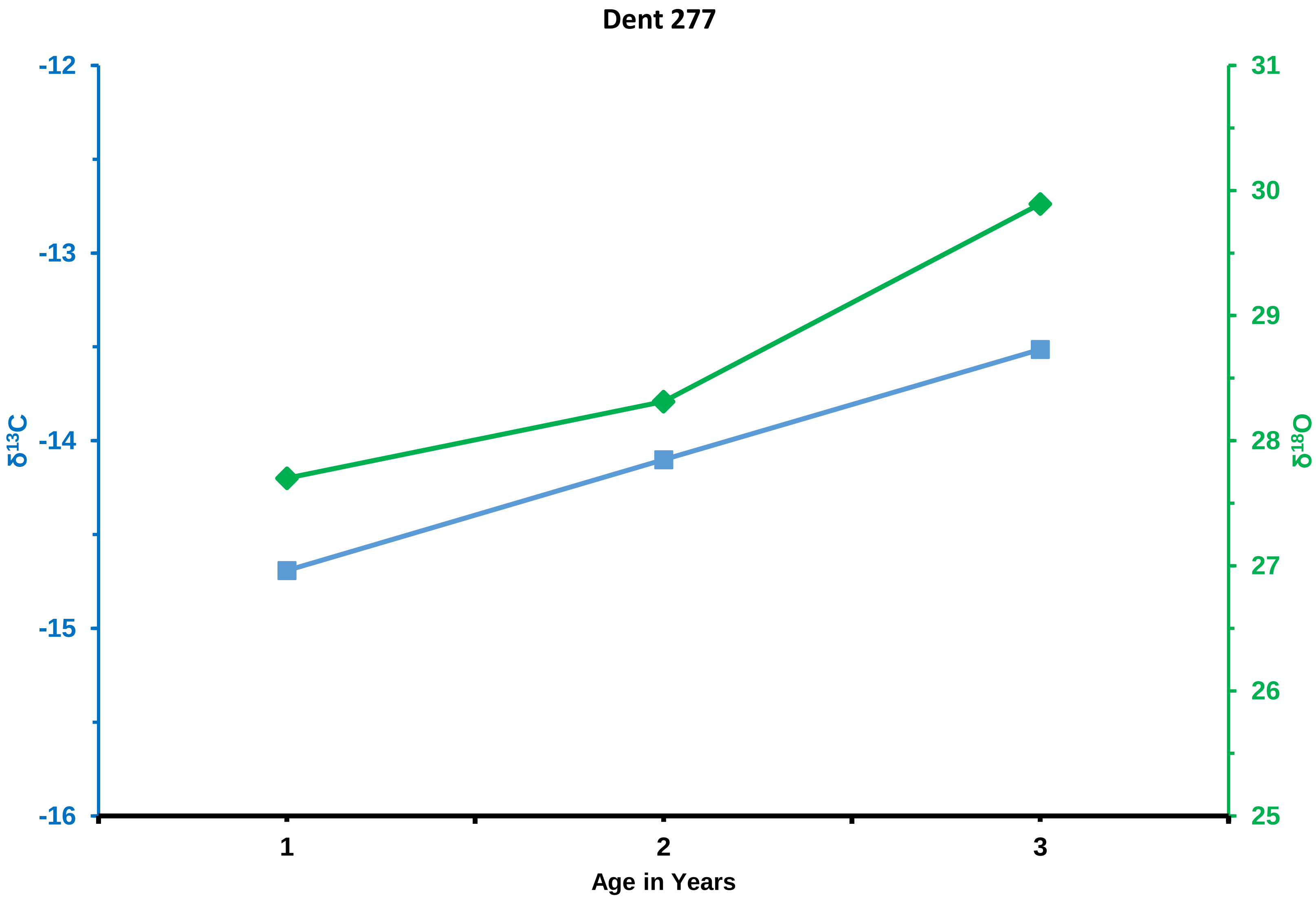

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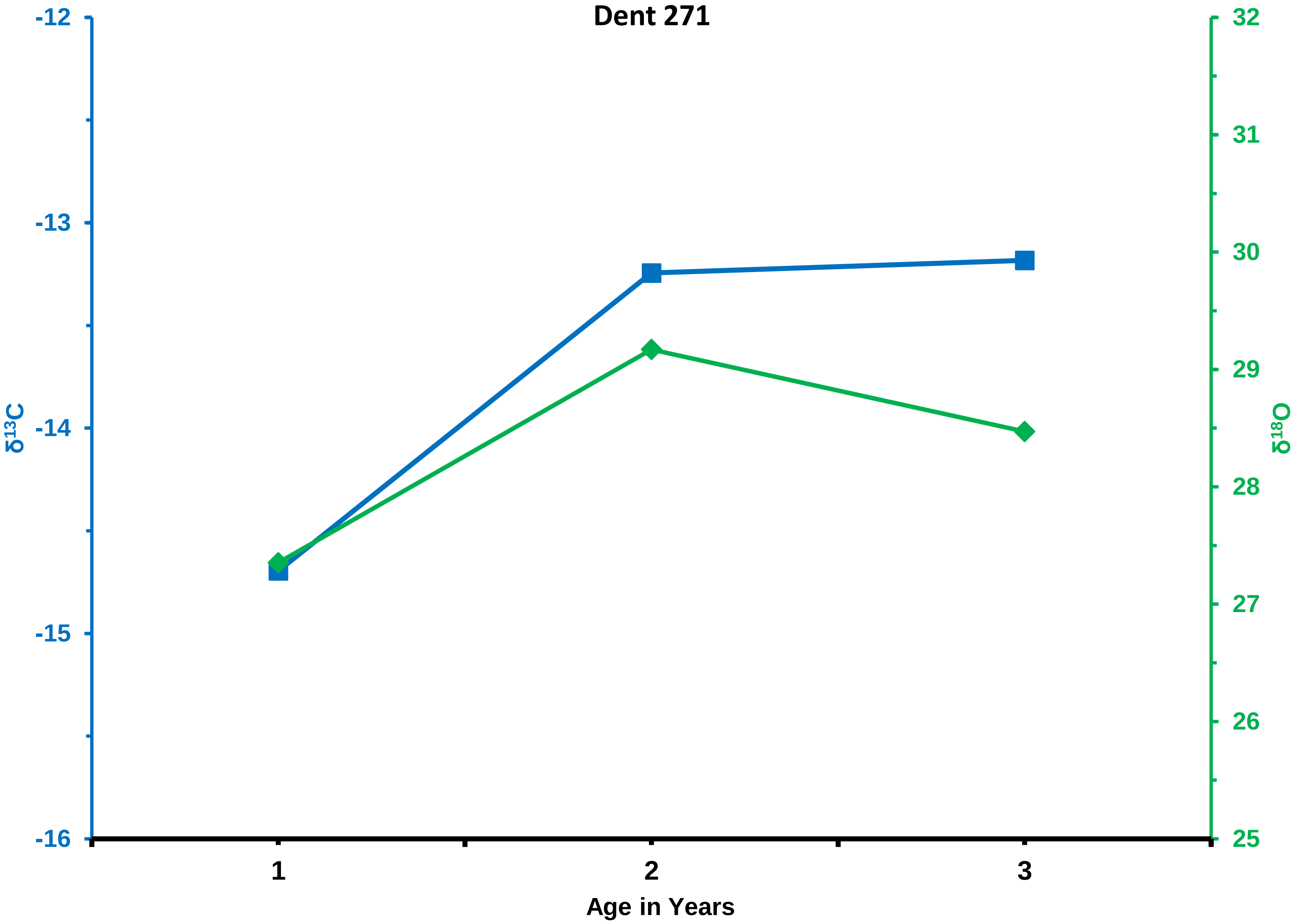

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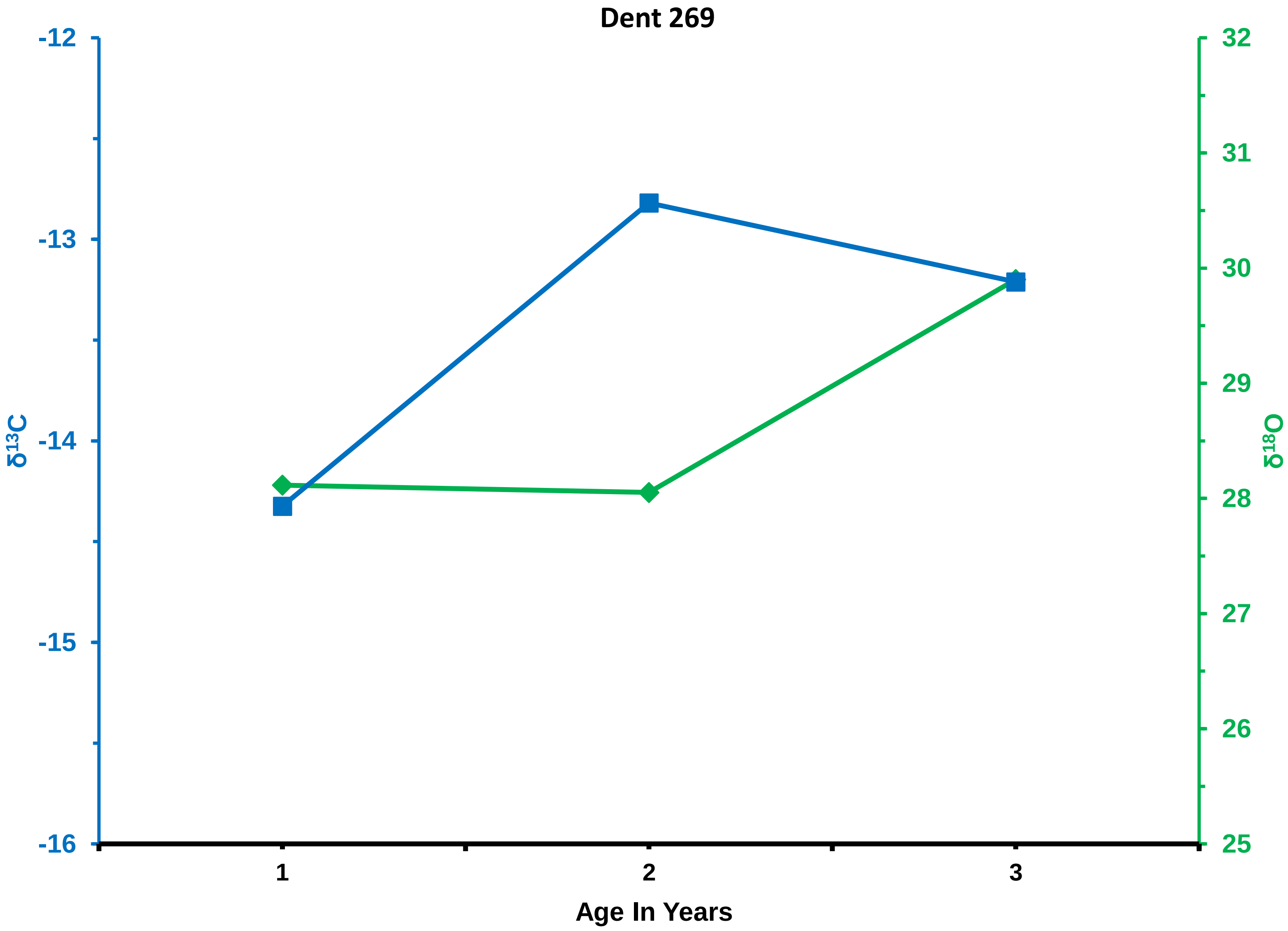

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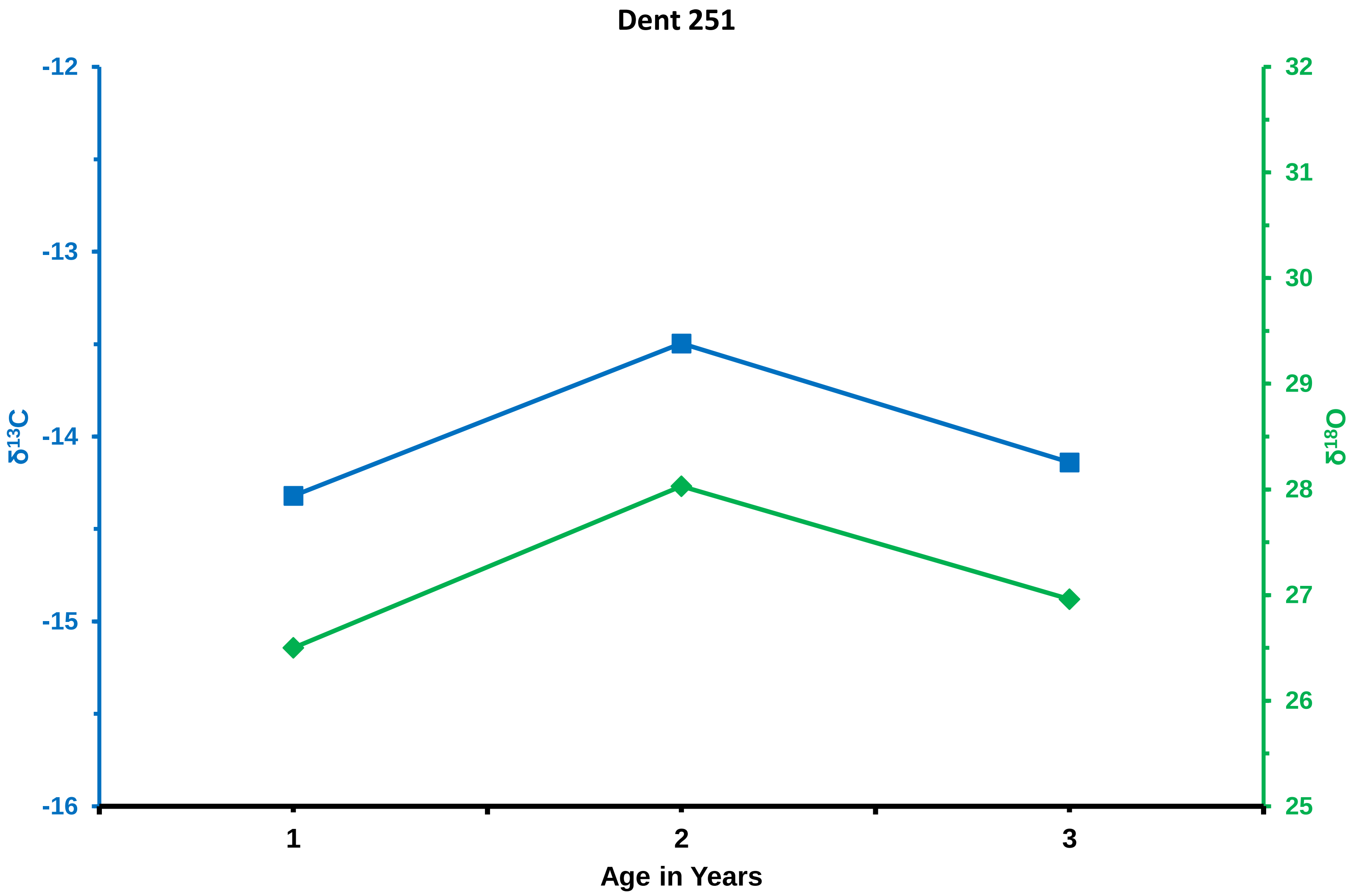


Figure B-9: Northern fur seal canine tooth showing enrichment of $\delta^{18}O$ at year two.

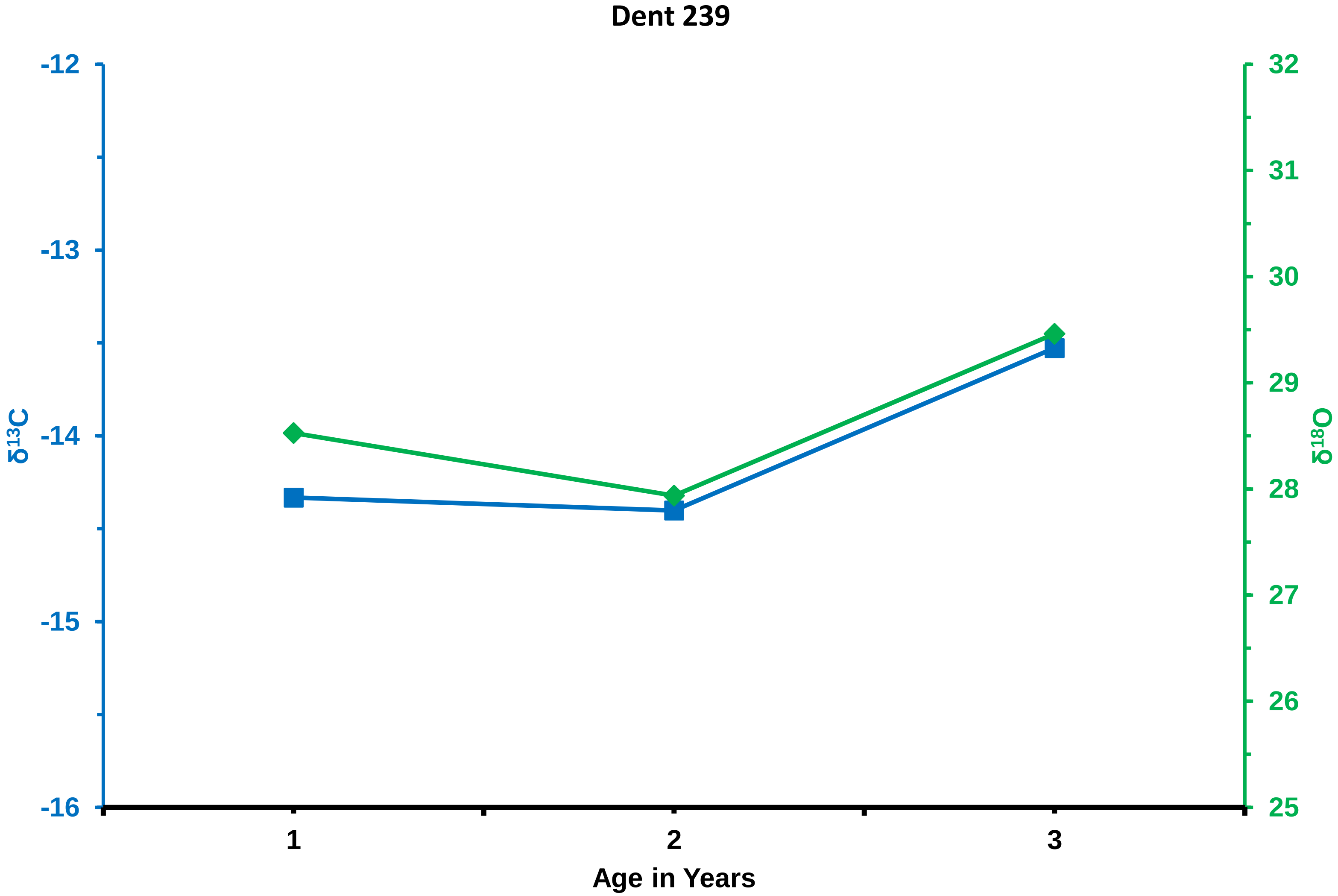


Figure B-10: Northern fur seal canine tooth showing enrichment of $\delta^{18}O$ at year two.

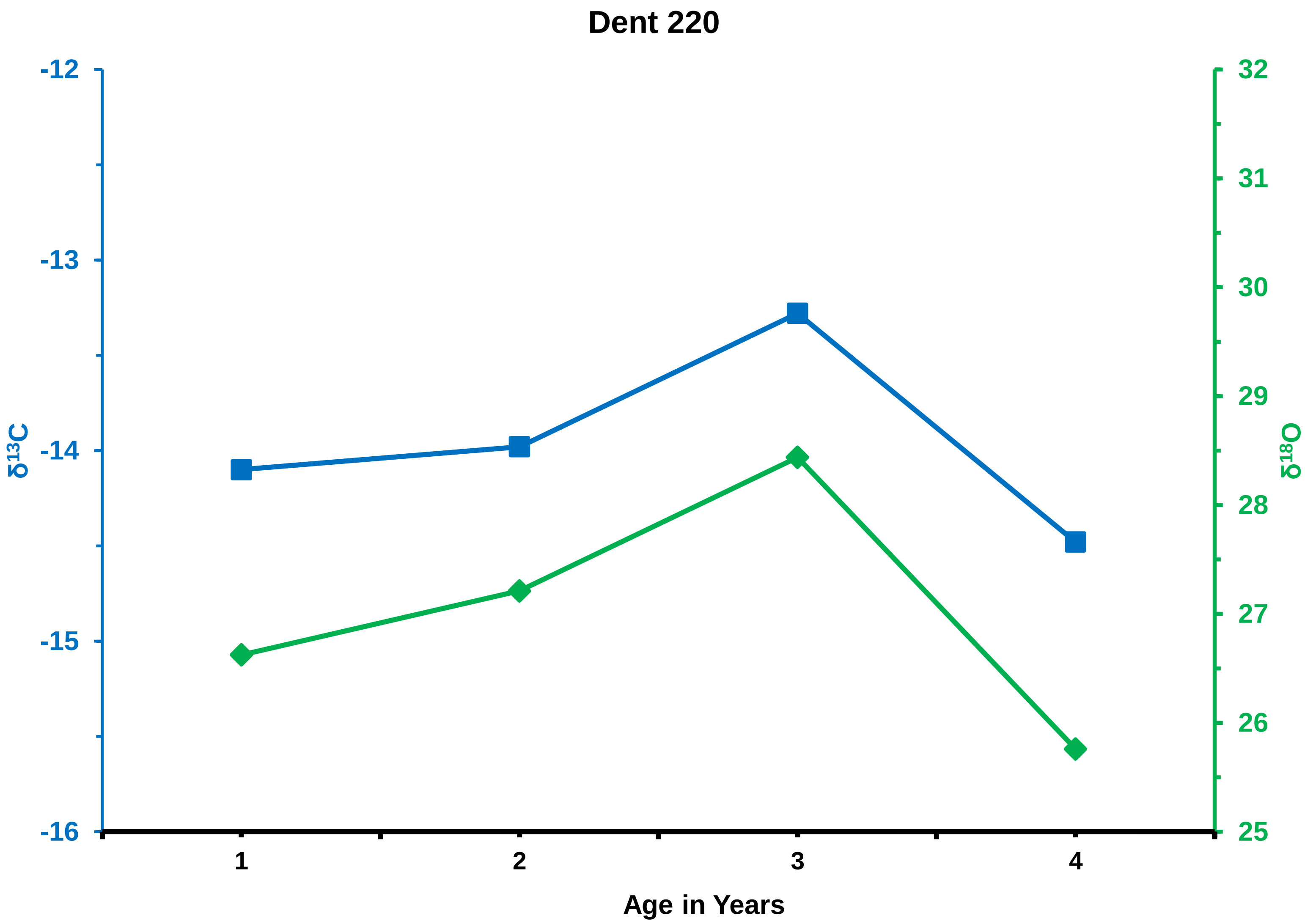
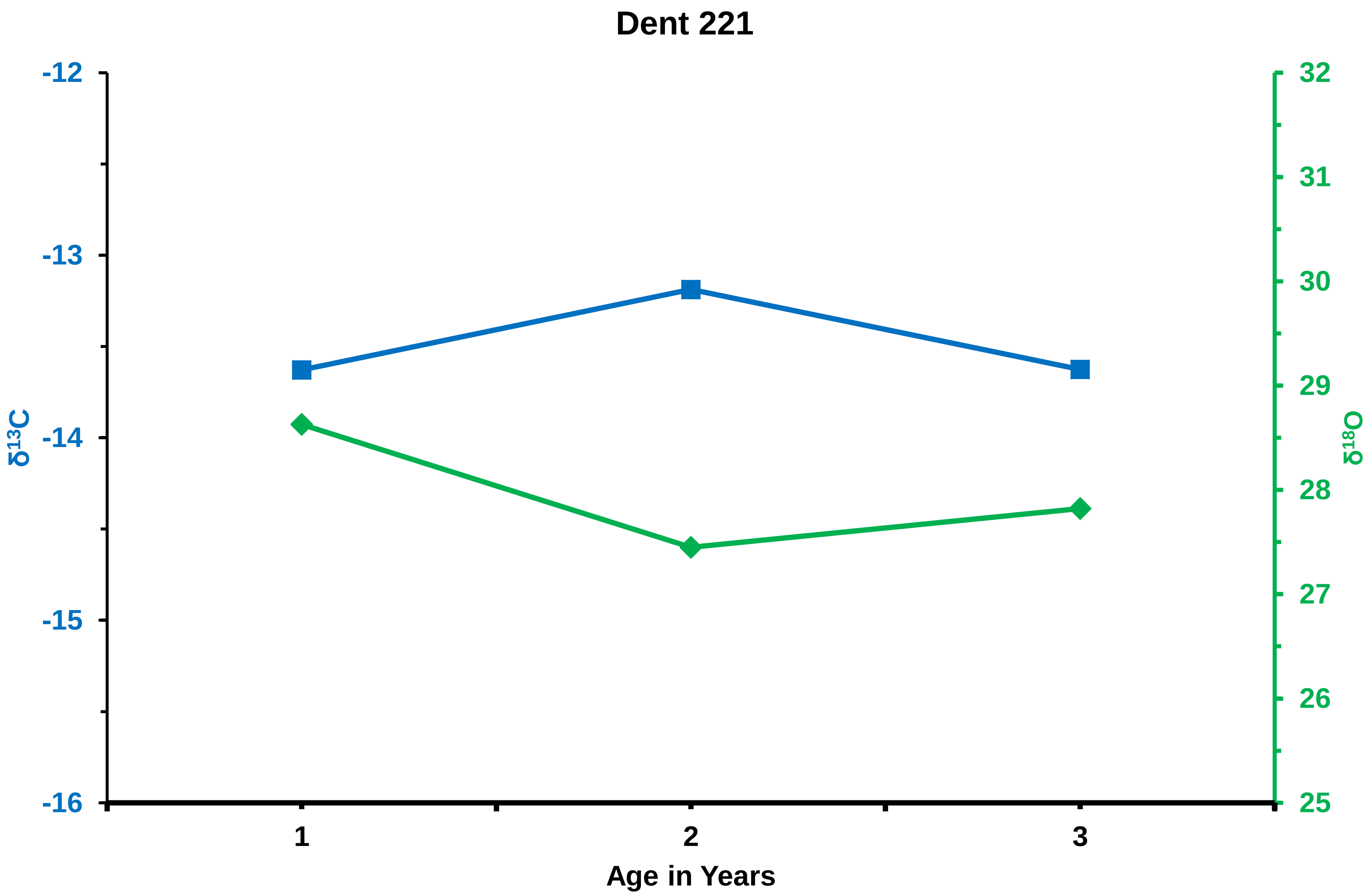


Figure B-11: Northern fur seal canine tooth showing enrichment of $\delta^{18}O$ at year two.



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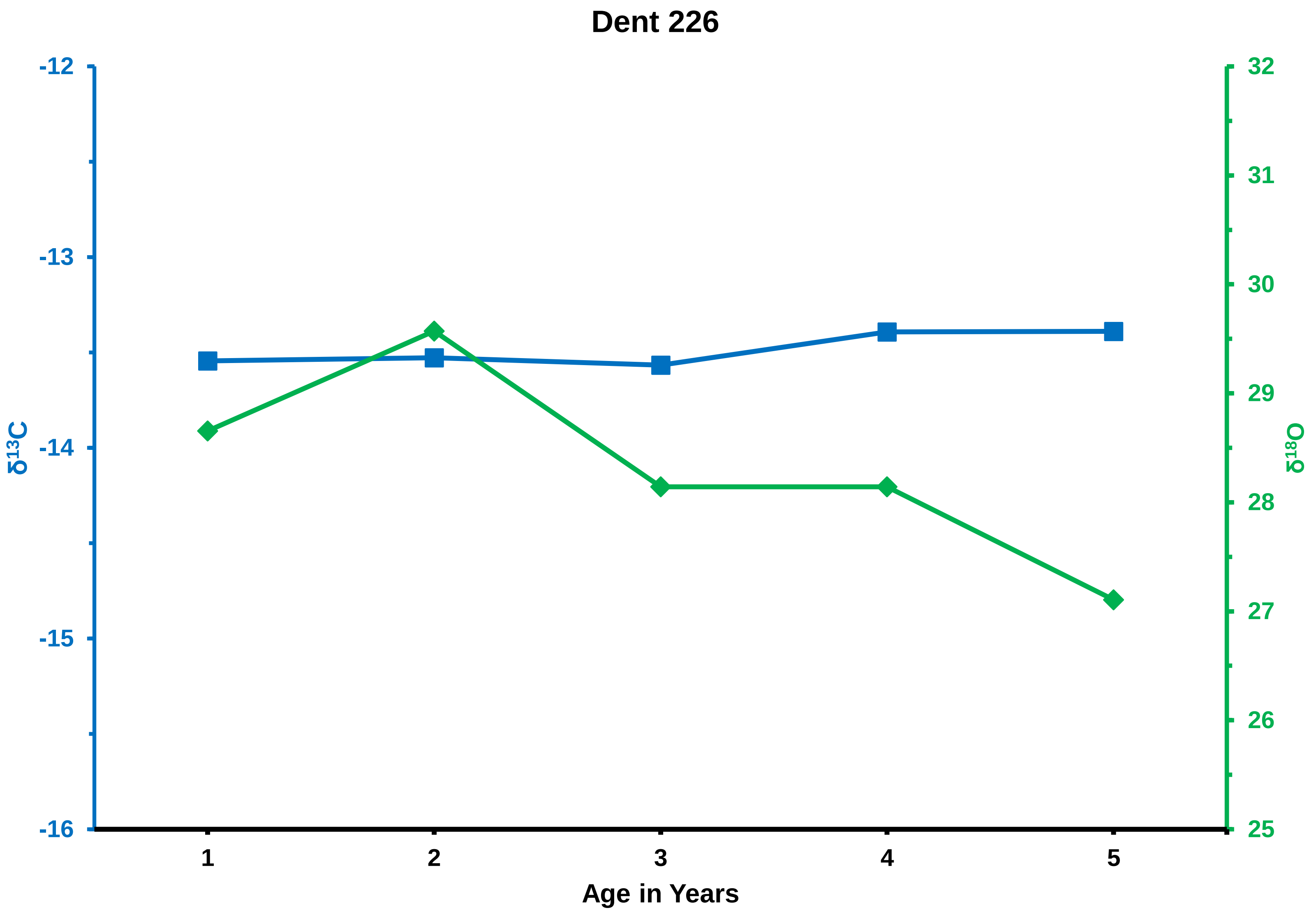

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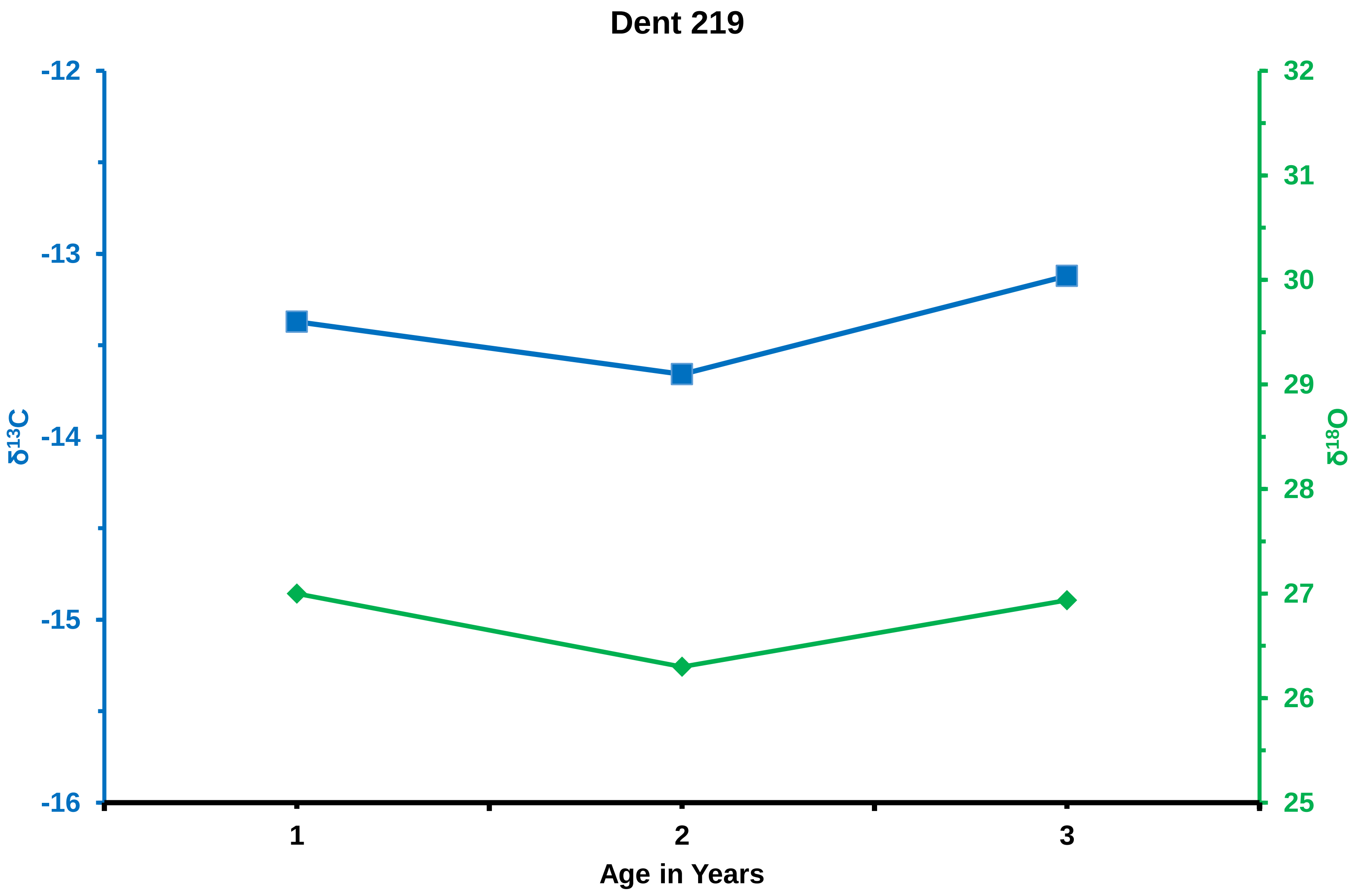
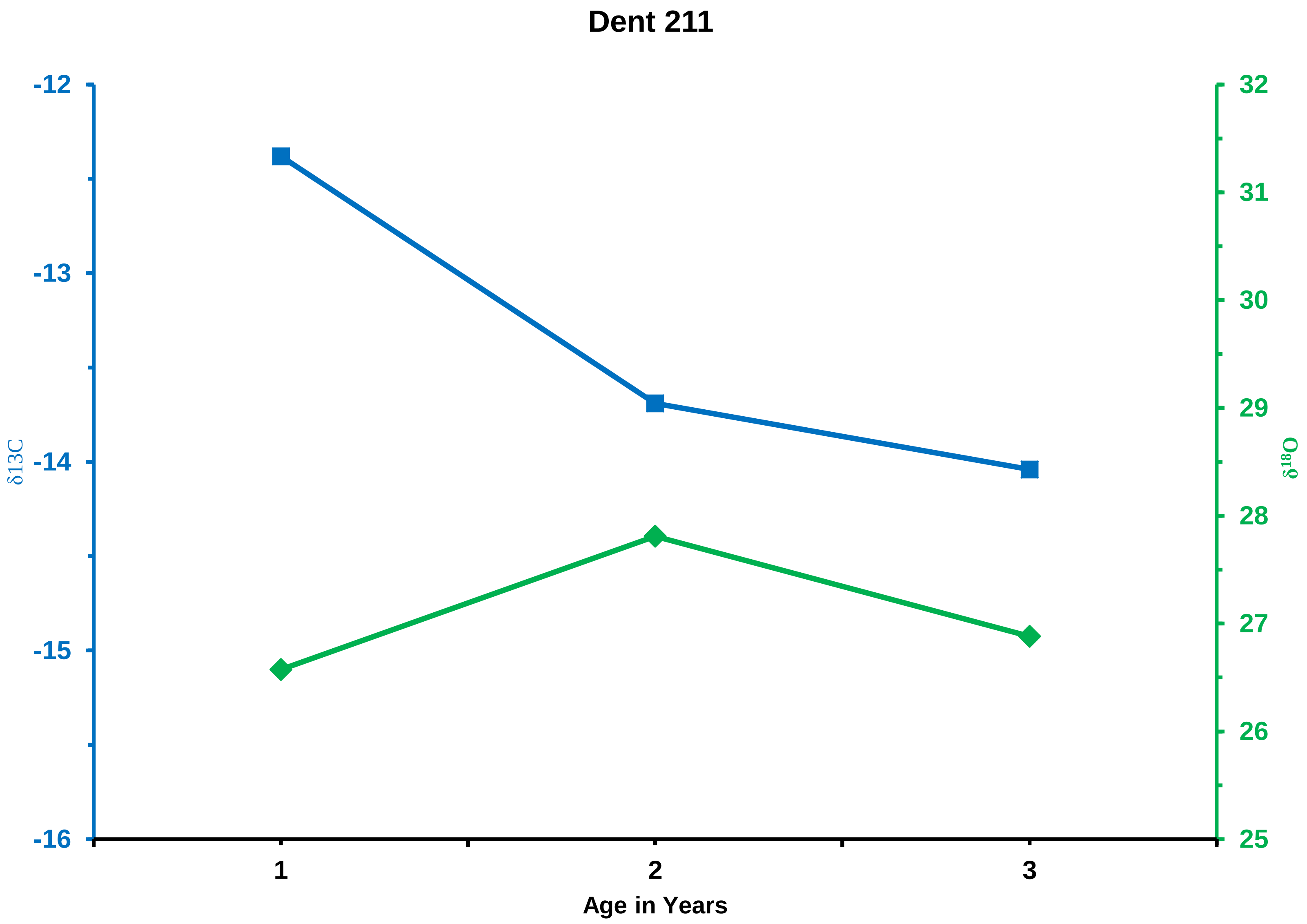


Figure B-14: Northern fur seal canine tooth showing depletion of $\delta^{18}O$ at year two.



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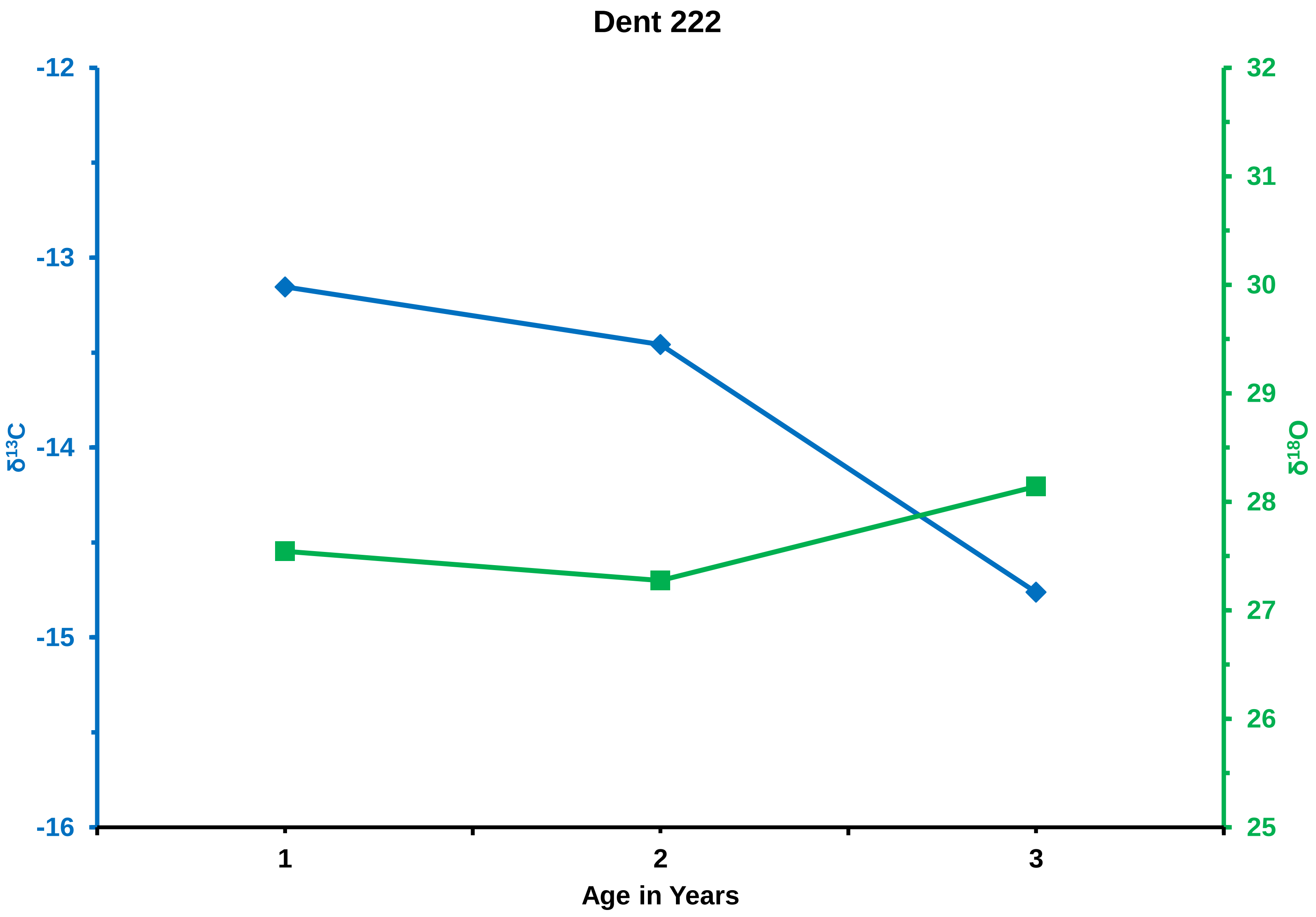

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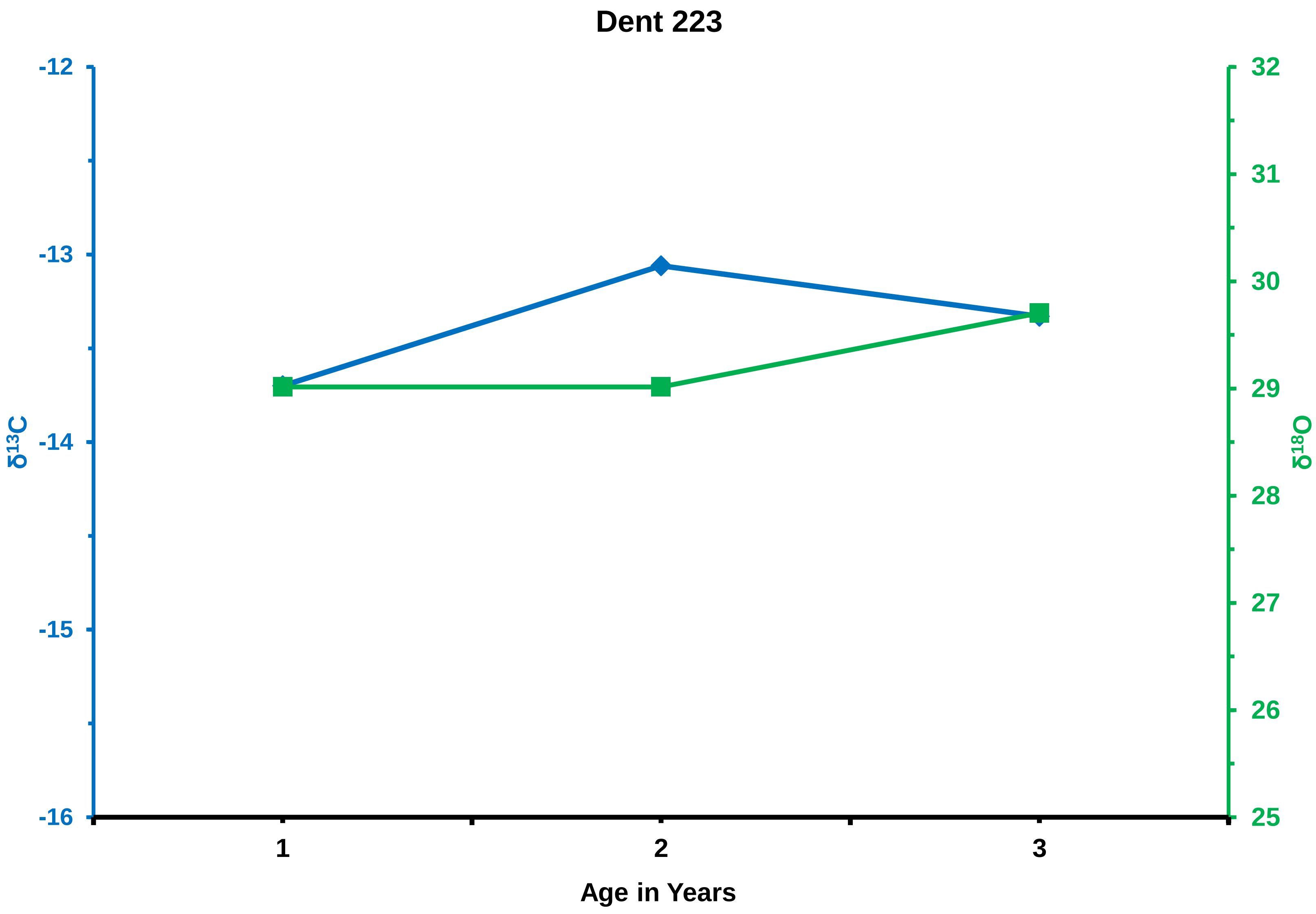

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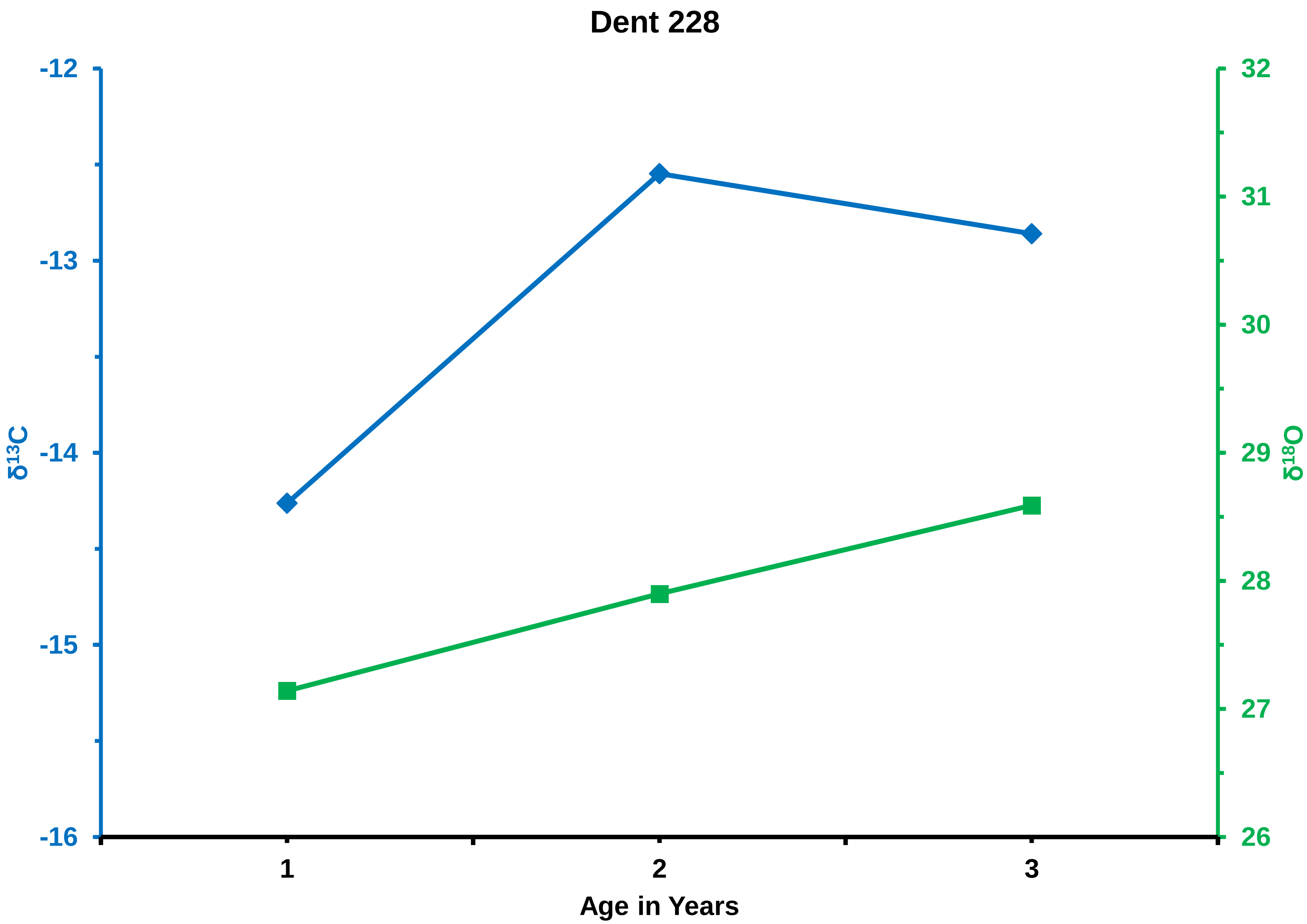

Figure B-18: Northern fur seal canine tooth showing enrichment of $\delta^{18}O$ at year two.

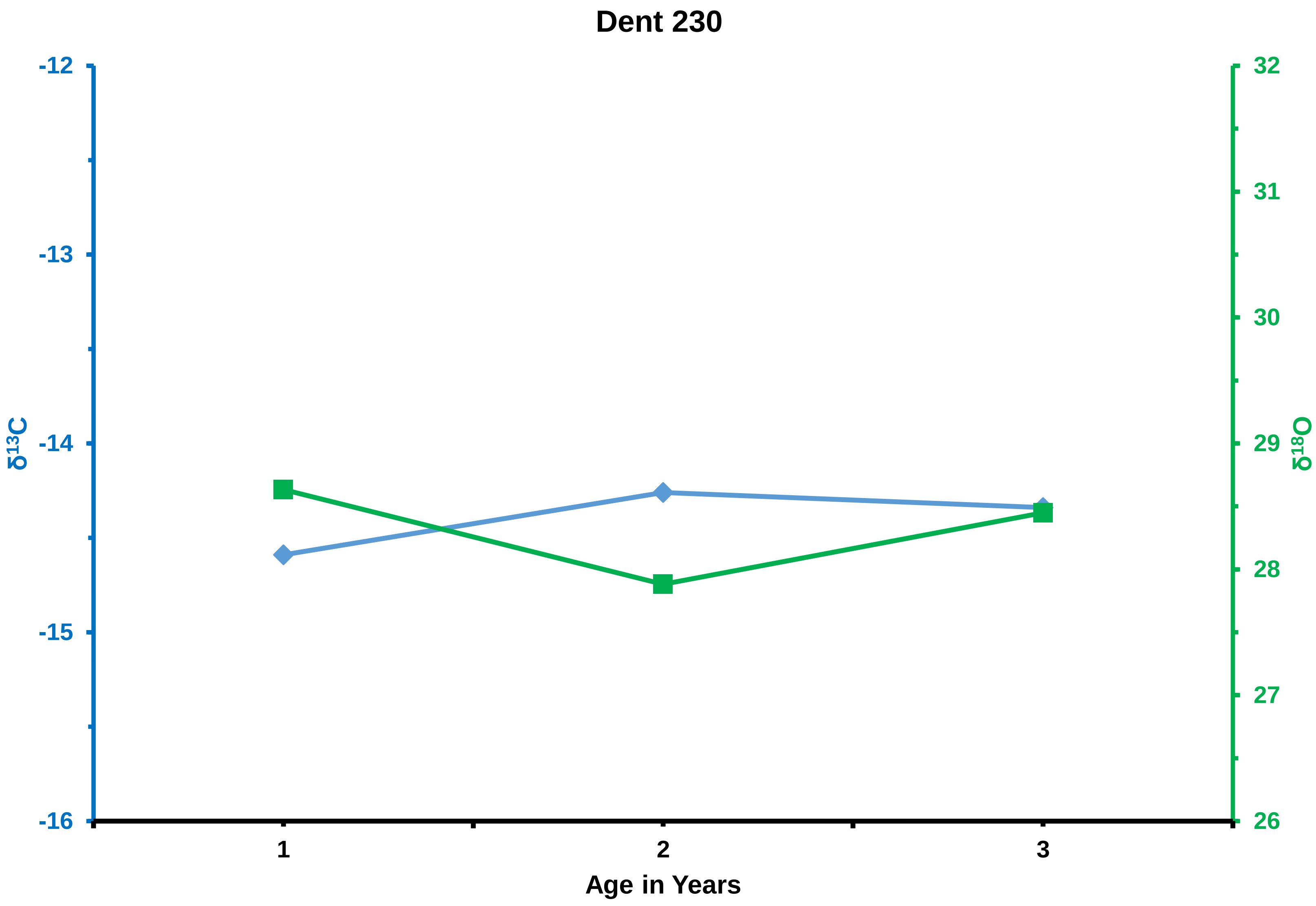

Figure B-19: Northern fur seal canine tooth showing depletion of $\delta^{18}O$ at year two.

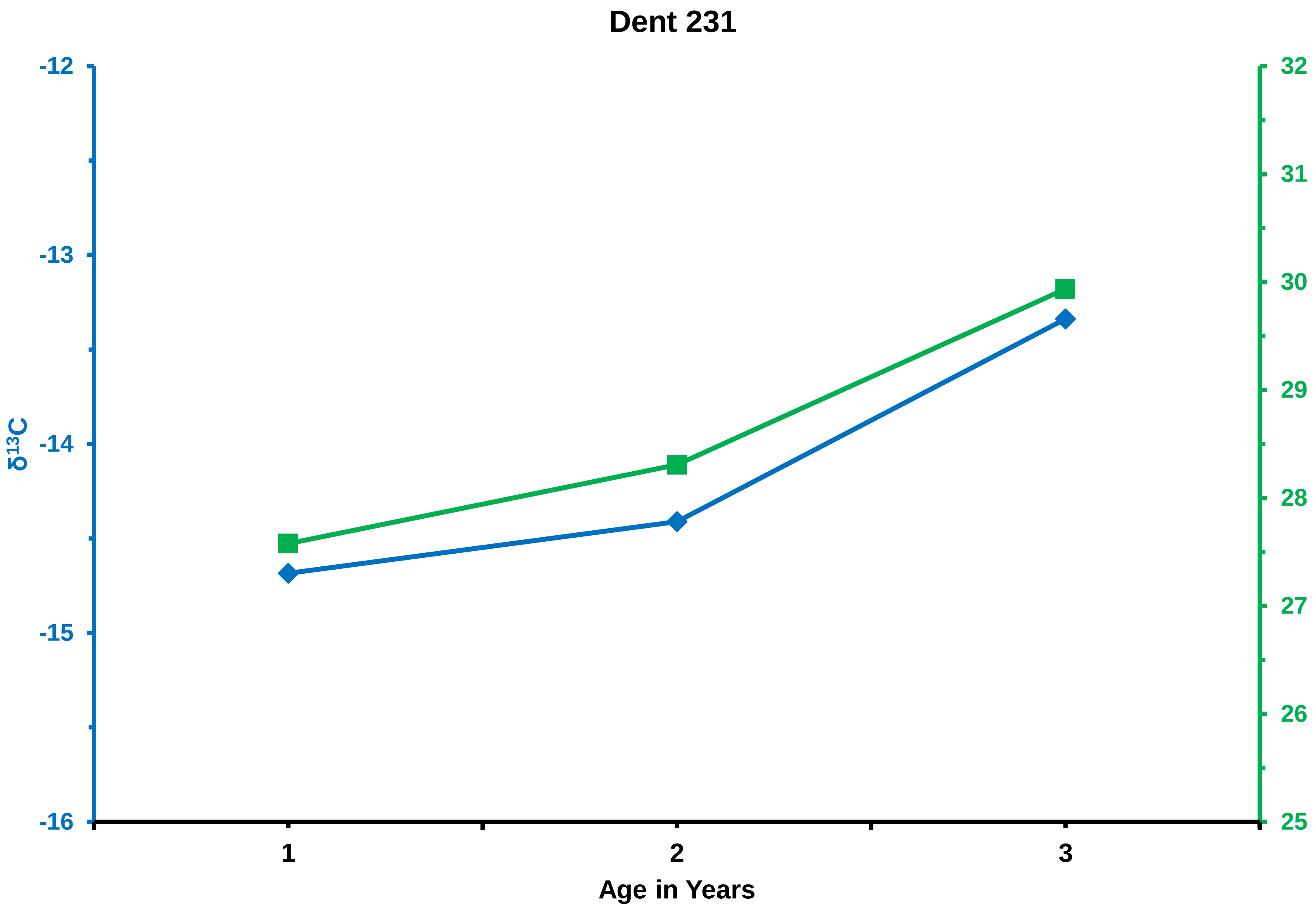

Figure B-20: Northern fur seal canine tooth showing enrichment of $\delta^{18}O$ at year two.