Isotopes in teeth and a cryptic population of coastal freshwater seals

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Abstract: Human activities threaten the biodiversity of aquatic mammals across the globe. Conservation of these species hinges on the ability to delineate movements and foraging behaviors of animals, but gaining such insights is hampered by difficulties in tracing individuals over their lives. We determined isotope ratios in teeth ($^{87}$Sr/$^{86}$Sr, $^{13}$C/$^{12}$C, and $^{18}$O/$^{16}$O) to examine lifelong movement and resource-use patterns of a unique freshwater population of a wide-ranging pinniped species (harbor seal [Phoca vitulina]) that resides in Iliamna Lake, Alaska (U.S.A.). This population’s potentially unique migratory behavior and use of different trophic resources are unknown. The isotope ratios we measured in teeth showed that seals were born in the lake, remained lifelong residents, and relied principally on resources produced from in the lake, even when seasonally abundant and nutrient-dense spawning anadromous fish (i.e., sockeye salmon [Oncorhynchus nerka]) were available in the lake. Our results illustrate how serial isotope records in teeth, particularly $^{87}$Sr/$^{86}$Sr ratios, can be used to quantify how coastal mammal populations exploit both freshwater and marine ecosystems. Understanding lifelong patterns of habitat and resource use is essential information when designing effective conservation plans for threatened coastal mammals. We present the Iliamna Lake harbor seals as a unique case study into how isotope records within teeth can help reveal the cryptic ecology of such a population residing in an intact ecosystem. The results also provide critical baseline information for the Kvichak River system, which is facing an uncertain future due to proposed large-scale industrial development and a rapidly changing climate.

Keywords: biodiversity, habitat use, isotope ecology, life history, migration, resource use, strontium isotopes

Isotopos Dentales y una Población Criptica de Focas Costeras de Agua Dulce

Resumen: Las actividades humanas amenazan a la diversidad de mamíferos acuáticos en todo el mundo. La conservación de estas especies depende de la habilidad para delinear los movimientos y los comportamientos de búsqueda de alimento de los animales, pero la obtención de dicha información está obstaculizada por las dificultades en el rastreo de individuos a lo largo del transcurso de sus vidas. Determinamos la proporción de isótopos dentales ($^{87}$Sr/$^{86}$Sr, $^{13}$C/$^{12}$C y $^{18}$O/$^{16}$O) para examinar el movimiento a lo largo de la vida y los patrones de uso de recursos de una población única de una especie de pinnípedos de agua dulce con una distribución amplia (foca común [Phoca vitulina]), la cual reside en el lago Iliamna, Alaska (E.U.A.). Se desconocen el comportamiento migratorio potencialmente único de esta población y el uso que le dan a los diferentes recursos tróficos. La proporción de isótopos que medimos en los dientes mostró que las focas nacieron en el lago, permanecieron como residentes de toda la vida y dependieron principalmente de los recursos producidos en el lago, incluso cuando estaban disponibles en aquel lugar por razones reproductivas los peces anádromos abundantes estacionalmente y con densidad de nutrientes (es decir, el salmón rojo [Oncorhynchus nerka]). Nuestros resultados ilustran cómo los registros seriales de isótopos dentales, particu-
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Palabras Clave: biodiversidad, ecología de isótopos, historia de vida, isótopos de estroncio, migración, uso de hábitat, uso de recursos

Introduction

Coastal marine, estuarine, and freshwater mammals are threatened globally (Pompa et al. 2011). In particular, species and populations that migrate between estuarine and freshwater habitats, or that are freshwater dependent, include some of the most endangered mammals worldwide (He et al. 2018). At least 1 extinction has occurred during the last decade (the Yangtze River dolphin [Lipotes vexillifer]) (Turvey et al. 2007). Major threats to their persistence are directly due to human activity (Veron et al. 2008; He et al. 2018). Small and large hydropower dams are proliferating across the globe driving habitat fragmentation and changes to natural flow regimes with little consideration of consequences for aquatic mobile species, particularly mammals (Sabo et al. 2017; Couto & Olden 2018). Riverine and estuarine ecosystems also act as sinks for pollution generated by industrial and agricultural activities of densely populated regions posing significant risks to top predators that bioaccumulate toxins, such as cetaceans (Veron et al. 2008; Sinha & Kannan 2014). Incidental catches of endangered riverine and estuarine mammals during fisheries continue to threaten populations in some of the most intensely impacted rivers and estuaries of the world (e.g., Gulf of California, Ganges [Sinha & Kannan 2014], Mekong [Smith & Jefferson 2002], Yangtze [Turvey et al. 2007], Amazon and Orinoco [Gomez-Salazar et al. 2012] River basins.

The conservation of highly mobile species, including coastal aquatic mammals, is dependent on knowledge of complex life histories, population connectivity, and foraging behaviors (Runge et al. 2014). Unfortunately, for many species and populations these fundamental features of their biology remain unknown. This is because tracing the movements and foraging of individuals over the course of their lives is rarely possible, especially for rare and elusive species. Insights are often limited to studies based on visual observations or tagging efforts that yield relatively brief snapshot in time (Gomez-Salazar et al. 2012). Nonetheless, to ensure the persistence of such populations in the face of multiple environmental pressures, effective conservation plans must be able to identify critical habitats and trophic resources, how these vary through time, and how they vary among life stages.

We quantified the lifelong movement and foraging ecology of a unique and small population (~400 individuals) of a wide-ranging pinniped species (the Eastern Pacific harbor seal [Phoca vitulina richardii] that resides in Iliamna Lake, Alaska (U.S.A.) (Fig. 1) with serial isotope records in teeth. Like other cryptic aquatic mammals across the globe, the Iliamna harbor seal’s migratory and foraging behaviors are largely unknown (Burns et al. 2016). But, unlike most threatened populations, the Iliamna seals live in a relatively undisturbed ecosystem. Therefore, they provide a rare opportunity to gain insights into how populations that are at least in part freshwater dependent exploit the heterogenous landscapes and trophic resources characteristic of coastal ecosystems, and the extent to which they are connected with proximate marine-dependent populations. It is not known whether these seals migrate between the lake and
ocean (an ~80 km swim); nor is it known to what extent seals rely on trophic resources produced from within the lake versus the ocean (e.g., seasonally abundant sockeye salmon [Oncorhynchus nerka]). Thus, this case study is relevant to many of the world’s most threatened populations of aquatic mammals, but also provides critical baseline information for the Kvichak River (Fig. 1). This watershed is under increasing pressure from proposed large-scale mining activities within its headwaters (EPA 2014) and a rapidly changing climate. Iliamna Lake harbor seals are currently managed as if they are part of the nearby Bristol Bay marine population (Muto et al. 2017). We sought to determine whether this is an appropriate management strategy.

Isotope tracers in sequentially growing teeth are a powerful method for unraveling lifelong movement and resource use of elusive animal populations (Kohn & Cerling 2002; Koch 2007; Newsome et al. 2010). Because enamel in mammalian teeth is laid down sequentially during an animal’s first years of life (Koch 2007) and dentine grows continuously over the animal’s lifetime where layer thickness correlates with body size (Boyd & Roberts 1993; Hoffman et al. 2010), teeth yield lifelong chemical records of an animal’s diet and movements.

Stable isotope ratios, expressed as \( \delta^{18}O \), \( \delta^{13}C \), \( \delta^{15}N \), and \( \delta^{34}S \), are commonly used to study isotopic gradients within and among food webs and habitats of terrestrial, aquatic, and marine ecosystems. Strontium (Sr) isotope ratios (\( ^{87}Sr/^{86}Sr \)) represent a potentially useful tracer to understand movement and resource use patterns of aquatic mammals among freshwater and marine systems. But their use has been limited to a study on the paleoecology of extinct Miocene desmostylians (Clementz et al. 2003) and to a population of endangered beluga whales (Delphinapterus leucas) (Nelson et al. 2018). No one, however, has quantified 2 critical aspects of Sr biogeochemistry necessary to accurately interpret how \( ^{87}Sr/^{86}Sr \) ratios inform habitat and resource use of aquatic mammals among freshwater and marine ecosystems: isotopic changes of migratory prey (e.g., diadromous fishes) and concentration dependence. These are particularly important for coastal omnivores and carnivores, such as bears, cetaceans, and pinnipeds known to prey on diadromous fishes during their migrations among freshwater and marine systems. If left unconstrained, they can mislead interpretations of how \( ^{87}Sr/^{86}Sr \) ratios inform freshwater versus marine habitat and resource use.

Nonetheless, much of the world’s coastal freshwater habitat is characterized by \( ^{87}Sr/^{86}Sr \) ratios that differ substantially from their proximate marine ecosystems. The world’s oceans are isotopically homogenous (\( ^{87}Sr/^{86}Sr = 0.70918 \) [SD 0.00006]) (Faure & Mensing 2005). Due to their tectonic setting along continental margins or ancient shield terranes, many rivers draining regions, such as the Pacific Rim, Amazonian Craton, and the Tibetan Plateau, carve through rocks with \( ^{87}Sr/^{86}Sr \) ratios that differ widely from the ocean (Palmer & Edmond 1992). They are also home to the world’s most threatened mammal populations (Pompa et al. 2011). Given the ubiquity and predictability of such freshwater-marine isotopic
gradients across the globe, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios could be valuable for informing conservation efforts in coastal, estuarine, and riverine ecosystems worldwide. Strontium isotope ratios are an established and powerful tool in fish and terrestrial mammal ecology, but their use to study the movement and trophic resource use patterns of coastal mammals is relatively unexplored.

To quantify the lifelong movements and foraging ecology of Iliamna Lake harbor seals, we measured multiple isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$, $^{13}\text{C}/^{12}\text{C}$, and $^{18}\text{O}/^{16}\text{O}$) in the enamel and dentine of their canine teeth and characterized the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios and Sr concentrations ($\text{Sr}$, milligrams per kilogram) of potential trophic resources. Migratory diadromous fishes are a common trophic resource of coastal mammals and when exploited they can motivate movements among these ecosystems. Such fishes are also only ephemerally available, so understanding their relative importance to consumer energy budgets is crucial to understanding the ecosystem processes they support. To this end, we quantified the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios and $\text{Sr}$ of resident lake fishes and determined whether the isotopic ratio of the seasonally abundant adult sockeye salmon returning to Iliamna Lake changed over the course of their spawning migration. The physiological transformation that diadromous fish undergo when they migrate between marine and freshwater systems should induce isotopic variation among tissues (e.g., gonads, muscle, and blood) related to tissue turnover rates. Thus, we analyzed Sr concentrations and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in eggs, muscle, and blood from female sockeye salmon over the course of a spawning run (Supporting Information). Constraining time-dependent and tissue-specific $^{87}\text{Sr}/^{86}\text{Sr}$ changes in sockeye salmon was critical because consumers across the Pacific Rim exhibit selective feeding on anadromous fishes, including among different body parts (Gende et al. 2001; Hauser et al. 2008) and at different times over the course of a spawning run (Schindler et al. 2013; Deacy et al. 2016). Once constrained, the degree to which sockeye salmon isotopically changed over the course of spawning enabled us to test different hypotheses regarding whether Iliamna harbor seals migrate to the ocean and the extent to which they exploit trophic resources produced from within the lake versus the ocean. Furthermore, these time-dependent salmon tissue analyses demonstrate important aspects of the broader applicability of using the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope system to delineate the migratory and foraging patterns of coastal mammals.

**Methods**

We measured $^{87}\text{Sr}/^{86}\text{Sr}$, $^{18}\text{O}/^{16}\text{O}$, and $^{13}\text{C}/^{12}\text{C}$ ratios in the dentine and enamel of canine teeth of 4 Iliamna harbor seals and 3 marine harbor seals from proximate populations within Bristol Bay (Supporting Information). Iliamna Lake seal samples came from subsistence harvests and were collected in collaboration with the Alaska Native Harbor Seal Commission and the Bristol Bay Native Association and analyzed under Marine Mammal Protection Act permit number 15510 issued to J.M.B. Iliamna seal ages were determined in the cementum of teeth (Burns et al. 2016). Teeth from marine seals came from University of Alaska’s Museum of the North. Dentine was collected from the outside edge of each tooth toward the pulp cavity via ~100-μm-wide drill paths drilled parallel to visible growth layers with a microdrill (~30 samples/seal) (Supporting Information). Using a Dremel tool, we milled enamel from 3 locations: enamel-dentine junction near base, middle, and apex of each tooth. All $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, including salmon tissues, were measured via multicollector inductively coupled plasma mass spectrometry (MC-ICP-MS); $^{18}\text{O}/^{16}\text{O}$ and $^{13}\text{C}/^{12}\text{C}$ were measured via isotope ratio mass spectrometry with standard methods (Supporting Information). The $\text{Sr}$ of fish tissues were analyzed via single collector ICP-MS. We digested all tissues prior to $\text{Sr}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ analyses (Supporting Information).

Because of the large differences in $\text{Sr}$ between the marine and freshwater lake system, we used concentration-dependent mass-balance equations (Phillips & Koch 2002) to evaluate the degree to which anadromous sockeye salmon contribute to the assimilated biomass of Iliamna harbor seals (Supporting Information). To account for the potentially high spatial and temporal uncertainty in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios and $\text{Sr}$ of spawning sockeye salmon in the lake, we evaluated 4 mass-balance scenarios differing in how the adult salmon endmember was characterized geochemically (Supporting Information). The marine endmember within these scenarios ranged from fully marine to near-senescent salmon (Supporting Information). In all scenarios, the lake endmember was based on measurements of resident fishes within lake (Supporting Information).

**Results**

**Sockeye Salmon Tissues**

The $^{87}\text{Sr}/^{86}\text{Sr}$ composition and $\text{Sr}$ of sockeye salmon tissues changed significantly over the course of the spawning run, and the rate and magnitude of the change was tissue dependent (Fig. 2 & Supporting Information).

**Isotopes in Teeth**

Early in the lives of all seals analyzed, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in dentine ranged from 0.7049 to 0.7059 and $\delta^{18}\text{O}$ values in enamel ranged from 16.2‰ to 17‰ (VSMOW | Vienna
Figure 2. (a) Strontium concentrations $[\text{Sr}]$ and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in tissues of adult sockeye salmon and resident lake fish (solid black circles, resident fish not scaled by $[\text{Sr}]$ because these analyses include $[\text{Sr}]$ in muscle and vertebrae of char and whole stickleback) over the course of the spawning run and (b) $[\text{Sr}]$ and (c) $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in different tissues of adult sockeye salmon and lake water (distributions represent samples collected across duration of spawning migration; horizontal line, median; upper whisker, $Q_3 + 1.5\text{IQR}$; lower whisker, $Q_1 - 1.5\text{IQR}$ [$Q_1$ and $Q_3$ are the lower and upper quartiles, and $\text{IQR} = Q_3 - Q_1$]).

standard mean ocean water] standard scale). These values were consistent with Iliamna Lake values (Fig. 3 & Supporting Information). Later in life, however, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in tooth dentine of all 4 individuals increased to ratios intermediate (0.7065–0.7085) of the global marine and Iliamna Lake values (Fig. 3a). Enamel $\delta^{13}\text{C}$ values of all 4 seals ranged from $-17.9\permil$ to $-13.2\permil$ (VPDB [Vienna Pee Dee Belemnite] standard scale), consistent with other freshwater aquatic mammals (Fig. 3b). The 16-year-old seal had more enriched enamel $\delta^{13}\text{C}$ values than the other seals (5–6 years old). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in dentine and enamel of Bristol Bay seals ranged from 0.70911 to 0.70926, consistent with the global marine value (0.70918) (Fig. 3a & Supporting Information). The $\delta^{18}\text{O}$ values in enamel of marine harbor seals from Bristol Bay ranged from 22.2‰ to 24.9‰ (VSMOW); $\delta^{13}\text{C}$ values ranged from $-10.9\permil$ to $-8.4\permil$ (VPDB) (Fig. 3b).

Mass-Balance of Resource use

Fractional contributions of salmon to seal diets varied depending on whether the salmon assimilated was fully marine, had just entered freshwater, was just about to spawn, or was near senescence (Fig. 4 & Supporting Information). These differences were due to rapid changes in the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios and $[\text{Sr}]$ of spawning adult sockeye salmon after entering freshwater (Fig. 2a & Supporting Information). From the perspective of assimilated biomass (Fig. 4a–c), scenarios where seals ate either fully marine salmon or salmon just entering freshwater resulted in estimated fractional contributions of salmon of <23%, including the periods later in life. Contributions estimated later in life for the scenarios assuming salmon were just about to spawn or were near senescence ranged from 10% to 100%. Early in seal’s lives, however, fractional contributions estimated via all scenarios from eating salmon were estimated as <10% assimilated biomass (Fig. 4 & Supporting Information). Due to relatively high $[\text{Sr}]$ in adult salmon tissues, fractional contributions to biomass were always lower than those estimated for the elemental mass of Sr (Supporting Information).

Discussion

Movement Ecology of Iliamna Seals

Isotopes in teeth indicated adult seals were born in Iliamna Lake and remained lifelong residents. The $^{87}\text{Sr}/^{86}\text{Sr}$
Figure 3. (a) $^{87}\text{Sr}/^{86}\text{Sr}$ profiles in dentine of Iliamna and marine harbor seals (light gray box, range in marine harbor seal [$n = 3$ seals: UAM99605, UAM52183, and UAM42152] enamel, dentine, and ocean water [Supporting Information]; dark gray box, range in Iliamna Lake fish and water) and (b) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in tooth enamel of Iliamna and Bristol Bay seals, including seals from California and Oregon (U.S.A.) (OS, offshore; NS, nearshore; E, estuarine; FW, freshwater. Data source: Clementz & Koch [2001]; VPDB, Vienna Pee Dee Belemnite scale; VSMOW, Vienna Standard Mean Ocean Water scale).

The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in tooth dentine and $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in enamel of 4 Iliamna seals revealed general coherence among the early life-history patterns of individuals (Figs. 3 and 4). During this period, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in enamel fell within ranges consistent with the enamel of freshwater aquatic mammals (Fig. 3b) (Clementz & Koch 2001). Similarly, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios recorded in the earliest dentine layers also reflected freshwater residence (Fig. 3a).

We inferred lifelong residence of Iliamna harbor seals in the lake based on our evaluation of different mass-balance scenarios, which indicated that, given high $[\text{Sr}]$ of salmon prior to entering freshwater, it was unlikely seals had a fully marine diet. If seals migrated to the ocean down the Kvichak River, they would have been required to have fed entirely on marine resources. Assimilation of even relatively small amounts of such resources would have resulted in tooth $^{87}\text{Sr}/^{86}\text{Sr}$ ratios that reflected the marine value (Fig. 4c). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in teeth were always <14% fully marine salmon. We assessed whether such a fraction could be explained by short migrations to the ocean by computing the expected $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in teeth if seals assimilated a mixture of fully marine salmon, salmon just prior to spawning, and resident lake fish in the approximately 2-month period corresponding to each 100-μm drill path that made up each tooth measurement (Fig. 4c & Supporting Information). We estimated that the maximum amount of time during this period that a seal (maximum $^{87}\text{Sr}/^{86}\text{Sr}$ ratio = 0.7085) could have spent eating fully marine fish in the ocean or estuary would have been ~2 weeks (0.14 × 2 months) (Fig. 4c & Supporting Information). This is also based on the assumption that while the seal was in the lake during the remainder of this period it ate only resident lake fish. If, instead, it also ate spawning salmon, the length of such a foray to the ocean would have been correspondingly shorter (Fig. 4c & Supporting Information). Although such migrations seem biologically unrealistic due to their short duration and associated energetic cost, they are within the range of movements of marine populations (Lowry et al. 2001). Stomach contents, however, of harvested seals from Iliamna Lake contained no evidence of marine prey items (Burns et al. 2016).

Foraging Ecology of Iliamna Seals

Isotopes in dentine suggest that earlier in life, seals relied principally on lake food resources. Later in life, seals shifted to rely more heavily on the seasonally abundant sockeye salmon. All mass-balance scenarios indicated that adult sockeye salmon contributed a small proportion of the Sr (Supporting Information) and biomass (Fig. 4) as assimilated by Iliamna seals early in life. The $\delta^{13}\text{C}$ ratios in enamel also indicated a primarily freshwater diet during this period (Fig. 3b). All individuals exhibited a large shift in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios later in life toward the global marine ratio (Figs. 3a and 4). This isotopic change likely reflected an ontogenetic shift in diet toward increased...
Figure 4. Scenarios of the proportion of adult sockeye salmon biomass assimilated by Iliamna seals if seals fed solely on (a) marine salmon, (b) bright salmon, (c) salmon just prior to spawning, or (d) salmon near senescence (i.e., zombie) versus lake resources. Endmembers for each mass balance scenario are described in Supporting Information. (e) Expected $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in teeth based on concentration-weighted mass balance if seals ate a mixture of fully marine salmon (fm), spawning salmon (fs), and resident lake fish (fl).

consumption of salmon. Similar shifts have been documented in coastal bear (Ursus arctos) populations (Van Daele et al. 2013), and also for estuarine bottlenose dolphins (Tursiops truncates) (Rossman et al. 2015a). Iliamna seals are almost always seen at the east end of the lake on a series of islands (Fig. 1) (Burns et al. 2016). Sockeye salmon are likely most vulnerable to seal predation once they start actively spawning along the island beaches. Sockeye salmon enter the Kvichak River in July and spawning in the lake occurs at the end of August. Actively spawning salmon have likely spent more time in freshwater than those that are holding. Thus, the salmon most vulnerable to seals would tend to have a geochemical composition reflecting salmon that have been in freshwater for an extended period (e.g., salmon just about to spawn or those near senescence) (Supporting Information). Observations of seal scat and seal-killed salmon on these islands indicate that during the spawning season, sockeye salmon represent a major diet source for seals (Hauser et al. 2008). But, seals often consumed only the belly of female fish ($>50\%$ of females), presumably seeking eggs, and typically consumed the whole body of male salmon ($>95\%$ of males). Sex ratios of sockeye salmon spawning on these island beaches have been reported as approximately 0.9:1 (female:male) (Stewart et al. 2003), but surveys of seal-killed salmon had sex ratios ranging from approximately 1.2:1 to 5.4:1 over 3 years (Hauser et al. 2008). Taken together, this suggests that seals may disproportionately eat female salmon that are just about to spawn. Such selective feeding behavior has been documented for other mobile consumers in salmon ecosystems and is thought to reflect animals seeking to optimize
nutrient density and the energetic costs of metabolism (Gende et al. 2001). Given that $^{87}$Sr/$^{86}$Sr ratios early in the life of seals show little influence from marine sources, it is unlikely that young seals consume large amounts of salmon prior to spawning or those that have spawned and are near senescence (Fig. 4).

Even late in life, sockeye salmon contribute 10% (minimum for salmon just about to spawn) to 100% (maximum for both salmon just about to spawn and those near senescence) to the assimilated biomass of seals. This large range later in life is in part due to differences among individual seals (Fig. 4), suggesting some seals rely more heavily on sockeye salmon (seal 03 and seal 07) and others less so (seal 02 and seal 04). Individual specialization of foraging habits has been documented for other generalist consumers, such as coastal cetaceans (Rossman et al. 2015b), sea otters (Enhydra lutris) (Estes et al. 2003), and bears (Decay et al. 2016). The food resources produced from within the lake available to seals include abundant juvenile sockeye salmon and a diverse array of resident fishes, all of which would isotopically reflect lake water (Figs. 2 and 3). Furthermore, gut and scat contents of seals contained resident fishes even during periods when spawning sockeye salmon were available (Hauser et al. 2008; Burns et al. 2016). The coherent ontogenetic switch to relying more heavily on sockeye salmon later in life may reflect that young seals are unable to effectively hunt adult salmon prior to spawning when fish are still spry.

The estimates of dietary contributions reported here may also be affected by Iliamna seals drinking lake water, which would constitute a source of freshwater Sr in addition to fishes produced from within the lake that contributed to the total assimilated mass by Iliamna seals. No study has constrained the degree to which drinking water influences the Sr recorded in teeth of aquatic mammals. Freshwater drinking is thought to be limited in pinnipeds because they achieve water balance via metabolic and dietary sources of water (Ortiz 2001). Studies of terrestrial mammals that do regularly drink freshwater indicate that drinking water contributes $<10\%$ of the assimilated biomass (Lewis et al. 2017). Because Iliamna Lake water $^{87}$Sr/$^{86}$Sr ratios are very similar to the ratios of resident lake fish (Figs. 2 and 3), a proportion of the assimilated mass of seals from lake resources could be from drinking water. However, this proportion is probably negligible given the low [Sr] in Iliamna Lake.

Quantifying Marine Versus Freshwater Habitat and Resource Use of Coastal Mammals with $^{87}$Sr/$^{86}$Sr Ratios

Although $^{87}$Sr/$^{86}$Sr ratios have been used extensively to study the ecology of migratory fishes and terrestrial mammals, their use to study how coastal mammals differentially use marine, freshwater, and terrestrial ecosystems is relatively unexplored, especially compared with the lighter stable isotope systems ($^{15}$N/$^{14}$N, $^{13}$C/$^{12}$C, and $^{34}$S/$^{32}$S). Our study demonstrates the importance of 2 critical aspects of using $^{87}$Sr/$^{86}$Sr ratios to quantify migration and trophic resource use of coastal mammals among ecosystems: concentration dependence and tissue turnover of migratory prey. In coastal areas situated along continental margins (e.g., Pacific Rim) or shield terranes (e.g., Laurentian Plateau and Amazonian Craton), marine environments have much higher [Sr] compared with proximate freshwater and terrestrial ecosystems (Palmer & Edmond 1992). This contrast in [Sr] results in high sensitivity of $^{87}$Sr/$^{86}$Sr to discern marine resource and habitat use of principally terrestrial or freshwater coastal consumers (e.g., bears). However, this [Sr] gradient yields less sensitivity to discern freshwater resource and habitat use of principally marine consumers. The mass-balance scenarios here illustrate that small fractions of the assimilated biomass from marine resources with high [Sr] ($<5\%$) will correspond to large $^{87}$Sr/$^{86}$Sr isotopic changes recorded in teeth (Fig. 4e). Thus, even ephemeral periods of marine resource use by freshwater or terrestrial consumers can be detected. However, $^{87}$Sr/$^{86}$Sr will be less sensitive for quantifying freshwater habitat and resource use of marine consumers because they would have to assimilate large amounts of freshwater resources for isotopic changes in their teeth to be detected. Furthermore, when coastal mammals exploit populations of diadromous fishes during their migrations between ocean and freshwater, this food resource will undergo rapid isotopic change. Therefore, $^{87}$Sr/$^{86}$Sr ratios in teeth of principally marine consumers known to target anadromous fishes during spawning migrations (e.g., beluga whales [Nelson et al. 2018]) should be interpreted with caution, as departures from the global marine value could be due to feeding on a marine resource that partially reflects the freshwater isotopic endmember (e.g., bright salmon [Supporting Information]). It is imperative to constrain such processes (i.e., concentration-dependence and isotopic changes of migratory prey) with respect to $^{87}$Sr/$^{86}$Sr ratios.

Conservation of Iliamna Seals

Using serial isotope records within teeth, we quantified 2 fundamental biological dimensions of an elusive freshwater-dependent pinniped population. These insights have important implications for their conservation. The patterns we revealed for 4 seals are suggestive for the population overall, but are still subject to the issues of a small sample size. Although small, it corresponds to 1% of the population (~400), which is a relatively large sampling density in ecological studies, including of Alaska’s harbor seal genetic population structure (~0.3%) (Muto et al. 2017). Nonetheless, Iliamna seals clearly exhibit distinct patterns of habitat and resource use compared
with proximate and closely related marine harbor seals in Bristol Bay. The absence of migratory connectivity among these populations further emphasizes the need to protect Iliamna seals as an ecologically unique population because endemic populations are more vulnerable to environmental change (Ceballos & Ehrlich 2002; Pompa et al. 2011). Furthermore, because Iliamna seals are principally dependent on lake resources, especially early in life, responses of this population to environmental change will most likely differ from that of Bristol Bay marine populations. Rapidly warming temperatures and increasing pressure of proposed mining activities in the region (EPA 2014) further emphasize the need to establish baseline ecological information and an effective conservation plan for this population.

Boveng et al.’s (2016) review of the conservation status of Iliamna harbor seals shows this population is genetically distinct, but due to a paucity of quantitative genetic, morphometric, and ecological data it is unclear whether this population is significant (i.e., biologically or ecologically important) to the broader *P. v. richardii* taxon. They identify the need for data that will show whether Iliamna seals have adapted to their unique environment as a measure of their genetic and ecological significance to the broader taxon. Adaptation of unique foraging behaviors in unusual ecological settings can constitute such a measure of this significance, as in the case of the island-associated Hawaiian false killer whales (*Pseudorca crassidens*) (Oleson et al. 2010). The unique foraging ecology of Iliamna seals, as shown here, supports the conclusion that this population has adapted to their unusual ecological setting. This includes their reliance on lake resources and consistent ontogenetic shift from a diet composed principally of lake resources to one that exploits seasonally abundant salmon. Both imply locally adapted abilities to exploit a food web unlike that of any other *P. v. richardii* population across the Eastern Pacific, which is significant to the evolutionary potential of the broader taxon.

The endemism and unique foraging ecology of Iliamna Lake harbor seals is important because wide-ranging generalist consumers (bears, pinnipeds, and cetaceans) are predicted to fare better than spatially restricted specialist consumers in the face of environmental change due to their increased ability to integrate across variable habitats and resources (Miller-Rushing et al. 2010). Food resources are often only available for short periods of time and their productivity can exhibit high spatial heterogeneity (Armstrong et al. 2016). Mobility, plus the ability to integrate across resources that exhibit asynchronous and complimentary temporal dynamics, enables generalist consumers to exploit emergent portfolio effects of ecosystems (the dampened variance typical of aggregate scales of complexity due to weak covariance at finer scales). Such effects buffer consumer populations from variability of single prey populations and extend the period of time they are available. Run timing varies by 2 weeks among sockeye salmon stocks returning to the major rivers of Bristol Bay, Alaska. These stocks also exhibit ~70% more interannual variability on average than the aggregate of all Bristol Bay stocks (Schindler et al. 2010). Coastal marine mammal populations have the ability to integrate across this spatial and temporal variability, which makes the resource more reliable (Schindler et al. 2010). However, consumer populations restricted within a single basin (e.g., Iliamna Lake) would not be able to exploit these portfolio effects in the same way. Iliamna sockeye stocks were the most abundant stocks prior to the mid-1990s in Bristol Bay, Alaska, but returns through the mid-2000s were some of the lowest on record (Hilborn et al. 2003). Harbor seals endemic to Iliamna Lake are subject to these large shifts; whereas, their closely related marine populations are not. The stability of the population over this period (Boveng et al. 2018) may in part be due to the Iliamna seal’s ability to integrate across lake and marine resources.

The insights we gained into the cryptic ecology of Iliamna’s seals are relevant to other transient and obligate freshwater coastal mammals across the globe—many of which constitute the world’s most threatened mammal species and populations. The Iliamna seals clearly integrate across trophic resources produced from disparate ecosystems. The degree to which one ecosystem versus another supports their energy budget depends on life stage and also the individual. The differential exploitation of resources among life stages reflects the fact that particular prey sources are needed or preferred during different times (Van Daele et al. 2013; Rossman et al. 2015a). Similarly, individual foraging behaviors suggest that individuals adopt various feeding strategies in the face of spatially and temporally dynamic prey sources (Estes et al. 2003; Rossman et al. 2015b; Deacy et al. 2016). In both instances, there is an important interaction between foraging strategy, trophic resources, and the role of heterogeneity. This highlights why conservation of ecosystem heterogeneity and the processes that generate it is essential to the persistence of consumer populations.

In addition to changing overriding climatic conditions, human activities across the globe are degrading (e.g., via pollution), reducing, and simplifying (e.g., fragmentation of habitats via dams) the habitats of aquatic mammals. Conservation in the face of such environmental change depends on identifying critical habitats and trophic resources over the lives of individuals. Many of the most threatened mammal populations, including those within the largest and most highly affected rivers and estuaries in the world, use coastal marine, estuarine and riverine habitats and resources that are defined by predictable isotopic gradients. Thus, isotopes in sequentially growing teeth represent a promising way to elucidate fundamental aspects of their ecology. We show here that isotopes
in teeth, in particular $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, are a powerful approach to understanding the movement and foraging ecology of these cryptic aquatic mammals.

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**Supporting Information**

Detailed description of analytical methods and mass balance calculations (Appendix S1), table of mass balance scenario endmembers (Appendix S2), figures of sockeye salmon sampling locations (Appendix S3), seal tooth anatomy and dentine sampling (Appendix S4), Keeling plots of adult sockeye salmon muscle (Appendix S5), change in [Sr] and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of eggs and blood of adult sockeye salmon through time (Appendix S6), mass balance scenarios with respect to elemental mass of Sr and biomass (Appendix S7), data sets of fish tissue $^{87}\text{Sr}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (Appendix S8), and seal teeth isotope data (Appendix S9) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

**Literature Cited**


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