Retrospective characterization of ontogenetic shifts in killer whale diets via δ^{13}C and δ^{15}N analysis of teeth

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ABSTRACT: Metabolically inert, accretionary structures such as the dentin growth layers in teeth provide a life history record of individual diet with near-annual resolution. We constructed ontogenetic δ^{13}C and δ^{15}N profiles by analyzing tooth dentin growth layers from 13 individual killer whales *Orcinus orca* collected in the eastern northeast Pacific Ocean between 1961 and 2003. The individuals sampled were 6 to 52 yr old, representing 2 ecotypes — resident and transient — collected across ~25° of latitude. The average isotopic values of transient individuals (n = 10) are consistent with a reliance on mammalian prey, while the average isotopic values of residents (n = 3) are consistent with piscivory. Regardless of ecotype, most individuals show a decrease in δ^{15}N values of ~2.5‰ through the first 3 yr of life, roughly equivalent to a decrease of one trophic level. We interpret this as evidence of gradual weaning, after which, ontogenetic shifts in isotopic values are highly variable. A few individuals (n = 2) maintained relatively stable δ^{15}N and δ^{13}C values throughout the remainder of their lives, whereas δ^{15}N values of most (n = 11) increased by ~1.5‰, suggestive of an ontogenetic increase in trophic level. Significant differences in mean δ^{13}C and δ^{15}N values among transients collected off California suggest that individuality in prey preferences may be prevalent within this ecotype. Our approach provides retrospective individual life history and dietary information that cannot be obtained through traditional field observations of free-ranging and elusive species such as killer whales, including unique historic ecological information that pre-dates modern studies. By providing insights into individual diet composition, stable isotope analysis of teeth and/or bones may be the only means of evaluating a number of hypothesized historical dietary shifts in killer whales of the northeast Pacific Ocean.

KEY WORDS: *Orcinus orca* · Stable isotopes · Weaning · Tooth annuli · Dietary specialization

INTRODUCTION

Two major ecotypes of killer whales *Orcinus orca*, termed resident and transient, inhabit northeast Pacific waters and are found sympatrically in coastal waters of British Columbia, Washington, and southeastern Alaska. A third ecotype, termed offshore, has also been identified in the northeast Pacific, but is not included in this study because of the rarity of stranded animals. The resident and transient ecotypes generally differ in geographic and seasonal distribution, with residents inhabiting relatively small and predictable areas during the summer months, and transients being generally less predictable and known to migrate over large distances in search of prey. Social structure, vocalization patterns, and more importantly, foraging behavior are also quite different (Baird & Stacey 1988, Heimlich-Boran 1988, Bigg et al. 1990, Ford et al. 1998, Baird & Whitehead 2000, Saulitis et al. 2000, Deecke et al. 2005). Resident types form relatively large stable groups that are mostly composed of mature females and their descendants, primarily consume fish, and predictably congregate in certain areas during the summer months (Heimlich-Boran 1988, Hoelzel 1993, Nichol & Shackleton 1996). Residents are important predators of various Pacific salmon species (*Oncorhyn-*

chus spp.), but are also known to consume herring *Clupea pallasii*, rockfish *Sebastes* spp., and halibut *Hippoglossus stenolepis* (Heimlich-Boran 1988, Nichol & Shackleton 1996, Ford et al. 1998, Matkin et al. 2007). Transient types form smaller groups with no defining social structure and do not associate with resident pods. They are known to migrate over large distances, and are believed to specialize on marine mammal prey. Transient groups are known to prey on pinnipeds (e.g. harbor seals *Phoca vitulina*, Steller sea lions *Eumetopias jubatus*), small odontocetes (e.g. harbor porpoise *Phocoena phocoena*, Dall's porpoise *Phocoenoides dalli*), large mysticetes (e.g. minke whale *Balaenoptera acutorostrata*, gray whale *Eschrichtius robustus*, humpback whale *Megaptera novaeangliae*) and large odontocetes (e.g. sperm whales *Physeter macrocephalus*) (Baird & Stacey 1988, Heimlich-Boran 1988, Baird & Dill 1995, Saulitis et al. 2000, Ford et al. 2005, Matkin et al. 2007).

Analysis of naturally occurring variations in the abundance of stable isotopes provides insights on animal foraging behavior and habitat use (Kelly 2000, Rubenstein & Hobson 2004, Newsome et al. 2007c). Studies of phytoplankton and zooplankton have shown that stable carbon isotope (δ^{13}C) values are higher in productive nearshore regions (especially in upwelling zones) than in offshore regions, as well as in temperate than in high-latitude ecosystems (Rau et al. 1982, Goericke & Fry 1994, Michener & Schell 1994, Schell et al. 1998). Stable nitrogen isotope (δ^{15}N) values in phytoplankton are also higher in temperate than in high-latitude ecosystems (Saino & Hattori 1987, Altabet et al. 1999, Voss et al. 2001, Kienast et al. 2002), although onshore/offshore differences are inconsistent, except in the Bering Sea where δ^{15}N (and δ^{13}C) values of zooplankton decrease from east to west along the Aleutian Island chain (Schell et al. 1998). These spatial gradients in food web isotope values have been used as proxies for foraging latitude in a variety of marine mammal species in this region (Burton & Koch 1999, Aurioles et al. 2006, Newsome et al. 2007b).

Isotopic differences cascade up food webs to top consumers (DeNiro & Epstein 1978, 1981, Minagawa & Wada 1984, Rau et al. 1992, Kelly 2000), albeit with carbon and nitrogen fractionations of ~1 to 2 and ~3 to 5‰, respectively, for each trophic step. These trophic-related isotopic discrimination factors have served as effective tools in prior studies of marine mammal and seabird foraging ecology and habitat use (Schoeninger & DeNiro 1984, Wada et al. 1987, Schell et al. 1989, Rau et al. 1992, Hobson et al. 1997, Burton & Koch 1999, Walker & Macko 1999, Kurle & Worthy 2001).

Isotopic discrimination associated with mother-to-offspring transfer of nutrients during lactation and weaning has also been the subject of several recent studies utilizing ontogenetic isotopic time series of isotope values from marine mammal teeth and bones (Hobson & Sease 1998, Newsome et al. 2006, 2007b, Niño-Torres et al. 2006, Mendes et al. 2007, Knoff et al. 2008). Theoretically, if lactating mothers catabolize their own tissues to produce milk, their nursing offspring should have isotope values that suggest feeding at a higher trophic level than their mother. Trophic level enrichment factors of ~3 to 4‰ are common for diets of fish or milk, which contain high-quality protein and thus have higher nitrogen concentrations compared to herbivorous diets. For carbon isotopes, the predicted trophic level enrichment is complicated by the fact that milk has a substantial lipid component, with lipids being more ^{13}C-depleted than proteins (DeNiro & Epstein 1978). An animal that produces milk with a high lipid content, such as a marine mammal with milk that is ~30 to 40% lipid by weight, feeds its young with food that has relatively low δ^{13}C value. There is no difference in δ^{15}N value between lipids and associated proteins, so the consumption of milk rich in lipids would not affect trophic-related ^{15}N enrichment.

Analyses of tooth annuli in Steller sea lions and California sea lions *Zalophus californianus* show that nursing young have higher tooth dentin δ^{15}N values (~2 to 3‰) and lower δ^{13}C values (~1 to 2‰) than adults (Hobson & Sease 1998, Newsome et al. 2006). Tooth dentin ontogenetic profiles from northern fur seals *Callorhinus ursinus* and northern elephant seals *Mirounga angustirosis* do not show significant isotopic shifts related to weaning. This is probably because these species wean their pups at a younger age compared to sea lions, and most of the dentin deposited in the first year of life may represent independent foraging for solid prey, rather than ^{15}N-enriched dentin deposited during the short nursing period (Hobson & Sease 1998, Newsome et al. 2006). Significant δ^{15}N shifts associated with weaning have also been observed in the teeth of sperm whales *Physeter macrocephalus* from the North Atlantic Ocean (Mendes et al. 2007), bottlenose dolphins *Tursiops truncatus* from the southeast United States (Knoff et al. 2008), and long-beaked common dolphins *Delphinus capensis* from the Gulf of California (Niño-Torres et al. 2006).

Longitudinal dietary records are difficult to obtain for many species, especially for elusive and wide-ranging animals such as killer whales. Predation events are seldom seen first-hand and it is impossible to compile an observation-based longitudinal foraging record for an individual top consumer that lives in the open ocean. Isotopic proxies offer promise to characterize temporal dietary shifts at the individual level for marine mammals, especially isotopes compiled from accretionary or continuously growing but metabolically inert tissues such as tooth dentin (Hobson & Sease

1998, Newsome et al. 2006, Mendes et al. 2007) or vibrissae (Newsome et al. in press). Tooth dentin growth layers are especially useful for examining historic dietary shifts because many museum and some archaeological collections contain teeth, albeit in usually small sample sizes. Furthermore, individual dentin growth layers in killer whales are believed to represent annuli. Although this has not been rigorously validated for killer whales as it has been for other odontocetes (e.g. *Delphinapterus leucas*, Lockyer et al. 2007; *Tursiops truncatus*, Hohn et al. 1989), and counts of dentin growth layers from historically or photographically known killer whales correspond closely to their estimated age (Mitchell & Baker 1980, Vos et al. 2006).

In this study, we use stable isotope analysis of killer whale tooth dentin growth layers to (1) evaluate ontogenetic shifts in diet at the individual level, and (2) characterize differences in foraging behavior among and within transient and resident ecotypes. We also discuss the advantages and limitations of using this approach to assess historic changes in killer whale foraging ecology. Using a high-resolution micromilling system, we sampled successive tooth dentin growth layers of transient and resident individuals that were collected or stranded in California (n = 8, all transients), Washington (n = 2, all residents), and Alaska (n = 3, 1 resident and 2 transients) over the past 3 decades. Ecotypes were designated using genetic analysis (Morin et al. 2006) and observational data, or estimated based on collection location.

MATERIALS AND METHODS

***Orcinus* teeth.** *Orcinus* have between 10 to 14 large (12 to 15 cm long) homodont teeth in both the man-

dible and the maxilla (Heyning & Dahlheim 1988). Teeth at the extreme anterior and posterior portion of the tooth row are notably smaller in length and diameter than those in the middle. The enamel crowns are formed *in utero*, with eruption of the teeth occurring within a few weeks of birth (Heyning 1988), and the teeth growing through deposition of dentin on the inner surface of the pulp cavity. Barring tooth loss from abscessed infections, teeth continue to grow throughout the lifetime of the individual until the pulp cavity is completely filled with dentin.

Although we had little or no control over which tooth was available from each individual, we generally tried to obtain large teeth with minimal occlusal wear or cracking (either ante- or post-mortem), from the middle of the tooth row. Some amount of wear on the occlusal tip was evident in some of the teeth analyzed, which was usually in the form of chipping and faceting from occlusion with the opposite tooth row. Teeth in which the occlusal tip was either too worn or too cracked for positive identification of the first growth layer (assumed to correspond to the first year of growth) were not included in the modeled calculations of weaning age (see below).

Micromill approach. We obtained 14 teeth from archived collections (Table 1). Genetic analysis identified 3 teeth as collected from residents including 1 recovered on Kiska Island in the Aleutians, and 2 collected in Puget Sound, Washington (Morin et al. 2006). The transient teeth included 2 identified as collected from AT1 transients found dead in Prince William Sound, Alaska, and 8 transients collected from whales that died in California. The identity of the AT1 transients was known based on photographs taken when the whales were stranded (C. Matkin pers. comm.). Two separate teeth from one AT1 transient were analyzed independently (NGOS 1 and NGOS 2) to mea-

Table 1. *Orcinus orca*. Number of dentin samples (DS) obtained, mean $\delta^{13}C$ and $\delta^{15}N$ (and SD) values, and whale age, sex, ecotype (R = resident, T = transient), approximate collection locality, and year collected for each tooth analyzed. Ecotype classifications were determined using previously published genetic data (Morin et al. 2006) and stranding/collection locality

Sample ID	DS	$\delta^{13}C$	SD	$\delta^{15}N$	SD	Age	Sex	Ecotype	Collection locality–Year
AF 57355	24	−14.3	0.3	15.3	0.4	32	M	R	Kiska Island, AK–2003
NMML 89	18	−11.1	0.3	18.1	0.3	20	M	R	Washington–1967
NMML 88	6	−11.7	0.2	19.1	1.7	6	−	R	Washington–1967
NMML 85	16	−13.6	0.3	19.9	0.4	16	F	T	California–1967
SBNHM-1546	22	−12.5	0.6	20.2	0.4	28	F	T	California–1977
NMML 78	27	−12.9	0.4	19.2	0.7	38	M	T	California–1961
NMML 79	34	−11.5	0.5	22.5	0.9	52	M	T	California–1963
NMML 81	16	−14.0	0.3	18.2	0.3	16	M	T	California–1965
NMML 82	28	−13.3	0.4	18.5	0.5	40	M	T	California–1966
NMML 84	16	−12.4	0.4	19.5	0.2	16	M	T	California–1967
NMML 87	15	−13.0	0.6	19.2	0.6	16	M	T	California–1966
LL EYAK	24	−11.8	0.3	20.3	0.3	32	M	T	Prince William Sound, AK–2000
NGOS 1	27	−12.6	0.6	20.1	0.7	36	M	T	Prince William Sound, AK–2001
NGOS 2	25	−12.2	0.5	20.0	0.8	36	M	T	Prince William Sound, AK–2001

sure inter-tooth variability within a single individual. Based on counts of individual growth layers, the whales ranged in age from 6 to 52 yr old at death. All were males except for 2 female transients, both of which were collected off California.

Teeth were sectioned longitudinally with a water-cooled diamond-edged saw blade and polished on a lapidary wheel. In cases where dentin growth layers were obscure or difficult to follow, polished teeth were soaked in a 10% formic acid solution for ~12 h (Pierce & Kajimura 1980). We assume that acid etching did not influence $\delta^{13}C$ and $\delta^{15}N$ values because the surface portion of the tooth represents only a small fraction of the total sample (Hobson & Sease 1998, Newsome et al. 2006). Each section was examined at 50× magnification under transmitted polarized light to enhance distinction of dentin layers. We obtained powdered dentin for isotopic analysis using a high-resolution micromill system (Merchantek), which can drill along specified paths of ~300 µm width (Fig. 1). Tooth dentin is primarily composed of the mineral hydroxylapatite, intergrown with an organic matrix, which is chiefly composed of the protein collagen and comprises ~30% of the dentin dry weight (Koch 2007). We used drill bits ranging in size from 300 to 1200 µm. Growth layers were drilled to a depth of ~400–500 µm and powdered dentin samples were collected using small forceps. The rate of dentin growth may slow and the layers become thin over the lifetime of an individual. For example, the

growth layers adjacent to the pulp cavity of the sectioned killer whale tooth in Fig. 1 are thinner (~200 to 400 µm) than those adjacent to the exterior enamel surface (>1 mm) that represent the first few years of the individual's life. Thus, in some specimens, we were unable to sub-sample the individual growth layers that represent the last several years before the whale died and had to group several growth layers to provide enough material for isotopic analysis. We report the number of discrete samples milled from each individual, as well as the age of that individual determined through visual analysis of each tooth by counting the growth layers (Table 1).

Stable isotope analysis. To isolate collagen, powdered dentin samples were demineralized with repeated aliquots of 0.25N hydrochloric acid for ~12 to 15 h at 5°C, rinsed with distilled water until neutrality and then lyophilized. Approximately 1.5 mg of dentin collagen was weighed into tin boats for isotopic analysis. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were determined using a Carlo-Erba elemental analyzer NC 2500 interfaced with a Finnigan Delta Plus XL mass spectrometer at the stable isotope biochemistry facility of the Geophysical Laboratory, Carnegie Institution of Washington (Washington, DC). As a control for the quality of dentin collagen, considering that the powdered tooth dentin samples were not lipid-extracted prior to analysis, we measured the carbon to nitrogen (C/N) ratios of all samples to ensure that they did not contain ^{13}C-depleted lipids, which would lead to higher C/N ratios relative to pure protein (DeNiro & Epstein 1978). The C/N ratios of all tooth dentin samples ranged from 2.8 to 3.0, which are well within the range for unaltered collagen (DeNiro & Epstein 1978).

Isotopic results are expressed in parts per thousand (‰) as: $\delta^{13}C$ or $\delta^{15}N = 1000 \times [(R_{sample}/R_{standard}) - 1]$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The standards are Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon, and atmospheric N_2 nitrogen. Results were calibrated to international standards through repeated measurements of an acetanilide standard, which yielded a within-run SD of <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Duplicate isotopic measurements were performed on ~20% of all unknown samples and yielded a mean absolute difference of <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

Fig. 1. *Orcinus orca.* Sectioned and sampled tooth, with the occlusal tip to the right and the pulp cavity to the left. Top panel shows longitudinally sectioned tooth after acid etching and micromill sampling (growth layers highlighted with graphite). Lower panel shows the same image, with every 5th dentinal growth layer (blue dashes) and micromill paths (green solid lines) being indicated. Dentinal growth layers beyond the 25th year are narrow and difficult to distinguish

Statistical analysis. Ontogenetic changes in δ^{15}N values were modeled to determine the average weaning age and overall pattern of isotopic change from juvenile years to adulthood. We used 2-stage models to represent the weaning signal (*Fcn* 1) and post-weaning ontogenetic isotopic changes (*Fcn* 2). δ^{15}N values were standardized by subtracting the value for each growth layer from the value of the first (i.e. outer) growth layer. Thus, the modeled values are the relative changes in δ^{15}N from the birth-year value. Three whales were excluded in the model fitting: NMML 87 and AF 57355, which appeared to have very weak weaning signals due to the absence of the birth-year growth layer, possibly resulting from heavy wear or chipping of the enamel; and NMML 88, which had only 6 growth layers recovered from the young resident tooth.

Based on the pattern of observed δ^{15}N changes and some biological justifications, we choose 3 possible weaning functions to represent *Fcn* 1, which included a linear decline;

$$Fcn\ 1 = \text{Model 1: } Y = aX + b \tag{1}$$

a non-linear logarithmic decrease;

$$Fcn\ 1 = \text{Model 2: } Y = a + 1/\log (X + b) \tag{2}$$

or a non-linear 3rd-order inverse polynomial;

$$Fcn\ 1 = \text{Model 3: } Y = (a/X) + (b/X^2) + (c/X^3) \tag{3}$$

where X is the growth layer number, Y is the standardized δ^{15}N and a, b and c are fitted parameters. *Fcn* 2 always utilized a 4-parameter sigmoid function;

$$Fcn\ 2: Y = y0 + (d/(1 + \exp(-((X - x0)/e)))) \tag{4}$$

where X and Y are as defined above, and $y0$, d, e, and $x0$ are all fitted parameters. The biological justification for using this function is that it allowed for a change at some point in time, which could be interpreted as a change at maturation. We explicitly separate the 2 stages at a variety of potential weaning ages by specifying a particular growth layer group (i = 3 to 10), and then fitting *Fcn* 1 if $X < i$, and fitting *Fcn* 2 if $X \geq i$. In this context, weaning age is defined as the age when the relative δ^{15}N value reaches a post-weaning baseline value, and no enrichment due to nursing is detected. Model 1 allowed for a linear decline from growth layer 1 to 2 and therefore had 8 possible weaning ages (i.e. $i \geq 3$), while the other weaning models required at least 3 points from growth layers 1 to 3 and therefore had only 7 possible weaning ages (i.e. $i \geq 4$). One final model simply allowed *Fcn* 2 to begin at growth layer group (GLG) 2 and represents weaning by age 2. Thus, there were 3 possible *Fcn* 1 model forms, each with 7 or 8 possible weaning ages (22 possible models), plus one model where *Fcn* 1 was a constant and *Fcn* 2 began at GLG 2, or a grand total of 23 models.

The 2 model stages were fit simultaneously using an iterative maximum likelihood estimation method via a dual quasi-Newton optimization algorithm of non-linear regression within PROC NLMIXED (SAS statistical software, SAS Institute). Individuals (n = 11) were treated as a random effect, which allowed the model to account for autocorrelation within the individual GLG values (n = 234). For each of the 23 possible models, we calculated the best-fit parameter values. We then determined the 'best approximating model' given the observed data using Kullback-Leibler (K-L) information theory (Burnham & Anderson 2002) by using the 2nd-order Akaike's information criterion corrected for small sample size (AIC_c). In the K-L information theory, the best model has the lowest AIC_c value, with the difference between a particular model's AIC_c value and the smallest AIC_c value being referred to as its 'delta value'. Thus, the best model has a delta value of 0 and models with delta values >3 are generally considered to have relatively little support. Akaike weights (w_i) were derived from the delta values (Burnham & Anderson 2002), and can be interpreted as the probability that a particular model is the 'best' among those examined. We also calculated the model-averaged weaning age to account for model uncertainty (Burnham & Anderson 2002).

Differences in mean δ^{13}C and δ^{15}N values among individuals were assessed using 1-way ANOVA, followed by a post-hoc Tukey's HSD pairwise comparison test. ANOVAs were performed using the software program JMP (v 7.0).

RESULTS

Generally, isotopic sampling of each growth layer represents sampling of annual growth from birth year to ~15 to 20 yr of age (Fig. 1). After this point, each sample represents 2 to 3 annuli and likely integrates dietary information over these longer time periods. Isotope values for individual growth layers ranged over ~10‰, from 14.5 to 24.1‰, for δ^{15}N (Fig. 2A) and ~5‰, from –10.4 to –15.4‰, for δ^{13}C. δ^{13}C and δ^{15}N ontogenetic profiles for each tooth are presented in Fig. 2 and show similar patterns in δ^{15}N values for most individuals; nitrogen isotope values are higher in growth layers 1 to 3 than in growth layers that represent the juvenile age class (age ~4 to 12). Moreover, most individuals show an ontogenetic increase in δ^{15}N values of ~1.5‰ from juvenile to adult age classes. δ^{13}C values also show ontogenetic shifts, but without an obviously consistent pattern of change among individuals (Fig. 2B). The patterns of change in the duplicate teeth (NGOS 1 and NGOS 2) correlated well but were not identical.
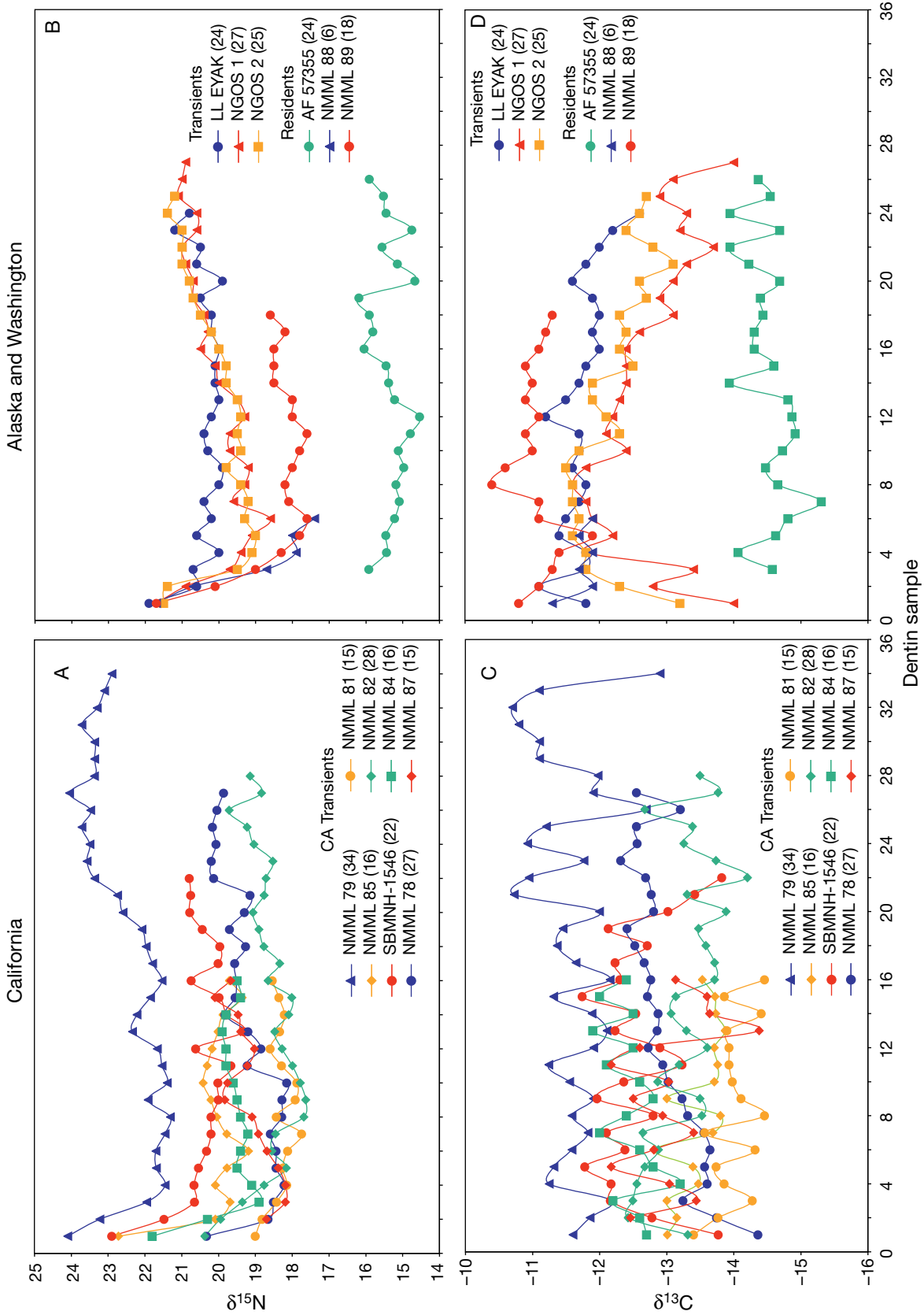
Fig. 2. *Orcinus orca*. Individual ontogenetic time series of $\delta^{15}N$ (A & B) and $\delta^{13}C$ (C & D) values for killer whales from California (A & C) and Alaska/Washington (B & D). The first dentin sample (left side of each panel) corresponds to the first growth layer adjacent to the enamel (see Fig. 1); numbers in parentheses denote the number of dentin samples obtained from each individual tooth. Dentin samples beyond the 15th growth layer generally integrate 2 or more annual growth layers
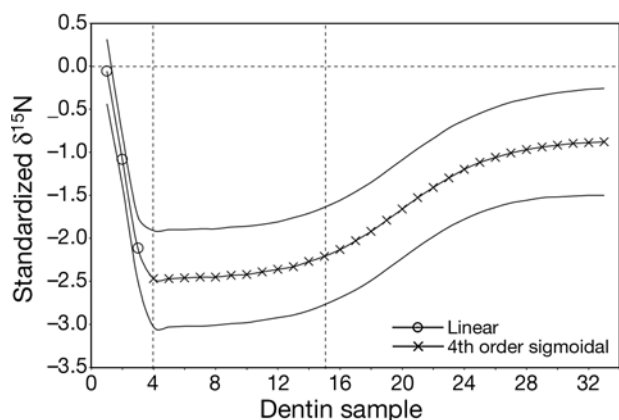
Fig. 3. *Orcinus orca*. Predicted pattern of change in standardized $\delta^{15}N$ values using the 'best' 2-stage model of ontogenic changes (see parameter estimates in Table 3); the first dentin sample corresponds to the first growth layer (i.e. birth year) adjacent to the enamel (see Fig. 1). The solid lines parallel to the modeled functions represent 95% CIs of the model. This model includes a linear weaning function with a weaning age of 4 yr and a sigmoidal post-weaning function. Dentin samples beyond the 15th growth layer group generally integrate 2 or more annual growth layers

Modeling the ontogenetic changes in standardized $\delta^{15}N$ values suggests that a linear decline of ~1.0‰ yr^{-1} best described the decrease in values from birth year to age 4 ($w_i = 0.396$), at which time values stabilize for ~10 yr, and then increase after ~14 yr of age (Fig. 3). The second best model also suggests a weaning age of 4, but with a non-linear decline in $\delta^{15}N$ occurring mostly in years 1 and 2 ($w_i = 0.288$). Thus, there was essentially no support for a complete cessation of nursing before age 3, with a cumulative w_i value of 0.694 for a weaning of 4 yr (Table 2). Hence, there is almost 70% probability that weaning in killer whales occurs sometime in the 3rd year of life, with a total cessation of nursing by age 4. The model-averaged weaning age was also 4 yr. Table 3 shows the parameter estimates for the 'best' ontogenetic model (bold in Table 2).

Based on the ontogenetic model, we assumed weaning by age 4, and used only growth layers deposited after age 3 to calculate mean post-weaning isotopic values (Table 1, Figs. 4 & 5). Isotopic variability was generally smaller within than among individuals (Fig. 4). In general, mean $\delta^{13}C$ and $\delta^{15}N$ values for the Alaskan AT1 transients are higher and more tightly clustered than values for transients collected off California, with the exception of a single California transient (NMML 79) that

Table 2. *Orcinus orca*. Likelihood comparison of models representing average ontogenetic changes in relative $\delta^{15}N$ for 11 whales (234 individual growth layers) showing number of model parameters (K), –2log-likelihood (–2LL), AIC$_c$ (Akaike information criterion corrected for small sample size), delta values, and Akaike weights (w_i) comparing 2-stage models of ontogenic changes in standardized $\delta^{15}N$ values. Stage 1 functions model the general decline in $\delta^{15}N$ from birth year to weaning age and uses either a linear function (Model 1), logarithmic decrease (Model 2) or 3rd-order inverse polynomial (Model 3). The Stage 2 function models post-weaning changes and uses a 4-parameter sigmoid function in all cases. Each of the 3 weaning models was assessed assuming weaning to occur at ages 3 to 10; only weaning ages 3 to 6 are presented as there was essentially no support for later weaning ages. One final model allowed weaning by age 2; *Fcn* 1 was a constant (0) and *Fcn* 2 began at growth layer 2. The single 'best' model (in bold) has the lowest AIC$_c$ score and highest w_i value. Models with delta values >3 are considered to have relatively little support

Weaning age	Weaning model	K	–2LL	AIC$_c$	Delta	w_i
2	0	7	370.8	385.3	65.5	0.000
3	1	8	309.1	325.8	5.9	0.021
4	**1**	**8**	**303.2**	**319.9**	**0.0**	**0.396**
4	2	8	310.5	327.1	7.3	0.011
4	3	9	301.7	320.5	0.6	0.288
5	1	8	313.8	330.4	10.6	0.002
5	2	8	317.7	334.3	14.5	0.000
5	3	9	302.7	321.5	1.6	0.178
6	1	8	336.7	353.3	33.7	0.000
6	2	8	319.6	336.2	16.4	0.000
6	3	9	303.8	322.6	2.7	0.101

has significantly higher $\delta^{15}N$ values than any other individual analyzed in this study (ANOVA, p < 0.01). For residents, mean $\delta^{13}C$ and $\delta^{15}N$ values for the WA and AK individuals were significantly different (ANOVA, p < 0.01). No comparisons between the young resident from WA (NMML 88, Table 1) and the other individuals were made since mean values for the former were highly influenced by annuli deposited during nursing (Fig. 2B,D).

Table 3. *Orcinus orca*. Parameter estimates for the 'best' 2-stage model of ontogenetic changes in standardized $\delta^{15}N$ values. This model includes a linear weaning function (a = slope, b = intercept) with a weaning age of 4 yr (i.e. nursing ceases sometime in the third year). The sigmoidal post-weaning function (Eq. 4) suggests a general increase in $\delta^{15}N$ values beginning at ~14 yr of age (see Fig. 3). LCI and UCI are lower and upper CIs, respectively

Function	Parameter	Estimate	SE	df	p	LCI	UCI
Fcn 1 = Linear	a	–1.03	0.09	10	<0.0001	–1.23	–0.83
	b	0.97	0.28	10	0.007	0.34	1.60
Fcn 2 = Sigmoid	$y0$	–2.45	0.22	10	<0.0001	–2.94	–1.97
	d	1.67	0.21	10	<0.0001	1.21	2.12
	e	3.24	0.75	10	0.002	1.56	4.92
	$x0$	19.94	0.92	10	<0.0001	17.90	21.98

DISCUSSION

Ontogenetic shifts in $\delta^{15}N$

Although captive studies indicate that *Orcinus* will eat a mix of solid food and milk up to 18 to 24 mo (Asper et al. 1988, Kastelein et al. 2003), there is little or no direct data

Fig. 4. *Orcinus orca*. Mean tooth dentin $\delta^{13}C$ and $\delta^{15}N$ values (±SDs) for individual killer whales. As in Table 1, isotopic data for the first 3 growth layers were not included in calculating mean values for each individual; numbers in parentheses denote number of dentin samples after the third growth layer that were collected from each individual. Stranding localities for individuals that were not collected in California are shown. Mean isotopic values for NGOS 1 and NGOS 2 are results for 2 separate teeth from a single AT1 transient that were analyzed independently (see Fig. 2 for isotopic profiles). Data for the juvenile resident from WA (NMML 88) are not shown

on age at weaning in wild, free-ranging killer whales. In the northeast Pacific, a single observation has been recorded of a known-age resident suckling (A69) at ~2.5 yr of age (B. Paterson pers. comm., 18 Jun 2008). Other than this single observation, data from captive studies (Asper et al. 1988, Kastelein et al. 2003) or from stomach contents of stranded calves (Heyning 1988) provide little indication of when individuals in the wild are fully weaned.

The longitudinal isotopic records presented here provide insight into the nature of and approximate age at final weaning of killer whales. The standardized $\delta^{15}N$ model presented in Fig. 3 shows a mean $\delta^{15}N$ decrease of ~2.5‰ from the 1st to the 4th year of life that likely corresponds to a decreasing reliance on milk and a concomitant increase in consumption of solid (fish or mammalian) prey. Mean $\delta^{15}N$ values for the 2nd annulus are intermediate between that of the 1st and 3rd annuli, suggesting gradual weaning of calves and their consumption of a combination of milk and solid food in the 2nd and 3rd year. For killer whales, the sharing of prey between adult/juvenile individuals and calves is a commonly observed phenomenon and an extended nursing period (2 to 3 yr) is probably necessary for an animal to learn sophisticated, communal hunting behaviors (Heimlich-Boran 1988, Baird & Stacey 1988, Baird & Dill 1995, Baird & Whitehead 2000, Ford et al. 2005).

The second major ontogenetic shift in $\delta^{15}N$ values — a gradual increase of ~1.5‰ from the juvenile to adult age class — is more difficult to interpret since both transient and resident killer whale pods engage in cooperative hunting and are known to share captured prey among pod members. It is therefore assumed that
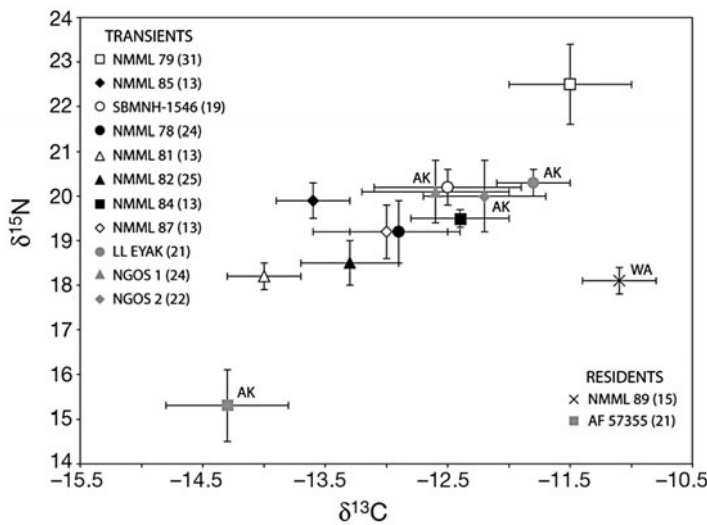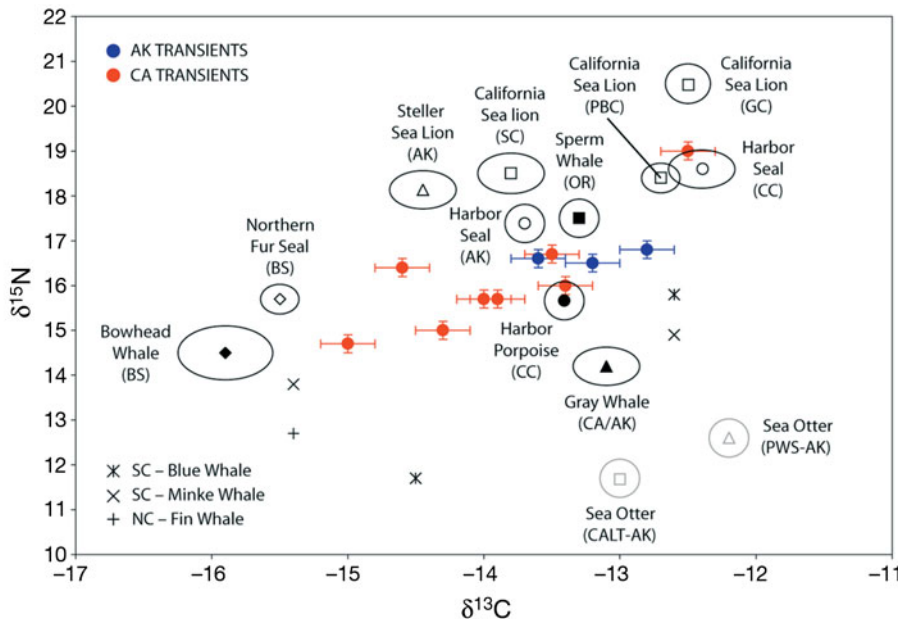

Fig. 5. Mean tooth dentin and bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of transient whales analyzed and possible marine mammal prey species. Mean tooth dentin $\delta^{13}C$ and $\delta^{15}N$ values for killer whales have been corrected for trophic discrimination by subtracting 1 and 3.5‰, respectively, from mean tooth dentin $\delta^{13}C$ and $\delta^{15}N$ values shown in Table 1 and presented in Fig. 4. As in Table 1 and Fig. 4, isotopic data for the first 3 growth layers (annuli) were not included in calculating mean values for each individual. Letter codes associated with prey denote collection localities; see Table 4 caption for a key to letter codes. For graphical clarity, error bars and ovals represent SEs; sample sizes for each prey species are presented in Table 4

Table 4. Mean bone collagen (BC) and tooth dentin (TD) $\delta^{13}C$ and $\delta^{15}N$ values (and SDs) of marine mammal prey collected in the northeast Pacific Ocean. Regional codes denote collection localities: GC = Gulf of California; SC = Southern California; CC = Central California; NC = Northern California; PBC = Pacific Baja California; AK = Alaska; BS = Bering Sea; OR = Oregon; CA = California; PWS-AK = Prince William Sound, AK; CALT-AK = Central Aleutian Islands, Alaska. Number codes for sources are (1) Newsome et al. unpubl. data, (2) Newsome et al. 2006, (3) Burton & Koch 1999, (4) Hirons et al. 2001, (5) Newsome et al. 2007a, (6) Toperoff 2002, and (7) Schoeninger & DeNiro 1984

Prey species	Region	n	$\delta^{13}C$	SD	$\delta^{15}N$	SD	Tissue	Source
California sea lions	GC	34	−12.5	0.6	20.5	1.6	TD	1
	PBC	34	−12.7	0.6	18.4	0.8	BC	2
	SC	15	−13.8	0.9	18.5	0.9	BC	3
Harbor seals	CC	18	−12.4	0.7	18.6	0.8	BC	3
	AK	37	−13.7	0.9	17.4	1.8	BC	4
Steller sea lions	AK	31	−14.4	1.1	18.1	1.4	BC	4
Northern fur seals	BS	230	−15.5	0.6	15.7	1.2	BC/TD	3, 5
Harbor porpoise	CC	29	−13.4	0.5	15.7	0.7	BC	6
Sperm whales	OR	24	−13.3	0.5	17.5	0.5	TD	1
Bowhead whales	BS	3	−15.9	0.6	14.5	0.8	BC	7
Minke whales	SC	2	−12.6/−15.4	–	13.8/14.9	–	BC	7
Gray whales	CA/AK	13	−13.1	0.8	14.2	0.7	BC	1
Blue whale	SC	2	−12.6/−14.5	–	11.7/15.8	–	BC	7
Fin whale	NC	1	−15.4	–	12.7	–	BC	7
Sea otters	PWS-AK	95	−12.2	0.5	12.6	0.6	BC	1
	CALT-AK	97	−13.3	1.3	11.7	1.2	BC	1

juvenile individuals consume, on average, the same prey in similar proportion as adults and should not experience significant ontogenetic shifts in prey type and/or trophic level throughout their post-weaning life. Despite this hypothesis, an ontogenetic shift in diet or trophic level must be considered as a possible explanation for the observed increase in $\delta^{15}N$ values at ~12 to 14 yr of age because the majority of our data is derived from transient males, which as adults leave the pod to lead largely solitary lives.

Transient males typically leave the pod upon reaching sexual maturity, which is believed to occur when they reach ~6 to 7 m in length at ~10 to 14 yr of age (Heimlich-Boran 1988). Adult males hunting alone or in small groups (2 or 3 ind.) could switch to higher trophic level prey relative to their maternal pod. Our model suggests that the juvenile to adult ontogenetic shift begins, on average, at ~14 to 15 yr of age. For transient males that lived ≥22 yr, the average relative shift in $\delta^{15}N$ from annulus 10 to the last GLG was 1.3‰ (n = 5, min = 0.9‰, max = 1.7‰). This scenario also implies that transient females should not show a shift to higher $\delta^{15}N$ values from juvenile to adult ages since they often remain in their pod after reaching sexual maturity. Only one transient female (SBMNH-1546) reached a comparable age, making statistical comparisons meaningless. Nevertheless, this transient female had a juvenile to adult $\delta^{15}N$ shift of 0.8‰, which is less than the minimum juvenile to adult $\delta^{15}N$ shift of the males. Future analyses of other transient females are required to further test this hypothesis.

A second plausible explanation for the increase in $\delta^{15}N$ values from juvenile to adult stages is associated with the influence of growth on trophic discrimination factors. Recent controlled feeding experiments on fish (Focken 2001, Gaye-Siessegger et al. 2003, Trueman et al. 2005) show that consumer tissue–diet discrimination factors significantly decrease with increasing protein accretion during periods of rapid and sustained growth. Theoretically, the isotopic composition of a consumer's tissues approaches that of its diet (i.e. small trophic discrimination factor) as more dietary protein is used directly for the synthesis of tissue protein to sustain growth (i.e. anabolic state). Thus, the ~1.5‰ increase in $\delta^{15}N$ values in the compiled killer whale ontogenetic series could have resulted from the decrease in growth rate, and concomitant increase in diet–tissue discrimination factor, that occurred between the juvenile and adult life stage when growth rates presumably decline. Hence, the observed increase in mean $\delta^{15}N$ values at the juvenile to adult transition may not be related to an increase in trophic level resulting from a change in diet, but rather a change in the diet–tissue discrimination factor associated with a decrease in growth rate. To our knowledge, however, this effect has not been observed in a large mammal.

Foraging ecology

The longitudinal data presented here show that a combination of carbon and nitrogen isotopes can be used to assess differences in foraging behavior among

ecotypes and sometimes within ecotypes from different regions. The AK resident stranded on Kiska Island (central Aleutian Islands) and recent studies suggest that Aleutian residents comprise a separate population that might be genetically distinct from other residents found in waters north and east of Kodiak Island (Matkin et al. 2007). After correcting for tissue-dependent $\delta^{13}C$ discrimination between skin and dentin collagen ($\delta^{13}C_{skin–collagen}$ = ~4‰; Koch 2007), the mean $\delta^{13}C$ value for the Kiska Island individual presented here is slightly lower (~1‰) than the mean $\delta^{13}C$ values for previously published central Aleutian individuals (Herman et al. 2005, Krahn et al. 2007). The adult WA resident has a slightly higher (~1‰) mean $\delta^{15}N$ value than the 4 west coast southern residents analyzed by Herman et al. (2005).

The highly significant differences in mean $\delta^{13}C$ and $\delta^{15}N$ values between the WA and AK residents (Fig. 4) cannot be explained by latitudinal differences alone and likely result from a combination of spatial differences in food web values and dissimilarities in prey preferences. As discussed earlier, food web $\delta^{13}C$ and $\delta^{15}N$ values decrease with increasing latitude in the northeast Pacific Ocean and from east to west along the Aleutian Island chain. Previous observational and gut content studies show that southern residents specialize on Chinook salmon *Oncorhynchus tshawytscha* (Ford et al. 1998). Little observational or gut content data has been compiled for Aleutian residents. However, since there are no large salmon runs in the Aleutian Archipelago, it is possible that resident whales in this area specialize on other types of fish. After accounting for a combination of tissue-dependent $\Delta^{13}C_{collagen–muscle}$ (~4‰) and trophic discrimination factors (1‰ for $\delta^{13}C$ and 3.5‰ for $\delta^{15}N$) by subtracting a total of 5.0 and 3.5‰ from respective dentin collagen $\delta^{13}C$ and $\delta^{15}N$ values (Koch 2007), comparison of killer whale data with previously published muscle data of potential fish prey in the Aleutians (Newsome et al. 2007a) suggests that walleye pollock *Theragra chalcogramma*, Pacific herring, and Atka mackerel *Pleurogrammus monopterygius* could be important prey species for the Alaskan (Aleutian) resident analyzed here.

When making inferences about dietary preferences in isotopic ecology, it is important to use data for prey that inhabit the same general area as the consumer of interest because of spatial gradients in isotope values at the base of the food web, which can complicate trophic interpretations. Isotopic data derived from prey collected in the Atlantic Ocean or even the northwestern Pacific Ocean are *not* useful for interpreting differences in isotopic composition among killer whales that inhabit the northeast Pacific (e.g. Herman et al. 2005). In Fig. 5, we have compiled bone

and tooth dentin collagen isotope data for various northeast Pacific marine mammals. This enables us to make direct, tissue-specific isotopic comparisons between the transients analyzed here and their potential prey without having to make assumptions regarding isotopic fractionation among tissue types, which is primarily driven by differences in amino acid composition (Koch 2007). Some general isotopic patterns among marine mammal species are important to note for interpreting killer whale isotopic data. For species that inhabit similar latitudes, nearshore foragers (e.g. harbor seals and sea otters *Enhydra lutris*) have significantly higher $\delta^{13}C$ values than those that forage on the continental shelf (e.g. California sea lions, Steller sea lions) or at the shelf-slope break (e.g. northern fur seals). $\delta^{15}N$ values, on the other hand, primarily highlight trophic differences between pinnipeds, mysticetes, and sea otters. There can be significant differences, however, in mean $\delta^{13}C$ and $\delta^{15}N$ values among populations of the same species, assumed to occupy the same trophic level, that inhabit different oceanographic regions (Aurioles et al. 2006); e.g. California sea lions sourced from breeding colonies within the Gulf of California versus colonies on the Channel Islands off southern California or the Pacific coast of Baja California (Fig. 5).

Most of the CA and AK transients have intermediate trophic-corrected $\delta^{15}N$ values relative to those for pinnipeds and mysticetes (Fig. 5). As in Fig. 4, we present mean $\delta^{13}C$ and $\delta^{15}N$ values in Fig. 5 for both of the teeth collected from the NGOS individual. Our isotopic results suggest that harbor seals are important prey for the 2 Alaska AT1 transients analyzed here and are consistent with what is known from observational studies of the AT1 transients, which shows that the AT1 pod specializes on harbor seals and Dall's porpoise, at least when found in Prince William Sound (Ford et al. 1998, Saulitis et al. 2000). Indeed, LL EYAK was an adult male believed to be a harbor seal specialist (C. Matkin pers. comm.) that at necropsy had the tags of several recently tagged harbor seals in its stomach (D. H. Monson pers. obs.).

Surprisingly, many of the CA transients have lower mean $\delta^{15}N$ values compared to the AK transients. Since food web $\delta^{15}N$ values generally decrease with increasing latitude in contrast to the pattern observed between AK and most CA transients, the CA transients likely consumed greater proportions of lower trophic level prey compared to AK transients. This interpretation is also supported by the carbon isotope data, since several of the CA transients have $\delta^{13}C$ values that are significantly lower than those of the 2 AK transients. This pattern also contrasts with the general trend of decreasing food web $\delta^{13}C$ values with increasing latitude in tissues of other top marine consumers in the

northeast Pacific Ocean (Burton & Koch 1999, Aurioles et al. 2006, Newsome et al. 2007a,b). Furthermore, post-hoc application of a +0.6‰ Seuss correction (0.16‰ per decade; Quay et al. 2003) to mean $\delta^{13}C$ values of relatively recently stranded AK transients (2000 to 2003) would only increase the carbon isotope difference between AK and most CA transients, all of which were collected in the 1960s (Table 1). Thus, consideration of latitudinal differences in food web isotope values and Seuss effects suggests that differences in $\delta^{13}C$ and $\delta^{15}N$ among transients from AK and CA result from differences in prey preference, and not from spatial or temporal shifts in isotope values at the base of the food chain.

At this time, however, definitive dietary interpretations for the historic CA transients are complicated by the lack of published isotopic data for northeast Pacific small odontocetes (Dall's porpoise, Pacific white-sided dolphin *Lagenorhynchus obliquidens*) and the small sample sizes for mysticetes (minke whales *Balaenoptera acutorostrata*, fin whales *Balaenoptera physalus*, blue whales *Balaenoptera musculus*) that are known prey for wide-ranging transient groups. Overall, the historic CA transients likely consumed a greater proportion of low trophic level prey that occur in offshore habitats compared to the 2 Alaskan AT1 transients known to specialize on piscivorous nearshore prey (Ford et al. 1998, Saulitis et al. 2000). Possible low trophic level, offshore prey consumed by CA transients include baleen whales, although observational data suggest that with the exception of minke whales, killer whales likely only take calves of large cetaceans (Ford et al. 2005, Matkin et al. 2007). Analogous to nursing killer whales, the $\delta^{15}N$ values of nursing baleen whales, dolphins, and seals/sea lions are likely to be higher than their adult counterparts. Killer whales that feed on ^{15}N-enriched calves would thus have higher $\delta^{15}N$ values than orcas that forage on adult mysticetes. Nevertheless, $\delta^{15}N$ values of mysticete calves would likely be significantly lower than most adult pinniped or odontocete prey.

There are 2 possible, but not mutually exclusive, explanations for the single California transient (adult male, NMML 79) that has significantly higher $\delta^{13}C$ and $\delta^{15}N$ values compared to other CA (or AK) transients (Figs. 4 & 5). First, this individual could have been a pinniped specialist and principally consumed high trophic level prey such as California sea lions sourced from rookeries on the Pacific coast of Baja California, or harbor seals along the California coast (Fig. 5). Second, he could have spent the majority of his life in the Gulf of California or areas further south. Particulate organic matter (POM) and sediments collected off southwestern Mexico and within the Gulf of California are significantly ^{15}N-enriched compared to similar material from southern/central California or southern Alaska Current (Altabet et al. 1999, Kienast et al. 2002). This latitudinal gradient in POM $\delta^{15}N$ values cascades up food chains to top consumers and has been previously used to determine the foraging location of several wide-ranging top marine consumers, including northern fur seals breeding in California and Alaska (Burton & Koch 1999, Newsome et al. 2007a), as well as northern elephant seals *Mirounga angustirosis* breeding off the coast of Baja California (Aurioles et al. 2006). An example of this phenomenon is the significant difference in mean bone collagen $\delta^{15}N$ values between California sea lions from breeding colonies within the Gulf of California and those sourced from the Pacific coast of Baja California (Fig. 5). While transient killer whales are occasionally sighted in the Gulf of California and the eastern tropical North Pacific, it is unknown if these groups remain in these areas throughout the year or if they visit on a seasonal basis from areas further north. If individuals or pods remain in southern waters year-round, they would likely have higher $\delta^{15}N$ values than transients that forage further north even if they foraged at similar trophic levels. Both these explanations imply that the mother of this individual also had similar foraging preferences or movement patterns, at least during the period when she was nursing the individual analyzed here.

Lastly, significant differences in mean $\delta^{13}C$ and $\delta^{15}N$ values among the CA transients analyzed suggest a high degree of individuality in prey preferences. Since transients are solitary foragers or hunt in smaller pods than residents, the relatively lower degree of intra- than inter-individual isotopic variability suggests that the CA transients analyzed here specialized on specific prey types or, more likely, proportions of different prey that did not change over their lifetime. Individual dietary specialization is increasingly being recognized as an important component of food web patterns and dynamics, which have significant implications for ecological and evolutionary processes at the community level (see review by Bolnick et al. 2003). Furthermore, recent work suggests that stable isotopes provide a reliable tool for examining foraging individuality in natural populations (Newsome et al. in press). Specialization may be particularly relevant for top-level predators such as killer whales exploiting a diverse prey base where each prey species or prey type (e.g. seal vs. dolphin) may require complex hunting strategies that could take years to learn and perfect. Individual- or pod-level specialization also has implications for accurate interpretation of isotopically derived foraging data, suggesting the need for caution when applying mixing models to isotopic data collected at the population or species level.

Potential of isotopic approach to constrain killer whale predation hypothesis

Killer whales have been the focus of much recent debate concerning their role in the historic declines of marine mammals in the northeast Pacific Ocean (Springer et al. 2003, 2008, Trites et al. 2007, Wade et al. 2007). The cause(s) of these declines is/are still unknown, despite substantial progress in understanding the current ecology of this system. Perhaps the most important reason for our failure to better understand this problem may be that too little attention has been paid to the past. Similar to ecological problems in coastal and coral reef ecosystems worldwide (Jackson et al. 2001, Pandolfi et al. 2003), the collapse of marine mammals in the North Pacific ecosystem is fundamentally a historical problem, because the events that led to marine mammal declines occurred before scientists were even aware of the problem.

Recent isotopic investigations of transient killer whales in the North Pacific Ocean report isotope values for biopsy samples (i.e. skin) collected after 2000 (Herman et al. 2005, Krahn et al. 2007). Since skin is a metabolically active tissue, its isotopic composition reflects dietary inputs in the months prior to collection, even for an animal the size of a killer whale (Martinez del Rio et al. in press). In contrast, the retrospective isotopic strategy undertaken here provides a unique perspective into the past foraging ecology of individual killer whales that are otherwise difficult or impossible to obtain through compilation of observational information (especially for wide-ranging transient whales), or through isotopic analysis of recently collected soft tissues (e.g. biopsy samples). Our ongoing analysis of teeth from other modern and historically collected individuals, especially individuals sourced from Alaskan waters, may allow us to construct a timeline of foraging information for transient killer whales that could be the best way to evaluate the role of killer whales as potential drivers of historic marine mammal population declines in the northeast Pacific Ocean. The retrospective examination of historic shifts in killer whale diets, however, must consider the ontogenetic isotopic trends observed here, as well as previously recognized spatial gradients in food web isotope values. In addition, examination of historic shifts in killer whale prey preferences may be complicated by the possibility that the declines in some marine mammal prey (e.g. sea otters) could be driven by (1) a shift in the prey preferences of a relatively small number of individual whales sampling of which may be highly unlikely (Williams et al. 2004), and/or (2) subtle shifts in the diets of a large number of individual whales that may not be detectable using an isotopic approach. Despite these complications, it is widely accepted that increased killer whale predation is the main cause of the relatively recent (mid 1990s) sea otter declines in the central Aleutian Islands (Estes et al. 1998, Doroff et al. 2003) and is therefore the least challenged aspect of the killer whale predation hypothesis.

Retrospective stable isotope analysis could, however, offer insight into the earlier hypothesized dietary switch from mysticete to pinniped prey since energetic considerations suggest a greater number of individual killer whales were required to drive the observed regional declines of harbor seals, northern fur seals, and Steller sea lions (Williams et al. 2004) than in Aleutian Island sea otter populations. Retrospective analysis of additional killer whale teeth could also be used to evaluate bottom-up forcing scenarios through comparison with other historic $\delta^{13}C$ and $\delta^{15}N$ time series compiled from bowhead whales (Schell 2000), Steller sea lions (Hirons et al. 2001, Hobson et al. 2004), and northern fur seals (Newsome et al. 2007a) in the northeast Pacific Ocean.

Lastly, the relative importance of mysticetes as a significant prey for historic transient whales has recently been questioned. The isotopic data presented here suggest that many of the historic transients collected off California in the 1960s relied on prey that occupied a relatively lower trophic level than that of pinnipeds or harbor porpoises sourced from the California Current and foraged further offshore (Fig. 5). While the scant amount of isotopic data available for mysticetes or other small odontocetes from the northeast Pacific Ocean does not allow definitive interpretations to be made at this time, these prey types likely comprised a non-trivial proportion of the diets of historic California transients analyzed in this study.

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