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**Marine Mammals Stable Isotope Records as Indicators of Climate Change:
A Call to Re-Examine Previous Conclusions**

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Abstract

Long-term stable isotope records derived from marine mammals present a unique retrospective glimpse at historic conditions, as they record of the flow and sources of nutrients from the food webs in which an animal feeds. These isotope records also provide a baseline from which to judge recent changes in the environment, and the subsequent impacts on the ecology of higher consumers. This paper reviews published marine mammal stable isotope records and provides evidence for the need for re-interpretation of long term trends, given an emergent weight of evidence.

Marine Mammal Isotope Records, And The Need For Re-Analysis

Records derived from the stable isotope ratios of marine mammal tissues have been generated for several species, with many studies being focused in the North Pacific (Table 1). Stable isotope ratios of higher consumers provide evidence of the sources and flow of nutrients in ecosystems, since consumers derive their stable isotope value from their diet (Hobson 2007). This is particularly evident when examining carbon isotope signatures in consumers, as carbon isotopes are not transformed significantly between trophic levels (Michener and Schell 1995).

Multi-decadal stable isotope records derived from the tooth annuli and bone collagen of Steller sea lions (*Eumetopias jubatus*) and Northern fur seals (*Callorhinus ursinus*) exhibited statistically significant decreases in carbon ($\delta^{13}\text{C}$) values over time (Hirons et al. 2001, Hobson et al. 2004, Newsome et al. 2007). $\delta^{13}\text{C}$ records of harbor seals (*Phoca vitulina*) also decreased, but the trend was not significant at $\alpha = 0.05$ (Hirons et al. 2001). Nitrogen ($\delta^{15}\text{N}$) records from the same studies showed mixed results, with the $\delta^{15}\text{N}$ values of Steller sea lion teeth increasing over time (Hobson et al. 2004) and the $\delta^{15}\text{N}$ values of Northern fur seal teeth and harbor seal bone remaining consistent over the length of each record (Hirons et al. 2001, Newsome et al. 2007). These authors each suggested that these data reflect changes in the Gulf of Alaska and Bering Sea ecosystems, specifically a decline in primary production. Since positive relationships between phytoplankton $\delta^{13}\text{C}$ and growth rate have been empirically demonstrated (Laws et al. 1995), the long-term $\delta^{13}\text{C}$ decline observed in marine mammal tissues was attributed to a decrease in phytoplankton growth rates across the region.

In an extensive study of bowhead whale (*Balaena mysticetus*) foraging ecology and migration, Schell (2000, 2001) also generated a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ record from baleen plates collected from 37 whales, all of which were incrementally sampled. This sampling technique provided a higher-resolution isotope record than those generated from pinniped tissue, as each baleen isotope data point reflected approximately 2 weeks of assimilated dietary information, as opposed to 1 year (from tooth annuli) or a lifetime average (from bone) (Hobson 1999). Pronounced seasonal differences were observed in the bowhead whale baleen records, such that baleen formed in the Bering/Chukchi Seas (winter) vs. the Beaufort Sea (summer) could be differentiated (Schell et al. 1989, Lee et al. 2005). Isotope data from baleen formed in the Bering/Chukchi Seas were isolated, and a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baleen record representing nutrient assimilation from this region showed significant decreases in both isotopes over several decades (Figure 1). Schell (2000) estimated that the temporal decline in baleen $\delta^{13}\text{C}$ represented a decrease in phytoplankton growth rates and a corresponding 30-40% decrease of primary production in the Bering Sea. This is based on assumptions that the concentration and $\delta^{13}\text{C}$ of dissolved inorganic carbon ($\delta^{13}\text{C}_{\text{DIC}}$)

in the euphotic zone had remained constant over the study period, 1946-1998 (Schell 2000).

Two recent studies of stable isotope records created from North Atlantic marine mammals showed similar long term trends (Table 1). The first study, an analysis of harbor porpoise bone tissue collected in the North Sea from 1848-2002, observed decreases in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ over the time series (Christensen and Richardson 2008). In an examination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in North Atlantic right whale baleen, Lysiak (2008) observed a decrease in $\delta^{13}\text{C}$ and an increase in $\delta^{15}\text{N}$ in isotope records spanning 1883-2005. While the available marine mammal isotope datasets differ in many ways (species examined, trophic position, tissue analyzed, and geographic location), they also share a striking common characteristic – a decrease in $\delta^{13}\text{C}$ over time. Given the broad geographical representation of the marine mammal isotope records presented here and well-documented observations that $\delta^{13}\text{C}_{\text{DIC}}$ has not remained constant in recent decades, I argue that declining primary production in the Bering Sea and Gulf of Alaska is not the most likely explanation for the previously published trends. *Therefore, the exploration of alternative hypotheses is justified.*

Anthropogenic Inputs

It is well established that the carbon dioxide (CO_2) concentration of the atmosphere has not remained constant over time, and has increased dramatically in recent decades (IPCC 2004). Much of this CO_2 , attributed to anthropogenic sources such as the burning of fossil fuels, has a disproportionately “light” $\delta^{13}\text{C}$ signature (Körtzinger and Quay 2003). Oceanic uptake of CO_2 accounts for nearly a third of anthropogenic carbon that is added to the atmosphere (Sabine et al. 2004). As anthropogenic-derived atmospheric CO_2 exchanges with the surface ocean, the net effect is an increase in $[\text{CO}_2]_{\text{aq}}$ coupled with a decrease in $\delta^{13}\text{C}_{\text{DIC}}$, termed the [oceanic ^{13}C] Suess effect (Quay et al. 1992). Concomitant to increases in oceanic $[\text{CO}_2]_{\text{aq}}$, reductions in seawater pH and alterations in seawater calcium carbonate saturation are occurring – phenomena collectively known as ocean acidification (Doney et al. 2009). Long-term studies addressing increased anthropogenic inputs of CO_2 to the ocean and the resulting biogeochemical consequences have been conducted at several sites, including the waters off Bermuda (related to the Bermuda Atlantic Time-Series Study, BATS). Gruber et al. (2002) documented an increase in oceanic pCO_2 since the 1980s, along with a persistent $\delta^{13}\text{C}$ isotopic dilution of DIC (Figure 2). Researchers have also observed a 0.02 unit per decade decrease in pH and lower calcium carbonate saturation states of surface waters at BATS during the same time period (IPCC 2007).

The biological effects of increasing anthropogenic CO_2 concentrations and ocean acidification are largely unknown, although calcifying organisms will likely be the most negatively affected (Doney et al. 2009). The responses of phytoplankton to elevated $[\text{CO}_2]_{\text{aq}}$ have been mixed (Beardall and Raven 2004, Dason and Colman 2004). Small (< 10%) increases in phytoplankton photosynthesis have been documented in some laboratory studies, although it has been impossible to examine photosynthetic rate separately from the effects of reduced pH (Raven et al. 2005). In a recent mesocosm experiment with a diatom- and coccolithophore-dominated phytoplankton community, CO_2 uptake was 27% and 39% higher in 700 μatm (high CO_2) and 1050 μatm (very high CO_2) treatments, respectively (Riebesell et al. 2007). Similarly, the cyanobacteria *Synechococcus* exhibited a greatly elevated photosynthetic rate under high CO_2 conditions (Fu et al. 2007). At BATS, Gruber et al. (2002) also reported an increase in net primary and annual community production since 1980. Given the documented increase in atmospheric and oceanic $[\text{CO}_2]$ and associated evidence of increases in primary productivity, it seems reasonable that long-term decrease in marine mammal $\delta^{13}\text{C}$ are strongly affected by anthropogenic CO_2 input (and the resulting effects to the ecosystem) rather than decreases in primary productivity. Additionally, Cullen et al. (2001) suggested that phytoplankton may increase the magnitude of their carbon isotope fractionation in response to increasing $[\text{CO}_2]_{\text{aq}}$, effectively decreasing their observed $\delta^{13}\text{C}$ value.

Climate Variability

In addition to the impact of anthropogenic CO₂ inputs, climate variability likely contributes significant inter-annual variability to long-term marine mammal stable isotope datasets. Natural climatic fluctuations acting on marine ecosystems may exert pressures on marine mammal species and their prey. Inter-annual climate and oceanographic variability in the northeast Pacific has been linked to the El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) (Chavez et al. 1999).

The ENSO is a coupled instability in the ocean-atmosphere, triggered by feedback between sea-surface temperature anomalies, wind stress, and convective activity in the tropical Pacific (Peixoto and Oort 1992). The effect is warm (El Niño) and cold (La Niña) phases, responsible for a large portion of the inter-annual variability in the global climate system. The inter-annual variability of the ocean's carbon storage was also associated with El Niño and La Niña (Chavez et al. 1999). The effects of ENSO events on marine mammals are likely derived via trophic linkages. For example, during El Niño years, elephant seals (*Mirounga leonina*) at King George Island exhibited lower seal weaning masses than during La Niña years. Increased water temperatures in elephant seal foraging grounds during La Niña years led to rapid growth of squid, better foraging success of pregnant elephant seals, and higher seal weaning mass (Vergani et al. 2008). Additionally, Leaper et al. (2006) described a strong relationship between southern right whale (*Eubalaena australis*) breeding success and sea surface temperature (SST) anomalies, likely mediated by global climate drivers resulting in oceanographic changes and interannual variability in krill density.

The PDO refers to large-scale sea-surface temperatures in the North Pacific, and oscillates between a warm and cool phase (Bond and Harrison 2000). It is characterized by a long periodicity, approximately 20-30 years (Zhang et al. 1997). Shifts between warm and cool phases often result in dramatic changes in marine ecosystems, and these shifts are often characterized as “regime shifts” (Overland et al. 2008). Decadal scale regime shifts may have striking effects on fish productivity, often comparable to fishing activities (Mantua et al. 1997). One such regime shift occurred in 1977, when the PDO shifted from a warm to a cool phase (Beamish et al. 1999). In the northeast Pacific, this regime shift negatively influenced the recruitment of salmon, hake, and herring stocks (Beamish and Bouillon 1993, Francis and Hare 1994). Such changes in fish stock recruitment hindered the foraging success of piscivorous marine mammals like Steller sea lions (Trites et al. 2007).

Newsome et al. (2007) examined the impact of climate variability to Northern fur seal teeth $\delta^{13}\text{C}$ records, effectively removing the long-term anthropogenic CO₂ signal from the data by “de-trending” with linear regression. The [de-trended] $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios of Northern fur seal teeth fluctuated on a 20-25 year wavelength, suggesting that trophic conditions may have varied in concert with natural climatic fluctuations (specifically the PDO, Newsome et al. 2007). A similar relationship can be seen in the published $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bowhead baleen records (Figure 1), where there is a strong linear decrease in both isotopes across time and also a secondary oscillating trend.

Loss of Sea Ice

As the polar seas warm in response to a changing climate, the extent and quality of sea ice is decreasing (Parkinson et al. 1999, Perovich & Richter-Menge 2009). Concurrently, the flow of nutrients and energy through high latitude food webs may be transitioning to pelagic dominated production as sea ice and its associated ice-algae decline (Moline et al. 2008). The relative contribution of pelagic diatom- and ice algae-fixed carbon can be examined with stable isotopes, as ice algae carry a significantly higher $\delta^{13}\text{C}$ signature than pelagic diatoms (Budge et al. 2008). If the contribution of pelagic diatom-derived carbon increases in polar and sub-polar ecosystems, a general decrease in $\delta^{13}\text{C}$ would be observed in affected ecosystems/food webs and by extension, higher consumers.

Conclusions

This paper has outlined several physical, biological, and climatological variables that directly or indirectly influence the isotopic signature through the flow of nutrients through food webs. The relative importance of these variables to the health of marine ecosystems and the population biology of associated marine mammals is not well understood. Long-term stable isotope records derived from marine mammals, especially cetaceans which feed low in the food web, present a unique retrospective glimpse at historical conditions. These isotope records also provide a baseline with which to judge recent changes in the environment, and the subsequent impacts on the ecology of higher consumers. Therefore, continued study of marine mammal isotope records is warranted, and datasets should be created or updated when and where samples allow.

Table 1: *Summary of existing long-term marine mammal stable isotope records.*

Species	Tissue	Record	Location	Reference
Bowhead Whale	Baleen	1946-1998	Beaufort Sea, Bering Sea	Schell 2000, 2001 Lee et al. 2005 deHart 2006
Right Whale	Baleen	1883-2005	North Atlantic	Lysiak 2008
Harbor Porpoise	Bone	1848-2002	North Sea	Christensen & Richardson 2008
Steller Sea Lion	Bone, Teeth	1953-1997	Gulf of Alaska, Bering Sea	Hirons et al. 2001 Hobson et al. 2004
Harbor Seal	Bone	1951-1996	Gulf of Alaska, Bering Sea	Hirons et al. 2001
Northern Fur Seal	Bone, Teeth	1914-2000	Gulf of Alaska, Bering Sea	Hirons et al. 2001 Newsome et al. 2007
Ringed Seal	Teeth	1200-1998	Canadian Arctic	Outridge & Hobson 2008
Beluga Whale	Teeth	1200-1998	Canadian Arctic	Outridge & Hobson 2008

Figure 1: Annual average carbon and nitrogen stable isotope ratios measured in bowhead whale baleen, when whales were feeding in the Bering and Chukchi seas. Least-square linear fits are shown for the carbon (1965-1998) and nitrogen (1952-1998) data (from Schell 2001, Lee et al. 2005)

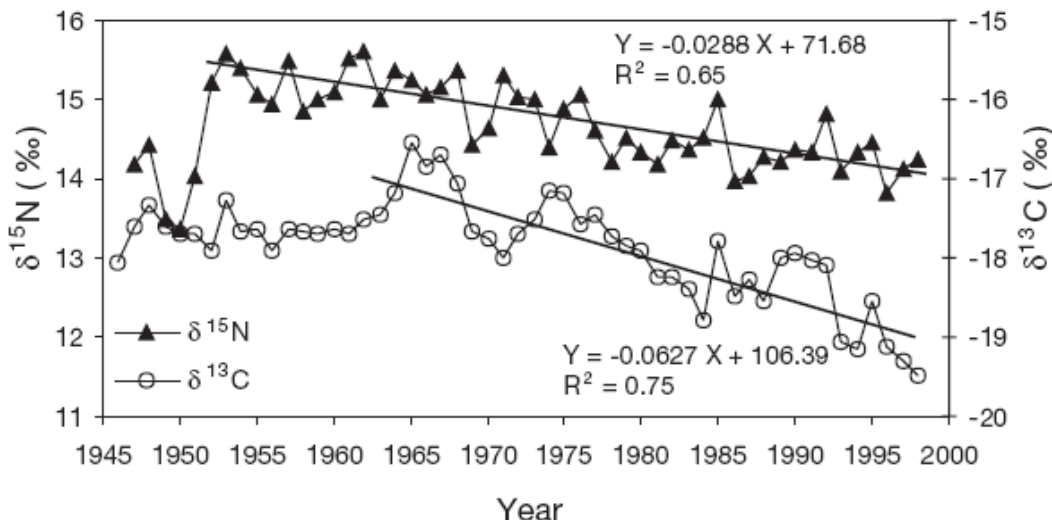
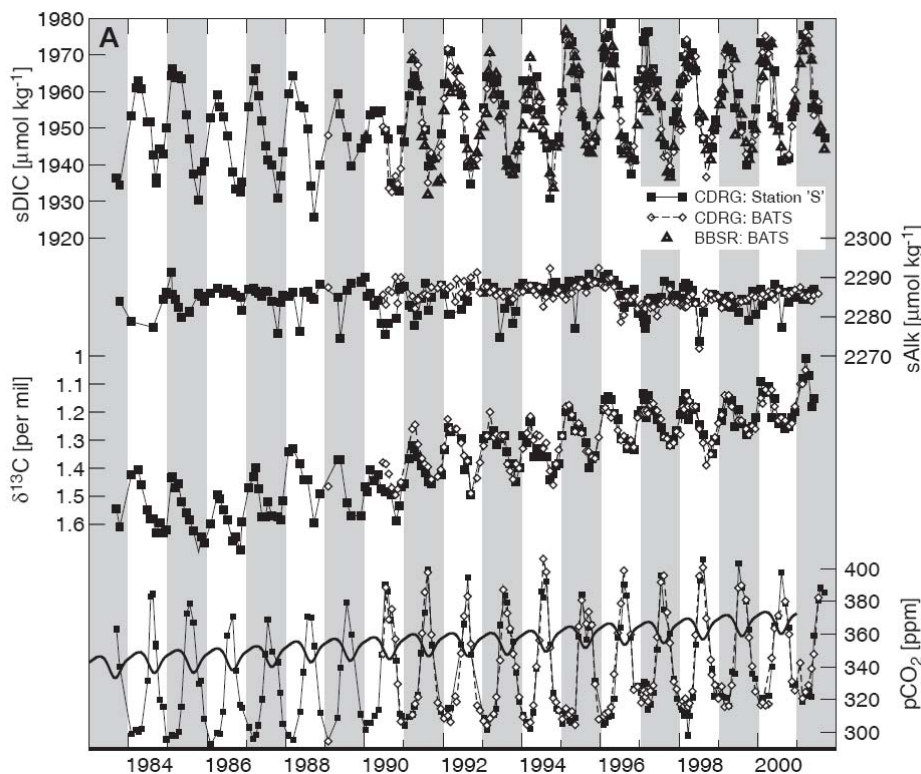


Figure 2: Time series of the properties of inorganic carbon in the upper-ocean mixed layer in waters of Bermuda. The $\delta^{13}\text{C}$ of DIC is inverted to make the long-term relation with DIC more evident. The concentrations of DIC and alkalinity (sDIC and sAlk) were normalized to a constant salinity (35 ppt). (from Gruber et al. 2002).



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