Journal of Archaeological Science 36 (2009) 2734–2741

Contents lists available at ScienceDirect

Journal of Archaeological Science

journal homepage: http://www.elsevier.com/locate/jas

A Late Holocene vertebrate food web from southern Haida Gwaii (Queen Charlotte Islands, British Columbia)

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ARTICLE INFO

Article history:
Received 11 June 2009
Received in revised form
29 July 2009
Accepted 31 August 2009

Keywords:
Stable isotopes
Trophic level
Marine diet
Ecology
Food web
Northwest Coast
Haida Gwaii

ABSTRACT

This study presents isotopic data (δ^{13}C and δ^{15}N from bone collagen) for 104 samples representing 29 vertebrate taxa from late pre-contact through to contact era (ca. 2000 – 100 BP) Haida Gwaii (British Columbia, Canada) from a wide variety of mostly marine organisms. The results demonstrate the considerable isotopic variability that characterizes potential prey items in coastal contexts and underscores the need for baseline faunal data to interpret human subsistence practices. Based on these data, a detailed marine food web was constructed, which provides insight into local ecological conditions. We present a simple method for quantifying the trophic level of ancient fauna using δ^{15}N of bone collagen. Finally, we discuss the implications of this study for the reconstruction of human diet.

1. Introduction

Since the early 1980s, isotopic analyses have played an important role in reconstructing diet in archaeological populations. Since stable carbon and nitrogen isotope values derived from bone collagen ($\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$) provide direct evidence of dietary intake, distinctions can be made with respect to the relative contributions of marine and terrestrial resources or C_3 and C_4 plants (for a comprehensive review, see Ambrose, 1993). In addition, $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ can be used to determine trophic level and reconstruct foraging behavior in both modern and ancient ecosystems (e.g. Bocherens and Drucker, 2003). Within a species, variability in local vegetation, climate, hydrology or soil composition can also affect the stable isotope values of bone collagen, thus allowing them to be utilized in the reconstruction of past environmental conditions.

In addition to being utilized in archaeological contexts, isotopic analyses have also regularly been used in ecological studies to assess a wide variety of problems ranging from the influence of anthropogenic nitrogen (e.g. Oczkowski et al., 2009) to trophic dynamics (e.g. Davenport and Bax, 2002). Because of the fairly regular enrichment in ^{15}N that occurs between prey and consumer tissues (Minagawa and Wada, 1984), it is possible to examine the trophic position of both marine and terrestrial organisms (Kaehler et al., 2000; Lesage et al., 2001; Palmqvist et al., 2008). In marine ecosystems, there are often multiple sources of carbon (e.g. benthic/pelagic in coastal systems or marine/terrestrial/riverine in estuaries), which are isotopically distinct (France, 1995; Michener and Schell, 1994; Middelburg and Nieuwenhuize, 1998). Based on δ^{13}C and δ^{15}N values, an isotopic food web can be constructed. This technique has been applied successfully to a number of different marine environments (e.g. Das et al., 2003; Davenport and Bax, 2002; Fry, 1988; Hobson and Welch, 1992; Kaehler et al., 2000). Isotopic data from archaeofaunal assemblages are now being utilized to address similar questions about past ecosystems and examine long-term ecological change (e.g. Corbett et al., 2008; Gifford-Gonzalez et al., 2005).

Modern ecological studies of trophic dynamics are often based on stomach contents and/or the isotopic analysis of tissues that turn over rapidly (e.g. muscle, blood, liver, feather). Stomach contents, however, provide insight into a consumer's diet for only a very short period of time (several days). Similarly, the turnover rate of protein in muscle is quite rapid (~2 weeks), owing to its relatively high metabolic costs (Hobson and Clark, 1992). Bone collagen remodels at a much slower rate than more metabolically

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doi:10.1016/j.jas.2009.08.013

active tissues (e.g. blood, muscle, liver); therefore, isotopic analyses of this tissue more accurately reflect what can be considered an average of a consumer's diet (Hobson, 1990) and can better account for temporal and spatial variability.

These principles have extended into archaeology and greatly increased the resolution with which it is possible to analyze human diet. Schwarcz (1991) emphasizes the need to understand the isotopic variability in items that may have been consumed when modeling dietary intake. Often, this is achieved through the examination of known isotopic values of modern potential food items (e.g. Keenleyside et al., 2009; White et al., 2001). Due to the fragmentary nature of the archaeological record, such an approach is often necessary, particularly for plants and invertebrates. The isotopic analysis of contemporaneous vertebrate faunal remains from archaeological sites, however, provides more direct evidence of dietary intake *and* allows for human isotopic data to be placed within the context of local ecology (e.g. Bösl et al., 2006; Coltrain, 2009; Keegan and DeNiro, 1988; Newsome et al., 2004; von Steinsdorff and Grupe, 2006). Although a considerable number of prehistoric human remains from the Northwest Coast have been analyzed for $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ (e.g. Chisholm et al., 1983; Schwarcz, 1991), these and similar data often lack baseline isotopic values from local flora and fauna, which precludes an in-depth understanding of subsistence practices. This problem, however, is not specific to the Northwest Coast of North America and it has become routine to interpret shifts in human consumption patterns in coastal environments in the absence of isotopic data from contemporaneous or modern prey items. This study was initiated to provide a more complete picture of the isotopic composition of fauna from Haida Gwaii, and to address ecological conditions in this region in the Late Holocene.

2. Archaeological context

Haida Gwaii (Queen Charlotte Islands) is located off the north coast of British Columbia (Canada) in traditional Haida territory and consists primarily of two large islands (Graham and Moresby) surrounded by hundreds of smaller islands and islets. The islands are extremely isolated, being separated from the nearest adjacent land by at least 55km (Fig. 1; Moss, 2008). Archaeological samples utilized in this analysis were collected from the southern portion of the archipelago, in Gwaii Hanaas National Park Reserve and Haida Heritage Site.

The indigenous terrestrial fauna of Haida Gwaii is quite limited and was of minor economic importance to the Haida, with terrestrial species tending to be insignificant in most vertebrate faunal assemblages. Conversely, a great diversity of both mammals and fish are distributed in the coastal waters surrounding Haida Gwaii.

The cultures of the Northwest Coast are well known for having developed complex, stratified societies with economies based largely on hunting and gathering. The abundance of marine resources, especially salmon, is often cited as being of paramount importance for the development of these complex societies (Ames, 2005). The cultural complexity as well as the intensive marine subsistence economies for which the Northwest Coast are so well known developed over several thousand years. Intensive exploitation of marine resources existed on the central coast by at least 4500 BP (Coupland, 1998), and by at least 3500 BP on the northern coast (Ames, 1998). In some areas, a strong maritime adaptation existed considerably earlier, with a marine focus evident at Namu back to ~7000 BP (Cannon, 1991) and at Kilgii Gwaay, in southern Haida Gwaii, by ~9500 BP (Fedje et al., 2005).

Material analyzed in this study is derived from the Late Graham Tradition (ca. 2000 BP – 200 BP) through to the period following European contact. During the Late Graham Tradition, there is archaeological evidence for extensive regional interaction and conflict, more efficient food procurement technology and an increased emphasis on marine resources (Fedje and Mackie, 2005; Fladmark et al., 1990; Mackie and Acheson, 2005). Owing to the rich suite of marine resources available, settlement was relatively dispersed and seasonal mobility was limited (Fedje and Mackie, 2005). There is also an increased degree of similarly to the coastal mainland with respect to site elements, suggesting some cultural continuity between the two regions (Mackie and Acheson, 2005).

Contact with Europeans and the subsequent maritime fur trade (1780 to 1830) exerted a tremendous impact on the people of the Northwest Coast, including the Haida. It brought prosperity, as well as European trade goods to many industrious individuals, though this prosperity was short-lived. Intensified trading and interaction between coastal and interior groups facilitated not only the exchange of goods, but also of cultural practices. Marriage traditions, descent systems, potlatches, and artistic traditions were among the practices 'exchanged' between groups during the fur trade era (Gibson, 1992).

3. Materials

Faunal samples utilized in this study are derived primarily from three village sites (699T, 781T, 785T), with a small number of samples from four additional villages (717T, 740T, 924T, 1134T), all located in the southeastern portion of Haida Gwaii (Fig. 1). The village of *Kaidsu* (781T) is located on the eastern shore of Moresby Island in Juan Perez Sound. The site is characterized by large but irregularly distributed shell midden deposits. Based on the volume of traditional, Late Graham Tradition artifacts and the relative scarcity of European trade goods, it is likely that this site was occupied for a long period of time prior to contact, followed by a relatively brief occupation in the early contact period (Orchard, 2007). Located on the west coast of Lyell Island, the village of *Xuud tsixwaas 'llnagaay* (785T) contains at least six house features and substantial shell midden deposits. Radiocarbon dates indicate an occupation stretching back into the Late Graham (ca. 2000 years BP). The presence of contact period goods (glass and copper beads) indicate that the site was occupied into the contact period (Orchard, 2007). The village of *Qayjuu 'llnagaay* (699T) is located on the southeast shore of Moresby Island and comprises sixteen house depression features and substantial shell midden deposits. This site appears to have been occupied from the late pre-contact through to the post fur trade periods, based on archaeological and ethnohistoric evidence (Acheson, 1998; Orchard, 2007). Both 717T and 924T likely represent pre-contact through contact period occupations, but the lack of temporally diagnostic artifacts and radiocarbon dates preclude more precise dating of these sites. *Huulaagwaans 'llnagaay* (1134T) appears to be a relatively short-lived and possibly entirely post-contact occupation (Orchard, 2007).

In all, 104 samples representing 32 vertebrate taxa were analyzed for stable carbon and nitrogen isotopes. The species selected represent those that are most likely to have been of the greatest economic importance to the Haida (following Blackman, 1990; Orchard, 2007). Ideally, multiple individuals from each species were analyzed to attempt to account for intraspecific variability in diet and physiology (cf. Barnes et al., 2008), though this was not always possible due to a lack of appropriate material.

4. Isotopic methodology

Bone collagen was extracted using a modified Longin (1971) method. Bone fragments (typically 50–300 mg) were sampled from faunal specimens; for most species of fish, the entire element was used. Since herring (*Clupea pallasii*) and prickleback (*Xiphister* sp.)

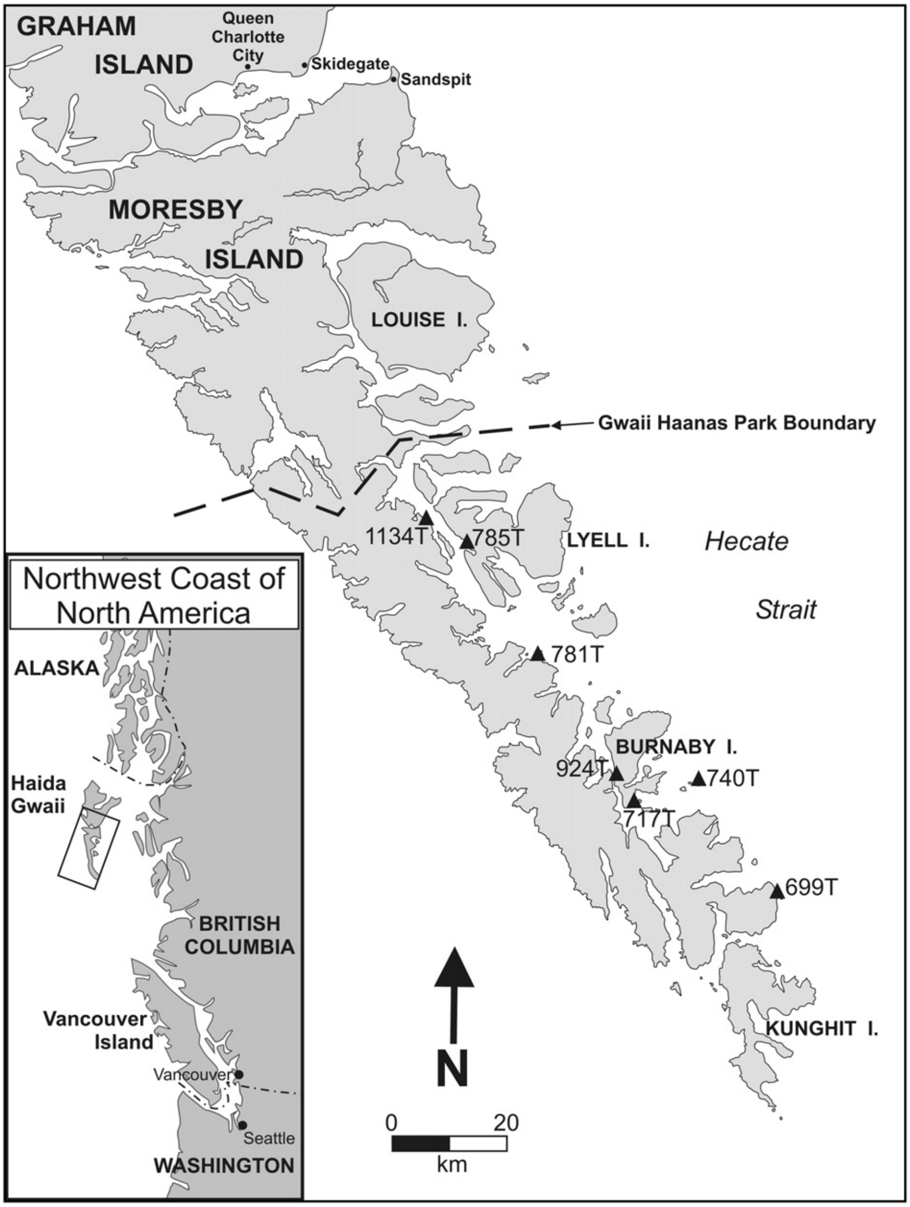

Fig. 1. Map of southern Haida Gwaii showing sites from which faunal material was sampled in this analysis.

are small, bulk samples were used for these species, with a number of elements being taken from the same archaeological context. For herring, twelve to sixteen vertebrae were used, whereas six vertebrae were used for prickleback. This type of bulk sampling for small taxa is common in ecological studies (e.g. Pinnegar and Polunin, 2000). Any visible foreign material was removed with a small brush. Samples were then reduced to a coarse powder (fragments 1.0–2.0 mm in diameter) and cleaned in an ultrasonic bath. Following cleaning, samples were dried and weighed.

Bone fragments were soaked in 0.50 M HCl until they were completely demineralized. They were rinsed with MQ water and treated with 0.10 M NaOH for 30 min to remove humic acids. This step was repeated until the solution was clear. Samples were then rinsed to neutrality with MQ water, rinsed with 0.25 M HCl and finally with MQ water, leaving the insoluble collagen in a slightly acidic solution (pH $\approx$ 3).

The solution containing the insoluble residue was heated in sealed glass tubes at 75 ± 2 °C for 24–36 h to gelatinize the collagen. Samples were then centrifuged and the gelatinized collagen was transferred into glass vials. Vials were placed in a sealed oven until all water was evaporated at 80 ± 2°C. The extracted collagen was then transferred into tin cups for isotopic analysis.

Stable isotope compositions of collagen ($\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$) and relative percentages of carbon and nitrogen were determined using a Thermo Finnigan DeltaPLUS XP continuous-flow mass-spectrometer at McMaster University. Stable carbon and nitrogen isotope ratios are reported versus VPDB and atmospheric nitrogen, respectively. Standard deviation was better than ±0.1‰ for $\delta^{13}C$ and ±0.2‰ for $\delta^{15}N$.

5. Results

Average isotopic values for all analyzed taxa are presented in Table 1 (see Supplementary Material for all data). All atomic C:N ratios are within the range of accepted values for well-preserved

Table 1
Mean stable isotope values by species.

Species		*N*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Trophic Level
Marine birds					
Ancient murrelet	*Synthliboramphus antiquus*	15	-14.2 ± 0.5	17.9 ± 0.7	3.8
Bald eagle	*Haliaeetus leucocephalus*	1	-11.8	17.5	3.7
Cassin's auklet	*Ptychoramphus aleuticus*	1	-14.0	16.9	3.6
Common loon	*Gavia immer*	1	-12.3	18.0	3.8
Common murre	*Uria aalge*	1	-13.5	19.3	4.2
Rhinoceros auklet	*Cerorhinca monocerata*	1	-13.8	18.0	3.8
Short-tailed albatross	*Phoebastria albatrus*	1	-14.6	20.0	4.3
Terrestrial birds					
Canada goose	*Branta canadensis*	1	-21.0	5.1	
Nearshore fish					
Cabezon	*Scorpaenichthys marmoratus*	2	-9.6 ± 0.4	15.4 ± 0.4	3.2
Dogfish	*Squalus acanthias*	3	-12.1 ± 1.6	13.4 ± 1.5	2.7
Greenling	*Hexagrammos* sp.	2	-10.7 ± 1.0	14.6 ± 0.5	3.0
Irish lord	*Hemilepidotus* sp.	2	-9.1 ± 0.1	15.5 ± 0.4	3.2
Lingcod	*Ophiodon elongates*	3	-10.4 ± 0.8	17.2 ± 0.6	3.6
Pacific cod	*Gadus macrocephalus*	2	-11.4 ± 0.4	17.3 ± 0.4	3.7
Pacific halibut	*Hippoglossus stenolepis*	2	-11.1 ± 2.3	17.5 ± 0.8	3.7
Prickleback	*Xiphister* sp.	2	-12.2 ± 1.2	13.4 ± 0.4	2.7
Ratfish	*Hydrolagus colliei*	2	-10.3 ± 0.3	16.0 ± 0.4	3.3
Rockfish	*Sebastes* sp.	9	-11.1 ± 0.8	15.9 ± 0.4	3.3
Pelagic fish					
Pacific herring	*Clupea pallasii*	3	-13.6 ± 0.9	13.5 ± 0.2	2.7
Anadromous fish					
Salmon	*Oncorhynchus* sp.	19	-15.1 ± 0.7	12.2 ± 0.8	
Marine mammals					
Harbour porpoise	*Phocoena phocoena*	2	-12.3 ± 0.3	19.3 ± 0.9	4.2*
Harbour seal	*Phoca vitulina*	3	-11.5 ± 1.0	18.4 ± 0.9	4.0*
Northern fur seal	*Callorhinus ursinus*	4	-12.6 ± 0.4	19.6 ± 0.6	4.2
Northern sea lion	*Eumetopias jubatus*	3	-12.0 ± 0.8	19.9 ± 0.7	4.2*
Pacific white-sided dolphin	*Lagenorhynchus obliquidens*	2	-11.3 ± 0.1	16.1 ± 0.2	3.4
River otter	*Lontra canadensis*	2	-10.7 ± 0.2	19.6 ± 0.4	4.2
Sea otter	*Enhydra lutris*	10	-10.9 ± 0.4	13.6 ± 0.5	2.7
Whale	Cetacae sp.	1	-13.1	17.3	3.7
Terrestrial mammals					
Black bear	*Ursus americanus*	3	-19.3 ± 1.5	4.0 ± 5.0	
Domestic dog	*Canis familiaris*	1	-12.2	17.9	

Taxa denoted with a (*) indicate that the trophic levels of these species were obtained from published sources and were used to estimate $\delta^{15}N_{POM}$.

bone collagen (2.9–3.6) as reported by DeNiro (1985). Figs. 2 and 3 graphically illustrate the $\delta^{13}C_{coll.}$ and $\delta^{15}N_{coll.}$ values of some of the major resources exploited by the Haida.

6. Discussion

6.1. Calculation of trophic position using bone collagen $\delta^{15}N$

The calculation of trophic positions for marine taxa in archaeological assemblages is of considerable importance. Knowing the trophic level of particular taxa not only facilitates a better understanding of the feeding ecology of the species in question, but also allows temporal changes in trophic position to be quantified. Since trophic level changes are indicative of large-scale alterations in the structuring of marine ecosystems (Pauly et al., 1998a), it is possible to examine the impacts of prehistoric, historic and modern populations on aquatic food webs using archaeofaunal material (e.g. Quitmyer and Reitz, 2006; Reitz, 2004; Wing, 2001). Stable nitrogen isotope measurements provide a direct way to quantify trophic level in animals.

It is common in ecological studies to assign numerical trophic levels to species based on the $\delta^{15}N$ values of their tissues. This is typically calculated with the following equation (following Das et al., 2003):

$$TL_{con} = 2 + (D_{con} - D_{POM} - TEF)/TEF$$

where TL_{CON} is the trophic level of the consumer, D_{CON} is the $\delta^{15}N$ value obtained for a consumer's tissue (bone collagen in this case), D_{POM} is the $\delta^{15}N$ value for particular organic matter (POM) for the area and TEF is the estimated trophic enrichment factor between

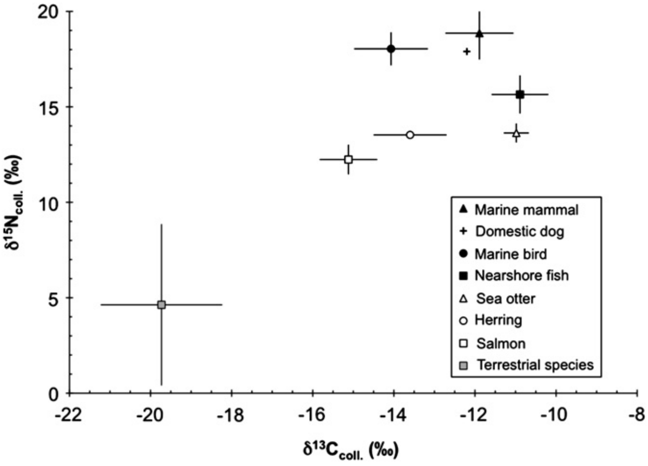

Fig. 2. Plot of $\delta^{13}C_{coll.}$ and $\delta^{15}N_{coll.}$ for major vertebrate groups from Haida Gwaii. All oceanic fish with the exception of salmon and herring are grouped together as nearshore fish. All birds except Canada goose are grouped as marine birds. Terrestrial species include black bear and Canada goose. Error bars represent one standard deviation.

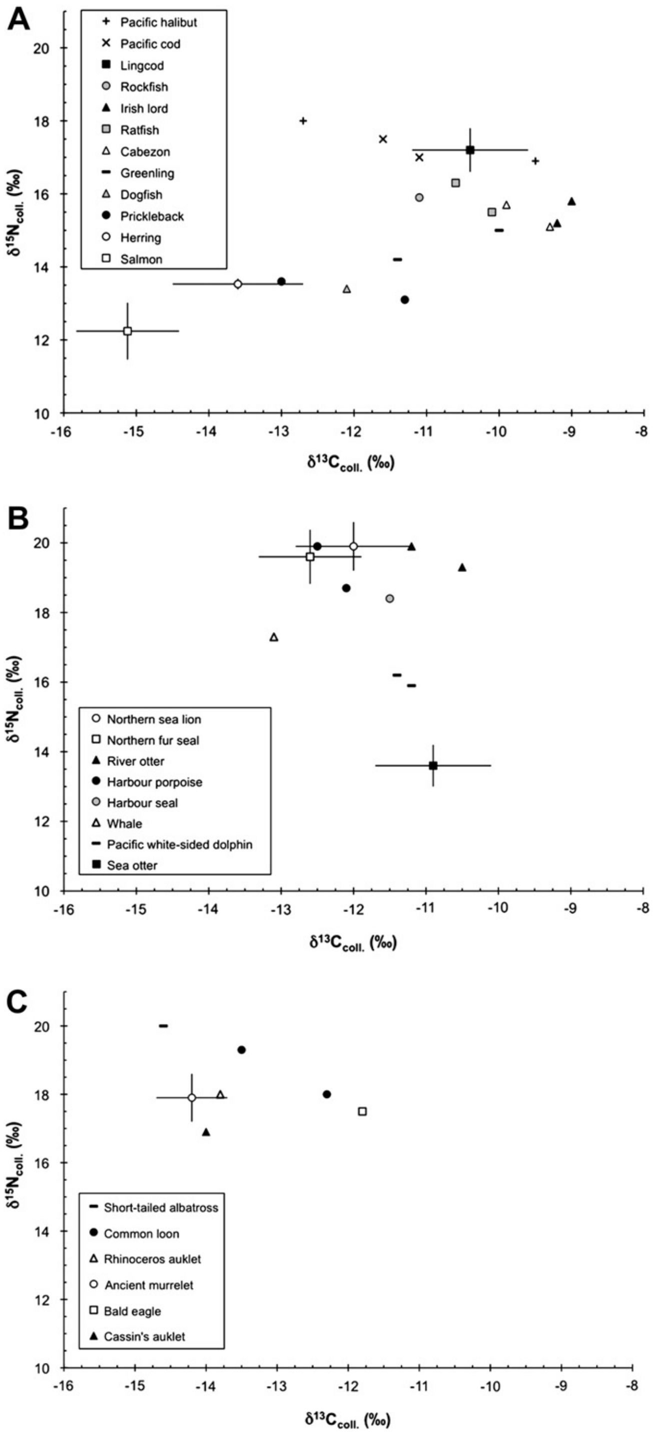

Fig. 3. Plot of $\delta^{13}C_{coll.}$ and $\delta^{15}N_{coll.}$ for individual species. A = fish, B = marine mammals, C = marine birds. Mean values with standard deviations (1σ) are shown for taxa where $N \geq 3$.

the consumer tissue and the diet. In marine ecosystems, the first trophic level is occupied by POM, and as a result $TL_{POM} = 1.0$. While in modern ecological studies $\delta^{15}N_{POM}$ can be measured directly (e.g. Middelburg and Nieuwenhuize, 1998), this is not possible in archaeological investigations. Furthermore, it may be unreasonable to use modern $\delta^{15}N_{POM}$ values for a given region since there is likely to be considerable temporal variability as a result of changes in nutrient availability, environmental conditions and/or alterations in the food web structure (Oczkowski et al., 2009). As a result, in archaeological contexts, it is necessary to work backwards through this equation to determine a value for $\delta^{15}N_{POM}$.

We used published trophic positions of three species (harbour seal [*Phoca vitulina*], northern sea lion [*Eumetopias jubatus*] and harbour porpoise [*Phocoena phocoena*]) from Pauly et al. (1998b) and Das et al. (2003). Similar trophic levels of ~4.0 are reported for modern pinnipeds and toothed cetaceans from the waters around Haida Gwaii (Beattie et al., 1999). For simplicity, the enrichment in ^{15}N between diet and bone collagen was assumed to be consistent between different taxa and across different trophic levels. While there may be some variability between species, Vander Zanden and Rasmussen (2001) have noted that the calculation of trophic position and results of mixing models are minimally affected by differences in $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ values. For all other species, an enrichment factor of 4.0‰ was used, based on average values obtained from a number of studies (see Bocherens and Drucker, 2003). $\delta^{15}N_{POM}$ was calculated using the published trophic levels of the three species mentioned above (values of 6.4‰, 7.1‰, 6.5‰) and the average value for $\delta^{15}N_{POM}$ was 6.7‰, which is very similar to other published data for the region. Hobson et al. (1994) reported a value of 6.8‰ for $\delta^{15}N_{POM}$ in southern British Columbia. Using the calculated value for $\delta^{15}N_{POM}$, the trophic levels of marine taxa were calculated (see Table 1).

6.2. *Ecological implications*

Isotopic analysis of marine animal tissues also provides insight with respect to the environment in which the animal lived, largely as a result of isotopic variability at the base of the food chain (phytoplankton and POM) that is passed along to consumers. Nearshore or benthic food webs tend to be characterized by more positive $\delta^{13}C$ and $\delta^{15}N$ values than offshore or pelagic food webs (Cherel and Hobson, 2007; France, 1995; Hobson, 1991; Hobson et al., 1994). Additionally, $\delta^{13}C$ values of primary producers vary with latitude (Quillfeldt et al., 2005). This latitudinal effect on $\delta^{13}C$ values is passed on to consumers and animals foraging at high-latitudes tend to record $\delta^{13}C$ values that are more ^{13}C-depleted than animals foraging at middle-latitudes (Burton and Koch, 1999).

In this study, taxa that are known to be primarily associated with nearshore habitats recorded less negative $\delta^{13}C$ values than those associated with pelagic habitats. For example, Pacific herring (*Clupea pallasii*) were considerably more depleted in ^{13}C than all other oceanic fish. Salmon (*Oncorhynchus* sp.) also exhibited more negative $\delta^{13}C$ values, which likely reflects both the pelagic nature of most salmon, as well as time spent in freshwater as juveniles (see Johnson and Schindler, 2009). The considerable range in Pacific halibut $\delta^{13}C$ values is accounted for by the life history strategy of this species, which spends the first several years of its life near shore, before moving further offshore as it matures (Gao and Beamish, 2003). Because offshore carbon is more ^{13}C-depleted than nearshore carbon, larger fish should exhibit more negative $\delta^{13}C$ values.

Although ratfish (*Hydrolagus colliei*) are a relatively small species known to feed primarily on benthic invertebrates (Armstrong, 1996), the $\delta^{15}N$ and calculated trophic level for this species were quite high, 16.0 and 3.3 respectively. These values most likely reflect a high contribution of crabs, prawns and shrimp (e.g. *Cancer* sp., *Pandalus* sp.) to the diet, all of which are abundant in the waters surrounding Haida Gwaii (Sloan et al., 2001). Since the trophic level of these invertebrates is commonly over 3.0 (Fredriksen, 2003; Lesage et al., 2001), it should not be unusual for ratfish to have recorded high $\delta^{15}N$ values. This highlights the fact that relatively small species of little economic value (cf. Cannon, 1995), may actually record very high $\delta^{15}N$ values.

Sea otters have been known to incorporate variable amounts of nearshore fish (greenling and rockfish) in their diets, with this behaviour occurring more frequently in areas where sea otter populations are higher (at or near equilibrium density) as is the case in some parts of Russia and Alaska (Riedman and Estes, 1988). Pauly et al. (1998b) estimated the trophic level of sea otters to be 3.4 based on a diet of 80% benthic invertebrates, 10% demersal fish, 5% small squids and 5% small pelagic fish. Accordingly, the otters analyzed in this study were likely consuming a diet of almost exclusively benthic invertebrates (e.g. sea urchins, clams and bivalve mollusks). This suggests that the sea otter populations in southern Haida Gwaii may have been below equilibrium density prior to the maritime fur trade. Such a pattern may result from human hunting pressure and the local extirpation of sea otters from the waters immediately surrounding village sites (e.g. Corbett et al., 2008; Simenstad et al., 1978). Certainly, sea otters are a ubiquitous and abundant contributor to mammalian assemblages from virtually all Late Holocene sites yet analyzed from southern Haida Gwaii (Orchard, 2007). Further isotopic analysis of archaeological sea otters may clarify this issue.

The isotopic composition of northern fur seal (*Callorhinus ursinus*) bone collagen merits some discussion because there has been considerable interest in the temporal variability in the breeding and migratory patterns of this species (e.g. Burton et al., 2001; Gustafson, 1968; Moss et al., 2006). Presently, northern fur seal populations breed at high latitudes, with the overwhelming majority of the North American population breeding in the Pribilof Islands in Alaska (Gifford-Gonzalez et al., 2005). Based on the distribution of northern fur seals in archaeofaunal assemblages on the Pacific coast of North America (e.g. Gustafson, 1968), however, it appears likely that the biogeography of this species through the Holocene was markedly different than it is today.

Burton and Koch (1999) demonstrated that harbour seal (a nearshore species) bone collagen was significantly less ^{13}C-depleted than male northern fur seals in Alaska and female northern elephant seals in California, both of which are offshore feeders. Ample evidence demonstrates that nearshore carbon is less depleted in ^{13}C than offshore carbon (France, 1995) and this is reflected in the organisms foraging in either location (Burton and Koch, 1999; Hobson et al., 1997; Kurle and Worthy, 2001). Moreover, because δ^{13}C values of phytoplankton are affected by latitude, pinnipeds foraging at middle latitudes should record δ^{13}C values that are less depleted in ^{13}C than those foraging at high latitudes (Burton and Koch, 1999). Burton et al. (2001) went on to analyze δ^{13}C and δ^{15}N of northern fur seal bone collagen from two Holocene coastal sites in California. They suggested that because the isotopic signatures of the archaeological northern fur seals from these locations were more similar to other pinnipeds, which forage offshore and remain at middle latitudes year-round, northern fur seals did not seasonally migrate from high-latitude rookeries, but remained at middle latitudes year round.

Given the relatively high-latitude of southern Haida Gwaii, we would expect that migratory northern fur seals would record isotopic signatures intermediate between northern fur seals from Alaska and California and likely more similar to individuals from the Pribilof Islands. Indeed, Moss et al. (2006) performed isotopic analysis (δ^{13}C and δ^{15}N of bone collagen) on northern fur seals from the Netarts site on the northern coast of Oregon and found the isotopic signatures were very similar to those obtained from animals in the Pribilof Islands. They go on to suggest that while fur seals from California may be isotopically distinct from those in Alaska, animals foraging north of California will tend to resemble modern individuals from the Pribilof Islands. The δ^{13}C values of northern fur seals from Haida Gwaii were, however, not significantly different (Student's t-test) than Holocene specimens from Mendocino ($p = 0.8211$) or Monterey Bay ($p = 0.1785$), but were significantly different than modern samples from the Pribilof Islands ($p = 0.0007$ for males, $p = 0.0135$ for females) and Holocene samples from Netarts ($p = 0.0090$ for males, $p = 0.0002$ for females) (Fig. 4). With respect to coeval species, Haida Gwaii fur seals were more ^{13}C-depleted than nearshore marine mammals (sea otters, harbour seals), suggesting they were not foraging locally close to shore (see Fig. 3). On this basis, we suggest that northern fur seals did not migrate from high-latitude rookeries into the waters around Haida Gwaii. Presently, only offshore, migratory northern fur seals that breed in the Pribilof Islands occur in these waters (Heise et al., 2003). The isotopic data, however, are not congruent with migratory fur seals from high-latitude rookeries. Instead, it is more likely that these individuals were either year-round residents or migrated from southern rookeries. Notably, site 699T (southern Haida Gwaii) produced two juvenile northern fur seal elements, including a measurable left radius with dimensions (greatest length = 63.12, greatest breadth of proximal end = 23.43, greatest breadth of distal end > 14.41) which suggest an age of ca. 6-9 weeks (after Crockford et al., 2002). Notably, pups of that age are restricted to rookeries among modern populations, and the presence of rookery-aged remains in archaeological deposits from southern Haida Gwaii provides further evidence for a locally-breeding population during the Late Holocene (e.g. Crockford et al., 2002). More generally, this supports suggestions for considerable regional variability in northern fur seal biogeography in the Holocene, and additional isotopic data from sites on the Pacific coast will provide further insight into this interpretation.

6.3. Implications for reconstructing human diet

Although no human samples were analyzed, the results of this study are very relevant to the reconstruction of ancient human diet. The subsistence economies of the Northwest Coast, while heavily focused on marine resources, were characterized by a considerable amount of regional and temporal variability (Butler and Campbell, 2004). Undoubtedly, this applies to coastal areas throughout the world where people may have intensively harvested small pelagic species (e.g. herring, sardines), marine mammals (e.g. whales, pinnipeds), anadromous fish (e.g. salmon), invertebrates (e.g. clams), nearshore fish (e.g. grouper, rockfish), or any combination

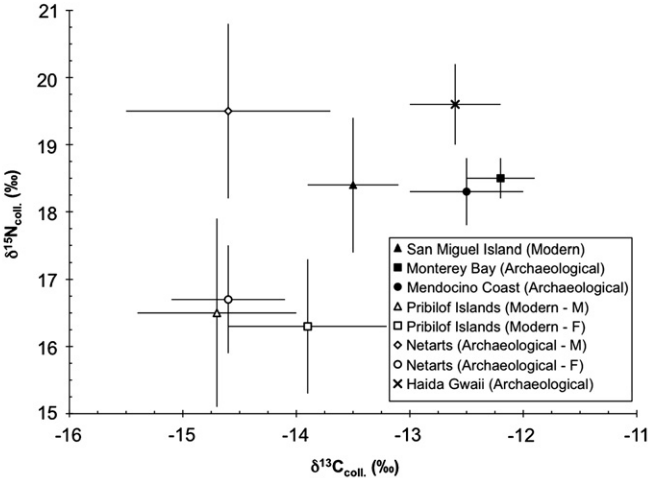

Fig. 4. Plot of $\delta^{13}C_{coll.}$ and $\delta^{15}N_{coll.}$ for modern and archaeological northern fur seals from the eastern North Pacific (M = male, F = female). Additional data obtained from Burton et al. (2001) and Moss et al. (2006). Error bars represent one standard deviation.

of these. Each of these economic modalities may be characterized by a diverse array of technological adaptations and settlement patterns. Thus, while the division between simply 'terrestrial' and 'marine' resource procurement in paleodietary studies is useful, it is also problematic in that it obscures considerable cultural variability. Moreover, discussions of 'higher' and 'lower' trophic level prey or 'lower quality' protein are also problematic when baseline isotopic data are lacking. For example, Moss et al. (2006) suggest that the anomalously high $\delta^{15}N$ values of harbour seal bone collagen at Netarts is indicative of access to higher trophic level prey, possibly salmon. In fact, of the twelve species of marine fish analyzed in the current study, salmon recorded the lowest $\delta^{15}N$ bone collagen values. In the data presented by Grier (2006) for Dionisio Point (southern coast of British Columbia) salmon were also the fish species with the lowest $\delta^{15}N$ values.

Baseline isotopic data are regionally specific for several reasons. First, species may exhibit geographic variability in foraging behaviour. For instance, sea otters in Alaska consuming proportionately more fish and fewer invertebrates than those in central California should possess tissues more enriched in ^{15}N. Isotopic variability in marine food webs is, however, ultimately controlled by primary producers. For $\delta^{15}N$, because oligotrophic (nutrient-poor) systems are dependent on recycled nitrogen, which is ^{15}N-depleted, $\delta^{15}N_{POM}$ in these systems tends to be lower than in eutrophic (nutrient-rich) systems (Michener and Schell, 1994). Many different sources of primary production can contribute to marine food webs, including: phytoplankton, seagrass and macrophyte algae. The relative contribution of each of these producers will affect the isotopic signatures of consumers living within these systems since they are often distinct (Duggins et al., 1989; Hemminga and Mateo, 1996). Since these differences are passed up the food web and there may be regional variability in consumer diets, it would be problematic to utilize isotopic values of fauna from regions other than the one in question for dietary reconstructions. Whenever possible, contemporaneous faunal remains should be analyzed in concert with human material to situate human diet within the local ecological context.

7. Summary

The isotopic analysis of archaeofauna can provide considerable insight into local ecological conditions, including: trophic dynamics, habitat preference and biogeography. These data, in turn, also provide a baseline with which to interpret human dietary patterns. Interpretations of these patterns are extremely difficult in the absence of such data, particularly in cases of productive coastal ecosystems with several isotopically distinct categories of marine resources.

Acknowledgements

Martin Knyf provided technical assistance. Financial support during the preparation of this paper was provided by a Social Science and Humanities Research Council of Canada Postdoctoral Fellowship to TJO and SSHRC Research Grant (No. 646-2006-1097) to DRG. The archaeological fieldwork on which this paper is based was made possible by the Council of the Haida Nation, the Archipelago Management Board, Parks Canada, Gwaii Haanas Staff, Marty Magne, Daryl Fedje, Ian Sumpter, Alan Davidson, Quentin Mackie, GHEAP Field Crews, Susan Crockford and Becky Wigen, the British Columbia Heritage Trust, SSHRC, the University of Toronto, and the University of Victoria. Two anonymous reviewers provided helpful comments on an earlier version of this manuscript.

Appendix. Supplementary data

The supplementary data associated with this article can be found in the on-line version at doi:10.1016/j.jas.2009.08.013.

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