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Changing gull diet in a changing world: A 150-year stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) record from feathers collected in the Pacific Northwest of North America

Running head: Changing gull diet in a changing world

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Abstract: The world's oceans have undergone significant ecological changes following European colonial expansion and associated industrialisation. Seabirds are useful indicators of marine food web structure and can be used to track multi-decadal environmental change, potentially reflecting long-term human impacts. We used stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) analysis of feathers from glaucous-winged gulls (*Larus glaucescens*) in a heavily disturbed region of the northeast Pacific to ask whether diets of this generalist forager changed in response to shifts in food availability over 150 years, and whether any detected change might explain long-term trends in gull abundance. Sampled feathers came from birds collected between 1860 and 2009 at nesting colonies in the Salish Sea, a transboundary marine system adjacent to Washington, USA and British Columbia, Canada. To determine whether temporal trends in stable isotope ratios might simply reflect changes to baseline environmental values, we also analysed muscle tissue from forage fishes collected in the same region over a multi-decadal timeframe. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ declined since 1860 in both sub-adult and adult gulls ($\delta^{13}\text{C}$, $\sim 2\text{--}6\text{‰}$; $\delta^{15}\text{N}$, $\sim 4\text{--}5\text{‰}$), indicating that their diet has become less marine over time, and that birds now feed at a lower trophic level than previously. Conversely, forage fish $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values showed no trends, supporting our conclusion that gull feather values were indicative of declines in marine food availability rather than of baseline environmental change. Gradual declines in feather isotope values are consistent with trends predicted had gulls consumed less fish over time, but were equivocal with respect to whether gulls had switched to a more garbage-based diet, or one comprising marine invertebrates. Nonetheless, our results suggest a long-term decrease in diet quality linked to declining fish abundance or other anthropogenic influences, and may help to explain regional population declines in this species and other piscivores.

Introduction

Marine ecosystems worldwide are responding to human-related stressors such as commercial fisheries, climate change, and pollution (Halpern *et al.*, 2008). Effects include degradation or loss of habitat, alteration of food webs, and declines in species richness and abundance, particularly in coastal areas (Roberts & Hawkins 1999; Crain *et al.*, 2009). The profound and potentially irreversible ecological consequences of such changes (Estes *et al.*, 2011) make it important to improve our understanding of them, particularly given their widespread nature and the growing public concern over ocean health (Crain *et al.*, 2009).

The inshore waters of southern British Columbia and northern Washington, collectively called the Salish Sea, have been ranked among the most disturbed coastal marine ecosystems on Earth (mean cumulative impact score for this region = 19.3, maximum study score = 19.5; Halpern *et al.*, 2008), and as such are targets for more effective conservation and management (Fraser *et al.*, 2006; Gaydos *et al.*, 2008). However, because of poor and incomplete monitoring, relatively few long-term population trends exist for individual species in the region (Pauly *et al.*, 1998; Gaydos & Pearson 2011), hampering the identification of ecological baselines and conservation targets.

In such cases, resident species for which long-term historical data exist stand as potential ecological indicators, particularly when their population growth, life history or diet can be linked to key ecosystem states or processes. Researchers have long recognised seabirds as useful indicators of marine food web structure and temporal changes (Ashmole & Ashmole 1968; Ainley & Boekelheide 1990; Furness & Greenwood 1993; Furness & Camphuysen 1997; Piatt *et al.*, 2007). Marine birds integrate ecosystem change across various spatio-temporal scales, yet as long-lived organisms they can be slow to show signs of alterations in the sampled environment

(Montevecchi 1993). Conducting studies spanning multiple decades overcomes this potential limitation, while simultaneously providing longer-term perspectives on ecological change.

Stable isotope analysis of museum specimens or archaeological samples is increasingly being used to assess long-term dietary changes for various avian taxa (Thompson *et al.*, 1995; Ainley *et al.*, 2006; Becker & Beissinger 2006). For example, Emslie & Patterson (2007) used stable isotope analysis of eggshell fragments ($\delta^{13}\text{C}$ in eggshell carbonate; $\delta^{15}\text{N}$ in eggshell membrane) from subfossil and modern samples to show that Adélie penguins (*Pygoscelis adeliae*) experienced an abrupt historical shift in diet from fish to krill in the 1700s, coincident with the industrial harvest and depletion of fur seals (*Arctocephalus gazella*) and whales. Norris *et al.*, (2007) and Gutowsky *et al.*, (2009) similarly used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of feathers to link population declines in British Columbia's marbled murrelet (*Brachramphus marmoratus*) to declines in fish prey over more than a century. Once grown, feathers are metabolically inert, so their isotopic values reflect diet during the period of feather generation (Mizutani *et al.*, 1990; Hobson 1999). In situations where consumers have access to marine foods, $\delta^{13}\text{C}$ values generally indicate the relative proportion of pelagic vs. inshore marine or terrestrial foods in the diet, while $\delta^{15}\text{N}$ values generally reflect the trophic level at which a bird was feeding at the time of feather growth.

Holarctic *Larus* gulls occur close to human settlements worldwide and have been studied in detail in many parts of their range, including the Salish Sea (Howell & Dunn 2007). Because gulls have been shown to respond strongly to variation in food availability and environmental change (Mills *et al.*, 2008), we identified them as a useful focal species for our study region. The glaucous-winged gull (*L. glaucescens*) is a common, marine-associated bird that has been studied

and collected for over 150 years (Anonymous 1908; Drent & Guiguet 1961; Hayward & Verbeek 2008). We were thus able to use archived specimens to test whether gulls could be used to determine long-term food web or dietary change in the Salish Sea (cf. Hobson 2007).

As a generalist consumer, glaucous-winged gulls should be buffered against ecological change. However, their populations in the Salish Sea increased rapidly during the mid-twentieth century, growing at c. 2.9% per annum from 1960 to 1986, before declining steeply to less than 50% of peak estimates (Galusha *et al.*, 1987; Vermeer & Devito 1989; Sullivan *et al.*, 2002; Hayward & Verbeek 2008; Blight *et al.* in revision). One hypothesis to explain variation in gull population growth invokes evolving waste management practices that first increased and then reduced gull access to garbage (Vermeer & Devito 1989; Vermeer 1992; Hayward *et al.*, 2010). However, there is conflicting evidence as to whether diets including garbage benefit gulls at the population level. For example, glaucous-winged gulls in British Columbia that fed their chicks marine diets (~90% fish) raised offspring that were heavier, grew faster (e.g., for 2-chick broods, mean asymptotic mass of 1014 vs. 883 g; 36 vs. 29 g d⁻¹), and fledged at a higher rate (84% vs. 68%) than those feeding chicks a diet containing garbage (Ward 1973). In the congeneric Western gull *L. occidentalis* in California, the most successful breeders also avoided garbage and fed themselves and their young primarily on fish (Pierotti & Annett 1990; Annett & Pierotti 1999). These findings imply, all things being equal, that we might expect declines in reproductive performance and population size if glaucous-winged gulls currently consume more garbage than they did historically. Indeed, Blight (2011) showed that glaucous-winged gulls in the Salish Sea have experienced a long-term decline in egg volume and clutch size, consistent with the hypothesis that dietary declines in high-quality fish and an increase in terrestrial sources of food reduces fecundity in this species. Conversely, for European herring gulls (*L. argentatus*) Spaans (1971) report-

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ed a positive correlation between amount of garbage in diet and brood size, and Pons (1992) reported a decline in reproductive rate coincident with the closure of a garbage disposal site.

Given the conflicting results above, we aimed to examine and quantify long-term trends in glaucous-winged gull diets to help elucidate how population trend, diet and environmental change may be linked in this species. Specifically, we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of adult and sub-adult glaucous-winged gull feathers collected in the Salish Sea between 1860 and 2009 to ask whether and how gull diets changed during the period of rapid human population increase following European colonization, and the associated industrialisation of coastal marine ecosystems in the region. If gull population trends were primarily driven by the declining availability of forage fish (Wallace 1998; Therriault *et al.*, 2009) and other fish foods (e.g., spawning salmon; Jewett 1953), we expected to observe an indication that the fraction of fish prey in gull diets declined over time, with feather isotope values showing declines in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as birds increasingly switched to feeding on marine invertebrates and/or C_3 -based garbage. Alternatively, we predicted that if glaucous-winged gull population growth was driven primarily by the availability of garbage, isotopic data should reflect an increase in terrestrially-based foods in gull diets up to the mid-1980s (i.e. decreases in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values), but a decline thereafter as management practices to restrict access to garbage were established and improved (Pons 1992; Hayward & Verbeek 2008). We further hypothesised that changes in the availability of garbage – or reduction of marine foods in gull diets – would affect sub-adults and adults differently, as adults are more proficient foragers in marine habitats (Verbeek 1977; Searcy 1978). Given this, and the fact that landfills are often used preferentially by sub-adults (Weiser & Powell 2011), we predicted that gull feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values would indicate a more marine (i.e. higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) and/or higher trophic level diets for adults than for sub-adults.

Interpretation of past diets via isotopic data derived over decades or centuries may be confounded by changes to baseline environmental values and it is now recommended that such retrospective studies address this limitation (e.g., Bond & Jones 2010). For example, the Suess effect describes the reduction in atmospheric $\delta^{13}\text{C}$ in CO_2 as a result of fossil fuel-derived carbon inputs (Gruber *et al.*, 1999; Sonnerup *et al.*, 1999), and this effect ultimately reaches ocean food webs, which can also show isotopic shifts due to changes in rates of primary productivity (Hilton *et al.*, 2006). Thus, to test for changes to baseline environmental values, we also used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements of muscle tissue from forage fish collected and archived from the Salish Sea over six decades of our study period.

Materials and methods

Study Area

Feather samples for stable isotope analyses came from glaucous-winged gull museum skins or moulted feathers collected between 1860 and 2009 (moulted feathers 2009 only) at nesting colonies in the Salish Sea, i.e., the inshore waters of the Strait of Georgia, BC, Canada, adjacent waters of Puget Sound, WA, USA, and the eastern Strait of Juan de Fuca; approximate range: $47.91^\circ - 50.02^\circ \text{ N}$, $121.95^\circ - 125.24^\circ \text{ W}$. This area includes all present-day colonies larger than 10s of pairs within the region, but excludes the more westerly colonies where diet is likely to have been influenced by the offshore marine conditions of the Pacific Ocean. Banding and telemetry data show that most glaucous-winged gulls breeding in the Salish Sea remain in or near the area year-round and that dispersal from natal to breeding sites is local (Pearse 1963; Butler *et al.* 1980; Reid 1988; J. Elliott, unpubl. data), and thus these birds primarily represent a single

oceanographic region. This assumption is relevant for stable isotope analysis, because baseline isotope values often vary among regions (Schell *et al.* 1989; Graham *et al.*, 2010).

Sample Collection and Stable Isotope Analysis – Feathers

To assess long-term changes in breeding-season diet we examined changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for a time series of feathers grown in and around the nesting season, a physiologically demanding period when birds must ingest foods that are energetically and nutritionally conducive to successful reproduction (Robbins 1981; Meijer & Drent 1999; Williams 2005). We analysed 270 feather samples from 216 glaucous-winged gulls collected over the 150 y study period. Of these 216 birds, 194 (90%) were held at eight museums in Canada, the US, and the UK (see Acknowledgements for all sources) with the remainder represented by feathers collected in the field. In total, of the feathers we sampled 138 were adult primaries, 55 adult head feathers, and 77 sub-adult primaries, with an average of 11 primary feathers per decade (with the exception of the years from 1860 – 1899, when only 10 museum specimens were available). To estimate diet of breeding adults, we used a section (~1 x 2 cm) cut from the tip of the innermost primary feathers as the first of these (P1) are generally moulted from mid-April to early May (Verbeek 1979), ca. 2 – 4 weeks before the lay date of first eggs (mid- to late May; Verbeek 1986; Blight 2011). Thus, isotope ratios in P1 feathers reflected a breeding bird's diet immediately prior to and during egg production the previous year. (Innermost primaries also had the advantage of being hidden from view in standard museum specimens, so that sampling did not alter external specimen appearance.) We obtained samples from each decade from 1860 – 2009 (except the 1870s; no specimens available), targeting P1, or P2 if P1 was absent. On rare occasions when P1 and P2 were absent, we sampled P3. We also collected moulted primaries in 2008 and 2009 (P1,

P2, and possibly P3 given appearance and timing; Verbeek 1979) from the ground in the glaucous-winged gull colony at Mandarte Island, British Columbia (48.63°N, 123.28°W).

Moulted feathers were collected from across the colony (c. 1800 breeding pairs) to minimise the chance that any individual was sampled more than once.

Adult brown-tipped (hereafter, “winter”) head feathers are grown during the post-breeding moult whereas white (hereafter, “summer”) head feathers are grown late winter to early spring, preceding or coincident with territory establishment (Hayward & Verbeek 2008; LKB pers. obs.). As both winter and summer head feathers are moulted at the extreme ends of the breeding season they do not entirely represent diets from critical periods (e.g., egg production and chick rearing), but as samples they have the advantage of causing minimal alteration to museum specimens. We therefore sampled from a subset of winter and summer adult head feathers taken from the same museum specimens to ask if these could be used as a proxy indicator of long-term diet change (i.e., by showing the same trends and isotope values as primary feathers grown during breeding). As we were also interested in long-term differences in the diet of adult and sub-adult gulls, we used the above protocol to sample primary feathers from museum specimens of sub-adults. Sub-adult birds moult their first primaries at a similar time as adults, but sub-adult head feather moult patterns can be more variable (Howell & Dunn 2007; P. Pyle, pers comm.), and thus a poor season-specific indicator of dietary change. For this reason we did not sample sub-adult head feathers from museum specimens.

Feather samples were prepared by soaking for 24 h in a 2:1 chloroform:methanol solution, and then rinsing in clean solution. Cleaned and rinsed samples were air dried in a fume hood for 48 h before loading 0.25 to 0.55 mg into tin capsules. All samples were processed at the Queen’s Facility for Isotope Research, Kingston, Ontario, using a ThermoFinnigan Delta Plus XP mass

spectrometer interfaced to a Costech elemental analyser for C and N isotope measurements. We ran 10% ($n=27$) duplication on feather samples, producing a repeatability of within $<0.3\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. During analysis, we ran standards NBS-21 graphite for $\delta^{13}\text{C}$ and NIST 8548 and NIST 8550 for $\delta^{15}\text{N}$, and an in-house standard, chicken blood (CK-1; Janssen *et al.*, 2011), for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Within-run error (SD) associated with in-house standards was $\pm 0.1\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Stable-carbon isotopic values are reported relative to Vienna Pee Dee Belemnite (VPDB) and $\delta^{15}\text{N}$ values relative to (atmospheric) Air.

Sample Collection and Stable Isotope Analysis – Fish

We sampled and assayed lateral muscle tissues from forage fishes collected in the Salish Sea from 1917 – 1960. Fish were collected by earlier researchers using largely unknown methods, and deposited in the year of their collection at the Beaty Biodiversity Museum, University of British Columbia. All specimens were initially preserved for 1 wk in buffered formalin, and stored thereafter in isopropanol (E. Taylor, pers. comm.). Preservation may deplete ^{13}C and ^{15}N concentrations in animal tissues (Hobson *et al.*, 1997; Arrington & Winemiller 2002; Edwards *et al.*, 2002), but we were interested in relative rather than absolute isotopic values of fish tissues, and assumed any depletion that did occur would have taken place for all samples, not affecting comparability. This assumption was supported by an apparent lack of effect of decadal preservation times on the tissue values of aquatic species (Rennie *et al.* 2012).

All fish were collected in the centre of our study area, near Vancouver or Nanaimo, Canada (49.28°N , 123.12°W , and 49.14°N , 123.95°W , respectively). We selected Pacific herring (*Clupea pallasii*), Pacific sandlance (*Ammodytes hexapterus*) and eulachon (*Thaleichthys*

pacificus) as candidates based on our own and published observations of dominant fish prey in modern and historical glaucous-winged gull diets (Hart & McHugh 1944; Ward 1973; Verbeek 1979; Vermeer 1983; Davis 2013; LKB unpubl. data). Fish were sampled from each decade represented in the museum's collection, with sample size limited by availability and size of specimens. We sampled only small fish (range: 43 to 97 mm in length; one tissue sample per individual) of the same approximate size as those regularly consumed by glaucous-winged gulls (LKB pers. obs.). Muscle tissue was prepared for analysis by freeze-drying for 3d, then grinding each sample in individual capsules in an amalgamator. Pulverised samples were weighed (0.40 – 0.55 mg), loaded into tin capsules, and processed in the same way as feather samples, but using tilapia (TIL-06-01) as the in-house standard. Repeatability and standards were otherwise the same as for feathers.

Because lipid extraction may affect $\delta^{15}\text{N}$ of processed tissues, and given our focus on fishes' relative vs. absolute isotope values over time, we did not perform lipid extraction as part of the fish sample preparation process. Instead, following Post *et al.*, (2007), we used C:N ratios of analysed samples to assess lipid content. C:N ratios for eulachon samples (mean 7.8 ± 2.4 SD) were high enough to indicate an elevated tissue lipid content and resulting biased estimates of $\delta^{13}\text{C}$ values (Post *et al.*, 2007); thus, we excluded eulachon data from analyses of $\delta^{13}\text{C}$ trends in fish (i.e., our proxy for environmental change). C:N ratios of herring and sandlance were relatively low (3.4 – 4.4), so we assumed no effect of lipid content on reported $\delta^{13}\text{C}$ values for these two species, again following Post *et al.* (2007).

We did not correct for the Suess effect as its presence and magnitude varies by geographic location in marine systems (e.g., Gruber *et al.*, 1999; Sonnerup *et al.*, 1999; Tanaka *et al.*, 2003), and fish stable isotope values showed no evidence for it affecting local isotopic trends in our study area (see Results).

Statistical Analyses

To assess temporal trends in feather isotope ratios of sub-adult and adult gulls, we conducted linear regressions on the time series of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary and head feathers. Given our prediction that a gull population driven primarily by garbage would show a pattern of increasing terrestrial foods in diet to the 1980s, and a decrease thereafter, we tested for quadratic trends in the $\delta^{13}\text{C}$ data from sub-adult and adult primary feathers. We used analysis of variance to test for differences among mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each feather type (adult winter head feathers, adult summer head feathers, adult primary feathers, sub-adult primary feathers). Post-hoc pairwise comparisons used Tukey-Kramer HSD tests.

In marine systems, $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ values are typically positively correlated, but this relationship can break down when birds forage across biomes (Hobson & Welch 1992), or when carbon is derived from lipids and carbohydrates in addition to protein. We therefore regressed feather values of $\delta^{13}\text{C}$ on $\delta^{15}\text{N}$ (primary feathers only) to provide an additional measure of the relative marine origin of the diet. Given our prediction that sub-adults would be more dependent on garbage, we expected to see stronger coupling between the two isotope systems for adults than for sub-adults, with the relationship breaking down with increased access to garbage.

We pooled isotope values for forage fish species and used the same linear modelling approach as above to assess temporal trends in $\delta^{13}\text{C}$ (herring and sandlance only; eulachon excluded due to high C:N ratios; see above) and $\delta^{15}\text{N}$ (herring, sandlance, eulachon) values of fish muscle tissues. To assess isotopic trends in forage fish to the present day, we performed additional tests using the same model and stable-isotope data derived from non-preserved muscle tissue of herring and sandlance caught adjacent to Mandarte Island in 2011 (M. Davis, unpubl. data; $n=14$; C:N ratios 3.3 – 3.9). As preservation techniques may or may not affect tissue $\delta^{13}\text{C}$ values in fish (Arrington & Winemiller 2002; Edwards *et al.*, 2002) we analysed trends in preserved museum specimens alone, as well as those for museum and modern fish combined. We also used linear regression of C:N ratios to test for any temporal trends in lipids in forage fish tissue (herring and sandlance only).

Results

Stable Isotope Analysis – Feather Samples

With one exception, analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values declined over time for all feather types sampled (Table 1). In adult primaries, $\delta^{13}\text{C}$ values declined $\sim 2.3\%$ since 1860 (Fig. 1a). Values of $\delta^{15}\text{N}$ in adult primary feathers also decreased, dropping $\sim 3.8\%$ from 1860 – 2009 (Fig. 1b). Feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for primaries of sub-adult birds showed similar trends (Fig. 1c, d). We observed a decline in $\delta^{13}\text{C}$ values for adult winter head feathers similar in magnitude to the declines reported above, but it was not statistically significant, perhaps due to small sample size (Table 1). Contrary to what would have been expected had amount of garbage increased and then decreased in gull diets over the study period, we did not find a quadratic trend in $\delta^{13}\text{C}$ values (i.e., were unable to fit a squared term) for sub-adult or adult primary feathers.

Comparing isotopic values by feather type and age-class suggested a slight but non-significant difference in mean $\delta^{13}\text{C}$ values between sub-adult and adult primaries, with sub-adult values suggesting a slightly less marine signal ($-15.4 \pm 0.2\text{‰}$ (sub-adult) vs. $-14.9 \pm 0.2\text{‰}$ (adult); $F=1.32$, $p=0.26$) and the lowest mean value among all four feather types. For $\delta^{15}\text{N}$, the only among-group difference detected was between adult primaries, grown during breeding, and adult summer head feathers, grown just prior to breeding ($16.0 \pm 0.2\text{‰}$ vs. $15.0 \pm 0.3\text{‰}$, respectively; $F=2.58$, $p=0.04$). Regressing $\delta^{13}\text{C}$ on $\delta^{15}\text{N}$ for primary feathers revealed statistically significant relationships, but as predicted, these values were less closely correlated for sub-adult ($R^2=0.24$) than adult birds ($R^2=0.41$).

Stable Isotope Analysis – Fish Samples

We obtained 37 tissue samples from forage fish collected from 1917 – 1960 (eulachon, $n=7$; herring, $n=16$; sandlance, $n=14$). Pooled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of forage fish muscle tissues showed no linear trend across years ($\delta^{13}\text{C}$: $F=0.01$, $p=0.94$; $\delta^{15}\text{N}$: $F=0.00$, $p=0.99$; Fig. 2a, b), indicating little change in average ecosystem productivity from 1917 – 1960. When stable isotope data from fish caught at Mandarte Island in 2011 were added to those from museum samples, fish $\delta^{13}\text{C}$ values became less negative over time, at a rate of 0.01‰ per annum ($F=5.15$, $p=0.03$). With these modern data included, forage fish $\delta^{15}\text{N}$ values also showed a weak (but not significant) increase over time ($F=2.44$, $p=0.12$). C:N ratios for herring and sandlance declined from 1917 to 1960 ($F=10.33$, $p<0.01$), and a similar trend in these ratios was maintained after including modern (2011) fish samples ($F=58.51$, $p<0.0001$).

Discussion

We found declines in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in gull primary and head feathers over our 150-year study period, indicating that the diets of glaucous-winged gulls in the Salish Sea have changed in both the degree of marine contribution and in trophic level over time. Because declines occurred in all feather types – adult primaries, sub-adult primaries, and adult summer and winter head feathers – our results imply that similar dietary changes occurred in all age classes, and that the shift occurred across seasons. Our interpretation of a dietary shift was supported by the isotopic data from a time series of museum-archived forage fish (1917 – 1960); together, these two datasets, fish and gull, provide parallel evidence that gull diets actually changed over time, rather than that feather isotope values reflected a baseline environmental shift. Although forage fish $\delta^{13}\text{C}$ values fluctuated (as would be expected in a dynamic marine system; Johannessen & Macdonald 2009) they did not show the incrementally declining baseline environmental $\delta^{13}\text{C}$ values predicted by the Suess effect (Gruber et al. 1999). Indeed, they showed the opposite trend with the addition of 2011 data, indicating that during the period sampled at least, conditions in the Salish Sea meant this effect was not detectable. Interpretation of isotopic values from terrestrial food webs can be complicated by the different $\delta^{13}\text{C}$ values of C_3 vs. C_4 plants, with C_4 plants more enriched in ^{13}C (Dawson & Siegwolf 2007). However, it is unlikely that C_4 isotopic inputs affected our results as the food industry in Canada is primarily C_3 based (cf. Hebert *et al.*, 1999), unlike the C_4 , corn-based industry in the USA (Jahren & Kraft 2008; but see Chesson *et al.*, 2009). About 98% of our feather samples were either from birds at Canadian colonies, or from the US but collected prior to the 1950s, when corn was widely adopted as feed for poultry and cattle (Pollan 2006).

The long-term changes we documented in gull feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are similar to those described for adult marbled murrelets sampled during the pre-breeding period (Feb – Apr) in the Georgia Basin from 1889 – 1996 (Norris *et al.*, 2007), and for juvenile murrelets sampled between 1854 and 2008 (Gutowsky *et al.*, 2009), wherein each group was observed to have declined in trophic level and the fraction of forage fish included in diets. Similar declines have been described for murrelets in California (Becker & Beissinger 2006) and herring gulls in the Great Lakes region (Hebert *et al.*, 2008).

The decline in $\delta^{13}\text{C}$ values we observed over time (Fig. 1a, c) differed from the dome-shaped trend we expected had glaucous-winged gulls increased and then reduced garbage intake over the 20th century. Instead, the gradual declines in marine origins ($\delta^{13}\text{C}$) and apparent trophic level ($\delta^{15}\text{N}$) of diets for both sub-adult and adult gulls were more consistent with the trend predicted had glaucous-winged gulls consumed less forage fish over time. Whether this suggests a gradual shift to a more garbage-based diet (rather than an initial increase followed by a decline) is unclear: declines in feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values would also be expected with increases in intertidal invertebrates in the diet, alone or in addition to garbage. However, because agricultural systems (and hence human food waste) are typically enriched due to fertiliser input (Nadelhoffer & Fry 1994; Hebert & Wassenaar 2001; Hobson 2007), a switch from a diet of fish to one of garbage would be less likely to show markedly declining $\delta^{15}\text{N}$ values.

Mean values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of feathers provided only equivocal support for our prediction that sub-adult gull diets would be less marine than those of adults on average. Mean $\delta^{13}\text{C}$ of sub-adult primary feathers was slightly, but not significantly, more negative than that of breeding

adults. We also found no difference in mean $\delta^{15}\text{N}$ of sub-adult vs. adult primaries, a difference we had expected if sub-adults relied to a greater degree on terrestrially-based foods (cf. Weiser & Powell 2011). As noted above, enrichment of modern agricultural food webs in ^{15}N may limit the ability to discriminate between a marine versus a garbage-based diet when considering only $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Nonetheless, the correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was stronger for adult than sub-adult primaries, supporting our prediction that sub-adults forage more frequently outside marine ecosystems during the breeding season, as seen in other sub-adult gulls (Butler *et al.*, 1980; Weiser & Powell 2011).

Differences in mean $\delta^{15}\text{N}$ values of adult summer head feather and adult primaries suggest that adult birds experienced a small downward trophic shift in the pre-breeding season, possibly due to being constrained by their proximity to the colony when courting and defending territories, or to requirements by egg-laying females for invertebrate-derived micronutrients. In contrast, the similarity of the mean isotopic values of adult primaries and winter head feathers suggest that adult gulls feed at similar trophic levels during and immediately after breeding. Given these similarities, winter head feathers appear to be a reasonable substitute for primaries when assessing historical gull diets given that head feather sampling causes less damage to museum specimens.

Little is known about population trends of forage fishes that are not commercially exploited, or for those commercially fished prior to 1950 but now rare in or absent from the system (Hay 1998; Wallace 1998; Moody & Pitcher 2010; Table 2). However, it is possible that forage fishes that are now scarce or absent from the Salish Sea (e.g., pilchard *Sardinops sagax*, capelin *Mallo-*

tus villosus) were once ecologically important in the region. Eulachon may have the highest lipid content of any marine fish species (range 15 – >50%), with tissue lipid levels often an order of magnitude higher than in other forage fishes (Payne *et al.*, 1999; Anthony *et al.*, 2000; Iverson *et al.*, 2002). Based on their C:N ratios, mean lipid levels of our sampled eulachon were in excess of 33% (cf. Post *et al.*, 2007). This species once provided gulls with high-quality food early in the breeding season; earlier researchers reported that glaucous-winged gulls fed “extensively” on eulachon in early spring (Hart & McHugh 1944; Verbeek 1979) but they no longer do so. Commercial catches of Georgia Basin eulachon peaked in the 1950s and ‘60s (Moody & Pitcher 2010) but the population reached a historic low in 2008 and was recently listed as a threatened species in the region (NOAA 2010; COSEWIC 2011). For Pacific herring, despite evidence of recovery since stocks crashed in the early 1960s (DFO 2008), spawning aggregations have contracted substantially in time and space and are now probably much less available to seabird predators than when they spawned in higher numbers and at more sites prior to 1970 (Stick & Lindquist 2009; Therriault *et al.*, 2009). Other seasonal sources of fish foods, such as roe and dead fish from spawning salmon runs in fall and winter, have also declined (Jewett 1953; Hayward & Verbeek 2008). Fisheries discards have played an important role in *Larus* gull population dynamics elsewhere (Oro *et al.*, 2004) and although discards occurred rarely in the diets of glaucous-winged gulls in the Salish Sea in the latter half of the 1900s (Ward 1973; Vermeer 1982; Vermeer 1983), they were likely more available historically. By 1930, BC fisheries were extracting more biomass than at any time after 1970 (Wallace 1998), and Salish Sea gulls presumably availed themselves of these resources when fisheries discards were high. Thus, the dietary changes suggested by our $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data likely reflect a general loss of fish (salmon, fish offal, forage fish) from diet over time, and across seasons. Such trends may also help explain

declining regional populations of marbled murrelets (Norris *et al.*, 2007; Gutowsky *et al.*, 2009) and other piscivores (Anderson *et al.*, 2009; Bower 2009; Vilchis *et al.*, 2014), and the re-distribution of Western grebes in western North America (Wilson *et al.*, 2013).

Herring and sandlance are currently the primary fish prey of breeding glaucous-winged gulls (Vermeer 1983; Davis 2013), but trends in the C:N ratios of herring and sandlance tissues we assayed suggest that lipid levels in these two species may have declined in the region over time.

A decline in forage fish quality via reduction in lipid content has been implicated in short-term declines in seabird productivity elsewhere, with poor food availability for fish a likely cause (Wanless *et al.*, 2005; Frederiksen *et al.*, 2007). Although isotopic techniques have yet to be used to describe declining tissue lipids over historical timeframes, we suggest long-term declines in food quality will be revealed elsewhere given further study. However, it should be noted that tracing dietary lipids using proteinaceous tissues like feathers is complicated due to differential routing of carbon from lipids and proteins to consumer tissues (e.g., Cherry *et al.* 2011).

Stable isotope analysis of feathers collected and archived over 150 years demonstrated long-term changes in diet in a generalist, mid-trophic predator living in an inshore sea heavily affected by human activity (Halpern *et al.*, 2008; Johannessen & Macdonald 2009). Most feathers we sampled integrated foods consumed early in the breeding season, when nesting gulls require high-protein foods to enhance body condition and facilitate egg production (Houston *et al.*, 1983; Bolton *et al.*, 1992, 1993). Our results point to a decline in diet quality – from a higher-trophic marine diet to one including more intertidal invertebrates and garbage – potentially contributing to ongoing population declines (Sullivan *et al.*, 2002; Bower 2009; Blight 2012). Glaucous-

winged gulls in the region also exhibit a long-term decline in clutch and egg size consistent with a hypothesis of declining food quality (Blight 2011). However, our ability to discriminate between marine vs. garbage-based diets was limited by using only $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; analyses using additional isotopes such as those of S, O, and H will be needed to fully characterise dietary changes over time. Causes of species declines and loss are complex, and while factors additional to the ones we identify here have presumably contributed to observed trends, we suggest that changes in food availability have been important. The trends identified here may assist in determining a subset of the factors contributing to marine piscivore declines in the Salish Sea and in coastal systems elsewhere.

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Accepted Article

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Figure legends

Figure 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of feathers from glaucous-winged gulls, 1860 – 2009 (adults) and 1893 – 2008 (sub-adults), Salish Sea region (SW British Columbia, Canada and NW Washing-

ton, USA); (a) $\delta^{13}\text{C}$, adult primary feathers; (b) $\delta^{15}\text{N}$, adult primary feathers; (c) $\delta^{13}\text{C}$, sub-adult primary feathers; (d) $\delta^{15}\text{N}$, sub-adult primary feathers. Note different scales for x-axes.

Figure 2. Trends in stable isotope values of preserved forage fish over time; (a) $\delta^{13}\text{C}$ (herring, sandlance); and (b) $\delta^{15}\text{N}$ (herring, sandlance, eulachon) of muscle tissue from forage fishes collected 1917 – 1960, Salish Sea region (SW British Columbia, Canada and NW Washington, USA). Stable isotope analysis of preserved forage fish tissues indicate there was no net change in baseline environmental values during the sampled time period (1917 – 1960).

Table 1. Trends in glaucous-winged gull feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, based on linear regression for all feather types; ‘*’ indicates significant results.

Feather type ($\delta^{13}\text{C}$)	<i>n</i>	<i>P</i>	Slope (SE)
Adult primary	138	<0.0001*	-0.015 (0.003)
Sub-adult primary	77	0.05*	-0.013 (0.006)
Adult head summer	31	<0.0001*	-0.042 (0.009)
Adult head winter	24	0.12	-0.018 (0.011)
Feather type ($\delta^{15}\text{N}$)			
Adult primary	138	<0.0001*	-0.025 (0.003)
Sub-adult primary	77	0.0005*	-0.026 (0.007)
Adult head summer	31	0.001*	-0.033 (0.009)
Adult head winter	24	0.003*	-0.030 (0.009)

Table 2. Estimated years of commencement of forage fish fisheries and population declines in Salish Sea, Canada and USA. Population trends for species other than Pacific herring are poorly documented.

Forage fish species	Common name	Timing of species' availability	Approx. year commercial/recreational fishery began	Year of documented or suspected decline(s)	Source
<i>Ammodytes hexapterus</i>	Pacific sandlance	Winter; breeding season	?	?	Therriault <i>et al.</i> , 2009
<i>Clupea pallasii</i>	Pacific herring	Winter/spring (spawning); breeding season (0+)	1890s	1960s, 2000s	Therriault <i>et al.</i> , 2009; DFO 2008
<i>Engraulis mordax</i>	Northern anchovy	?	1890	?	Pauly <i>et al.</i> , 1998; Therriault <i>et al.</i> , 2009
<i>Mallotus</i>	Capelin	Fall spawn-	1930	1970s	Hay 1998

Forage fish species	Common name	Timing of species' availability	Approx. year commercial/recreational fishery began	Year of documented or suspected decline(s)	Source
<i>villosus</i>		ing			
Osmeridae	“Smelts”	Fall, year-round?	1890	Decline uncertain	Pauly <i>et al.</i> , 1998; Therriault <i>et al.</i> , 2009
<i>Sardinops sagax</i>	Pilchard/sardine	?	1890s	1930s, 1960s	Pauly <i>et al.</i> , 1998; Wallace 1998;
<i>Thaleichthys pacificus</i>	Eulachon	March – May	1881	1930s, 1994	Hart & McHugh 1944; Hay 1998; Therriault <i>et al.</i> , 2009; Moody & Pitcher 2010



