

Long-term shifts in anthropogenic subsidies to gulls and implications for an imperiled fish



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ABSTRACT

Over the last century, human activities have altered coastal ecosystems by fishing through the marine food web and increasing anthropogenic resources (e.g. landfills), both of which may alter native predator–prey interactions. We conducted a 100-year retrospective stable isotope analysis to investigate temporal shifts in relative resource use and individual variation of a generalist seabird (Western Gull, *Larus occidentalis*) and the implications of gulls' shifting resource use on one of their native prey–threatened steelhead populations (*Oncorhynchus mykiss*). We applied a Bayesian mixing model (MixSIAR) to historical (early 1900s) and modern (early 2000s) populations of generalist gulls and compared changes in resource use to a piscivorous seabird population (Brandt's Cormorant, *Phalacrocorax penicillatus*) in Monterey Bay (California, USA). $\delta^{15}\text{N}$ significantly declined for both seabird species, suggesting shifts to lower trophic-level marine prey in the last 100 years. The shift in $\delta^{15}\text{N}$ was significantly larger for Western Gulls, suggesting a shift in gull resource use to prey not in the marine environment. Mixing models suggest anthropogenic resources (e.g., landfills) comprise the majority of modern gull diet (0.31; 0.18–0.44 95% CI), whereas it contributed relatively little to gull diet in the early 1900s (0.10; 0.01–0.26 CI). Furthermore, we found although steelhead contribute relatively less to overall modern gull diet, increasing gull populations and simultaneous steelhead population decline likely results in increased per capita predation risk to modern steelhead populations—our best estimate is that modern predation risk is ~2.4 times higher than historically, but this estimate depends on parameter values and overlaps with zero. This study highlights the impact of human activities on coastal predators and the potential consequences for native imperiled prey.

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1. Introduction

Human induced changes in food webs have altered coastal and marine ecosystems worldwide (Jackson et al., 2001; Oro et al., 2013; McCauley et al., 2015). However, these changes typically occur incrementally over many years and may remain unnoticed or underestimated (Pauly, 1995). Human over-exploitation has resulted in a slow decline in the mean trophic level of ocean fishes (Pauly et al., 1998), phase shifts in species abundance and diversity (Hughes, 1994), and species extinctions (Jackson, 2008). Anthropogenic effects

may also result in the addition of new resources that induce ecosystem change. For example, human subsidies from agriculture, commercial fishing, waste discharge, and refuse (e.g., landfills) can provide novel resources, which can alter food webs, population dynamics, and the state of ecosystems (Oro et al., 2013).

The introduction of novel food sources can subsidize generalist predator populations beyond what native prey can support, thereby increasing per capita predation risk for native prey (Polis et al., 1997). This effect is sometimes described as hyper-predation, apparent competition, or subsidized predation. Furthermore, human subsidies provide predictable and renewable food sources that sustain populations of generalist predators and can result in extinction of native prey (DeCesare et al., 2010). Thus, identifying shifting resource availability for generalist consumers and the impact on subsidized populations may provide insight into the management of imperiled species.

Seabirds reside at the nexus of two major human-induced changes, where overfishing has reduced the mean trophic level of their marine

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prey resource (Becker and Beissinger, 2006), and increased accessibility to fishery discards and human refuse can subsidize seabird diets and populations (Votier et al., 2004; Weiser and Powell, 2010). Consequences of shifting ocean and anthropogenic resources are particularly noticeable with gull populations (*Larus* spp.), where human trash (via landfills), increasing urban development, or fishery discards are thought to have contributed to the expansion and increase in gull populations worldwide (Pons, 1992; Smith and Carlile, 1993; Duhem et al., 2008; Skórka et al., 2014). Consequently, these subsidized populations may contribute to increased predation rates on native prey species. For example, increased availability to human food has contributed to a rising population of kelp gulls (*Larus dominicanus*) and subsequently increased predation pressure on a near-threatened Cape Cormorant (*Phalacrocorax capensis*) population (Voorbergen et al., 2012). Within subsidized seabird populations, the impact of an individual seabird on prey species can vary substantially due to the large variation in the composition of prey species that contribute to individual seabird diet (Votier et al., 2010). In central California (USA), Western Gulls (*Larus occidentalis*), are native generalist seabirds and are an important predator of imperiled steelhead (anadromous rainbow trout; *Oncorhynchus mykiss*; Frechette et al., 2012; Osterback et al., 2013). Furthermore, Western Gull populations in central California increased over the last 30 years (Carle et al., 2014). Although the exact mechanism for gull population increase remains unknown, it is possible that local landfills and urban waste have increasingly subsidized gulls. Understanding the relationship between anthropogenic subsidies, the gull population increase, and potential subsequent increase of predation risk to steelhead is important for recovery of imperiled salmonids, yet has not been investigated to date.

This study asked the question: how has the resource base of coastal avian predators changed over time and what are the potential implications of these shifts on native threatened prey? Shifting resource baselines can be illuminated through the use of retrospective stable isotope analyses; for example, the stable isotope signature of feathers can be sampled non-lethally from current populations of birds and can be compared to feathers of historical museum skins to infer changes in diet over time (Becker and Beissinger, 2006; Pedro et al., 2013). Specifically, we examined stable isotope signatures of a generalist consumer (Western Gull) and a marine piscivore (Brandt's Cormorant, *Phalacrocorax penicillatus*) in central California over the last 100 years. Three objectives of this study are to 1) compare shifts in the resource base over the last 100 years between a generalist consumer and a marine piscivore to determine potential shifts in the marine prey resource base versus other prey resources, 2) quantify temporal change in resource use and individual variation of the generalist consumer via stable isotope mixing models, and 3) explore shifts in predation risk of an imperiled estuarine fish (e.g., steelhead). This study illuminates the potential indirect impacts on imperiled prey resulting from anthropogenic subsidies, a potentially under-appreciated driver of environmental change.

2. Methods

2.1. Study system

We conducted our study on Western Gulls and Brandt's Cormorants in the Monterey Bay area (California), including Año Nuevo Island, Monterey Bay, and coastal creek mouths in Santa Cruz County. Año Nuevo Island (ANI) is a rookery just north of Monterey Bay that hosts a suite of seabirds and marine mammals including breeding populations of Brandt's Cormorants and the third largest Western Gull breeding population in California (Capitolo et al., 2009). Over the last two decades, the number of breeding Brandt's Cormorants on ANI has fluctuated, likely due to variation in ocean productivity (Carle et al., 2014). In contrast, the Western Gull breeding population on ANI has increased and the current breeding population is 2–4 times larger than in

the 1980s (Carle et al., 2014). Western Gulls are known to consume human refuse at landfills (Spear, 1988; Pierotti and Annett, 2001), thus one potential reason for the recent increase in Western Gull populations on ANI is due to an increase in anthropogenic resources (e.g., landfills, urban beaches) that subsidize gulls or buffer gulls from years with poor ocean productivity. Although human refuse and marine fishes often contribute to the majority of modern gull diet (Annett and Pierotti, 1989), gulls are opportunistic generalists that feed on a wide variety of organisms from marine mammals, intertidal organisms, and estuarine fishes, including federally threatened steelhead populations (Osterback et al., 2013).

We included Brandt's Cormorants, a marine piscivore, to examine the marine baseline resource over time. Brandt's cormorants are an appropriate seabird to provide a baseline for available marine prey in Monterey Bay for both seabird species over time because they consume similar prey to Western Gulls when gulls forage in the marine environment (for more information see Baltz and Morejohn, 1977; Ainley et al., 1981, and Annett and Pierotti, 1989). In addition, these two species likely experience spatial overlap while foraging in Monterey Bay because both species breed on ANI (Carle et al., 2014) and are commonly observed year-round in Monterey Bay (Baltz and Morejohn, 1977).

2.2. Sample collection and processing

We collected breast feathers for stable isotope analysis from the historical (1910–1941) and current (2008–2013) populations of adult Western Gulls and Brandt's Cormorants near Monterey Bay. Feathers integrate stable isotope signatures from diet items over the time period during which they were grown (Inger and Bearhop, 2008). Breast feather growth and molt are a relatively continual process and occur over a long time frame for Western Gulls (>6 months between May–December; Howell and Corben, 2000) and for Brandt's Cormorants (from late summer into winter; Bridge, 2006; Howell, 2010); therefore, stable isotopes from feathers should provide information on seabird dietary resources integrated across weeks to months. We assume feather samples collected for this study represent foraging in Monterey Bay because both species are considered year-round residents of Monterey Bay (Baltz and Morejohn, 1977). While younger Western Gulls may exhibit long migrations, a previous study has shown the majority of adult Western Gulls remain sedentary and are resighted within 80 km of their breeding colony during all times of the year (Spear, 1988).

In May 2008, and February and May 2009, we captured adult Western Gulls ($N = 41$) at two coastal creek mouths (Scott and Waddell Creeks, CA) and sampled breast feathers for stable isotope analysis (for more details on gull capture, see Frechette et al., 2015). Based on Western Gull molting patterns from Howell and Corben (2000), feathers collected in February were likely grown during the non-breeding season whereas feathers collected in May could have grown either during the breeding or non-breeding season. We pooled all modern samples together after insuring there were no significant differences among samples collected during modern seasons ($p > 0.40$ for $\delta^{13}\text{C}$ and $p > 0.31$ for $\delta^{15}\text{N}$) or years ($p > 0.28$ for $\delta^{13}\text{C}$ and $p > 0.13$ for $\delta^{15}\text{N}$) using a Welch's two sample t -test (R Development Core Team, 2013). All adults sampled were in adult plumage and assumed to be breeders. In collaboration with the Coastal Ocean Mammal and Bird Education and Research Surveys (BeachCOMBERS), we collected breast feathers from adult Brandt's Cormorant carcasses on beaches surrounding Monterey Bay (Nevins et al., 2011) in October 2012 and May 2013 ($N = 11$).

We sampled historical adult Western Gull ($N = 15$) and Brandt's Cormorant ($N = 13$) feathers from study skins at the University of California Berkeley's Museum of Vertebrate Zoology (MVZ) collected near Monterey Bay between 1910 and 1941. We only sampled individuals confirmed as adults by MVZ, and pooled all historical samples together after insuring there were no substantial effect of year on $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ stable isotope signatures of feathers. To correct for the change in carbon isotope ratios in atmospheric CO_2 over time (called the

'Suess Effect'), we applied the correction factor described in Eq. (4) by Verburg (2007) to $\delta^{13}\text{C}$ values for historical feathers only. We used 2000 as the reference year to compare with modern samples.

To clean feathers before stable isotope analysis, we rinsed a single feather from each individual in a 2:1 methanol–chloroform solution, rinsed twice with methanol, and dried feathers at 60 °C for 48 h. We homogenized feathers by cutting feather barbs into small pieces and ran 0.70 mg of each sample for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ on an isotope ratio mass spectrometer (University of California, Santa Cruz Stable Isotope Laboratory). All samples were corrected with standards (i.e., Pugel and Acetanilide), and we ran duplicates for 12% of the feather samples to ensure consistency of sample preparation ($R^2 > 0.96$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

2.3. Identifying shifts in resource baselines and relative resource use

To identify shifts in the resource baseline over the last 100 years, we compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of modern and historical breast feathers between a generalist consumer (Western Gulls) and a marine piscivore (Brandt's Cormorants). Mean stable isotope signatures were compared between species and time periods using Welch two sample t-tests (R Development Core Team, 2013).

To determine relative contributions of different resources to the current and historical diet of adult Western Gulls, we used MixSIAR, a Bayesian stable isotope mixing model that uses a mixed effects framework to estimate relative contributions of potential prey items to the consumer population (Stock and Semmens, 2013). MixSIAR allows for estimates of variation in diet among individuals by including individuals as a random effect. Within MixSIAR, we conducted Markov chain Monte Carlo (MCMC) sampling by running three replicate chains each with 1 020 000 draws. We removed the first 20 000 iterations as burn-in and kept every 200th posterior sample, resulting in 5 000 independent draws from the posterior distribution. We confirmed model convergence using Gelman–Rubin diagnostics (Gelman and Rubin, 1992). We used uninformative priors (i.e., flat) for gull diet because although common prey items of Western Gulls are known, published quantitative diet composition data is lacking for our system.

Based on a review of Western Gull diets (Hunt and Hunt, 1976; Annett and Pierotti, 1989) and our own observations (Frechette et al., 2012), we selected five potential prey sources that represent the prey items available within a range of habitats in which gulls forage: estuarine fishes (e.g., steelhead), human food (e.g., in landfills), intertidal invertebrates, marine fishes, and marine mammals (Table 1; for justification and description, see online Appendix). Stable isotope signatures of potential prey and fractionation factors were compiled directly from

published literature or from data collected during this study (Table 1), except for the following. First, stable isotope signatures of intertidal prey species from Newsome et al. (2009) were represented as a weighted average based on species-specific relative percent cover in Monterey Bay (PISCO, unpublished data; Table 1). Second, we applied an average diet-to-feather fractionation factor to both Western Gulls and Brandt's Cormorants by following methods similar to previous studies (Weiser and Powell, 2011; Steenweg et al., 2011), and calculated the mean fractionation factor and standard deviation of 11 seabird studies where birds were fed lipid-extracted muscle tissue (Becker et al., 2007a; Table 1). See online Appendix for more details.

2.4. Relating individual variation of gull diet to foraging locations

We investigated how individual variation in resource use and niche width varied with time period and foraging locations. First, we compared variation among individual inferred diets (i.e., posterior distributions of standard deviation across individuals estimated by MixSIAR) between historical and modern Western Gulls as an index of intra-population dietary differences. Second, we used a subset of the modern individual gulls to compare their inferred diet (relative proportions of prey) with their presence in different foraging locations around Monterey Bay, as quantified by a co-occurring radio-tracking study (Frechette et al., 2015). Tracking locations included Año Nuevo Island, coastal creek mouths, the Santa Cruz landfill, and the Santa Cruz wharf. Even though stable isotope diet data from feathers (inferred diet previous to sampling) and radio-tracking data (foraging after sampling) do not temporally overlap, these paired datasets may still reveal whether there are consistent patterns of foraging among gulls.

2.5. Exploring shifts to steelhead predation risk

We used results from the mixing models and previous research to explore how predation rates on steelhead may have changed over the last century. Specifically, we compared modern to historical per capita predation risk of steelhead by incorporating historical and modern estimates of Western Gull and steelhead population sizes, and the proportion of gull diet comprised of steelhead. Because estimates of Western Gull and steelhead abundances in the early 1900s are uncertain, we examined a suite of scenarios to include a range of realistic historical gull and steelhead abundances. The relative per capita predation risk (R) is defined as,

$$R = \text{Log} \left(\frac{dg}{s} \right)$$

where each factor in the equation is the ratio of modern to historical values: d is the ratio of the relative contribution of steelhead to modern gull diet compared to historical diet, g is the ratio of the modern to historical population size of Western Gulls on ANI, and s is the ratio of the modern to historical population size of steelhead. Values of R are log-transformed such that $R = 0$ suggests no change in relative risk to steelhead between modern and historical time periods, and negative and positive values of R suggest modern steelhead encounter decreased or increased predation risk to gulls, respectively.

We estimated change in predation risk to steelhead across a range of plausible parameter estimates. The relative contribution of steelhead to the diet of modern and historical Western Gull populations (d), was derived from the MixSIAR posterior distributions from both groups. We used the mean estimate as well as estimated 90% CI of d by bootstrapping, in which we calculated d from 15 000 draws from the modern and historic posterior distributions of the estimated contribution of steelhead to gull diets. We also explored a realistic range of the relative change in Western Gull populations (g) where the modern gull population is 0.5, 0.75, 1 (equal), 2, 3, 5 or 10 times the historical population. Among these possible values of g , previous research

Table 1
Literature values for stable isotope signatures and fractionation factors for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of five potential prey sources of Western Gulls that were incorporated into MixSIAR.

Sources	Sample size (n)	Stable Isotope Signatures (SIS)		Fractionation Factors (FF)	
		Mean \pm SD $\delta^{13}\text{C}$	Mean \pm SD $\delta^{15}\text{N}$	Mean \pm SD $\delta^{13}\text{C}$	Mean \pm SD $\delta^{15}\text{N}$
Steelhead ^a	11	-20.6 \pm 1.2	11.2 \pm 0.6	1.4 \pm 0.9	3.6 \pm 0.6
Human food ^b	485	-18.8 \pm 0.8	9.2 \pm 0.6	0.2 \pm 0.5	-1.45 \pm 0.6
Intertidal ^c	7	-16.2 \pm 0.8	9.9 \pm 0.3	1.4 \pm 0.9	3.6 \pm 0.6
Marine fishes ^d	11	-15.4 \pm 1.3	16.2 \pm 0.9	0 \pm 0.9	0 \pm 0.6
Marine mammals ^e	5	-15.2 \pm 0.5	19.8 \pm 0.6	1.4 \pm 0.9	3.6 \pm 0.6

^a SIS = Collins(2008) and FF = Becker et al.(2007a).

^b SIS = USGS(2006), FF = Schoeller et al.(1986), O'Connell et al.(2001) and Becker et al., 2007a.

^c SIS = Newsome et al.(2009), weighted for relative percent cover (PISCO, unpublished data) and FF = Becker et al.(2007a).

^d SIS = this study and FF = Becker et al.(2007a) (standard deviation only).

^e SIS = Sydeman et al.(1997) and FF = Becker et al.(2007a).

suggests the modern Western Gull population on ANI has increased (Carle et al., 2014) and may be at least three times larger than it was historically if it follows a similar trend to adjacent populations (Ainley and Lewis, 1974; Warzybok et al., 2012). We explored four scenarios of steelhead population change (s): where modern steelhead abundance is 0.1, 0.2, 0.3 and 1 (equal) to the historical population. Central California coast steelhead abundances were estimated to have declined by 80–90% in the last 50 years (Moyle et al., 2008), which prompted listing of these populations as threatened under the Endangered Species Act in 1997 (Federal Register, 2006). Further, modern steelhead returns are approximately 30% of historical accounts of Scott Creek run size from the early 1900s (Moore et al., 2011; Hayes et al., 2013). Thus, modern steelhead populations are likely less than one-third of the historical population.

3. Results

3.1. Identifying shifts in resource baselines and relative resource use

Stable isotope signatures of both Western Gulls and Brandt's Cormorants shifted to significantly lower mean $\delta^{15}\text{N}$ over time (historic vs. modern gulls, $t = 6.96$, $p < 0.01$; historic vs. modern cormorants, $t = 2.57$, $p < 0.02$; Fig. 1A and B). The difference in $\delta^{15}\text{N}$ for modern (14.7 ± 1.9 SD ‰ $\delta^{15}\text{N}$) and historical (17.4 ± 1.0 SD ‰ $\delta^{15}\text{N}$) Western Gulls was greater than the difference between modern (16.2 ± 0.9 SD ‰ $\delta^{15}\text{N}$) and historical (17.0 ± 0.7 SD ‰ $\delta^{15}\text{N}$) Brandt's Cormorants, suggesting different resource use between the two species (Fig. 1A and B). There were no significant differences between all pairwise comparisons of the mean $\delta^{13}\text{C}$ for modern gulls (-16.1 ± 0.8 SD ‰ $\delta^{13}\text{C}$), modern cormorants (-15.4 ± 1.3 SD ‰ $\delta^{13}\text{C}$), and mean Suess-corrected $\delta^{13}\text{C}$ for historical gulls (-16.2 ± 0.5 SD ‰ $\delta^{13}\text{C}$) and cormorants (-16.2 ± 1.6 SD ‰ $\delta^{13}\text{C}$; Fig. 1A and B). The range of stable isotope

signatures of potential prey sources was wide and encompassed the range of isotope signatures observed in both historical and modern Western Gull feathers (Fig. 1C). Prey sources spanned over 5 parts per mil for $\delta^{13}\text{C}$ and over 10 parts per mil for $\delta^{15}\text{N}$ (Table 1), with human food being particularly depleted in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Gull isotope signatures were distributed throughout this range, suggesting the relative contribution of prey sources varied among individuals (Fig. 1C).

The posterior distributions from MixSIAR suggest the relative contribution of prey sources to gull diet differed substantially between modern and historical Western Gulls (Fig. 2). The largest temporal difference in gull diet was the increase in the relative contribution of human food to modern gull diet (0.31; 0.18–0.44 95% credible intervals (CI)) when compared to historical gull diet (0.10; 0.01–0.26 CI). Another substantial difference was the smaller contribution of steelhead to modern gull diet (0.06; 0.00–0.16 CI) when compared to historical diet (0.25; 0.08–0.41 CI). Relative changes in the proportion of other prey sources to gull diet over time were less substantial.

3.2. Relating individual variation of gull diet to foraging locations

Individual variation in the diet of modern gulls was significantly larger than historical gulls ($p < 0.05$; Fig. 3A), suggesting modern gulls encompass a larger niche space. This difference is likely driven by significantly larger variance in $\delta^{15}\text{N}$ of modern gulls when compared to historical gulls (F test; $p = 0.011$; Fig. 1A, C). Based on the mixing model, the estimated proportion of human food comprises a large and variable proportion of modern gull diets (mean posteriors ranged from 0.23 to 0.43; Fig. 3B), whereas human food contributed a smaller and less variable proportion to historical gull diet (mean posteriors ranged from 0.09 to 0.11; Fig. 3B).

Paired stable isotope signatures and individual tracking data did not identify any systematic differences in relative proportion of human food

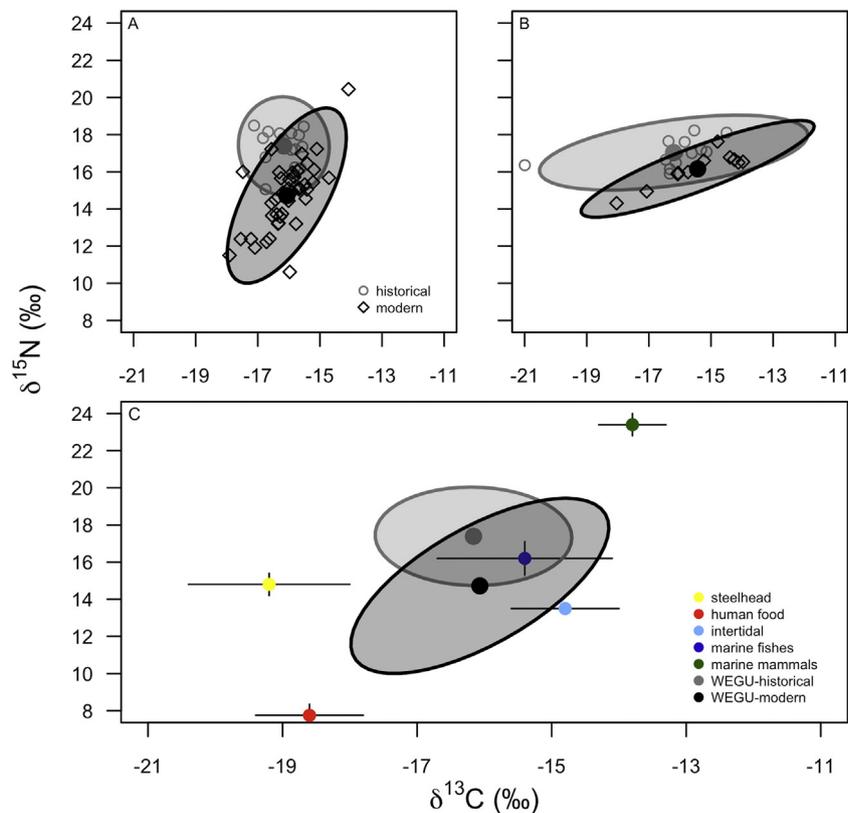


Fig. 1. Isotope signatures of $\delta^{13}\text{C}$ and of $\delta^{15}\text{N}$ of breast feathers from Suess-corrected historical and modern adult Western Gulls (A), Brandt's Cormorants (B), and Western Gulls with isotope signatures of potential prey sources, after accounting for fractionation (mean \pm SD; Table 1) (C). Note that ellipses contain identical data in 1A and 1C. Individual feather samples are indicated by open symbols, means are indicated by filled symbols, and 95% CI are represented by ellipses.

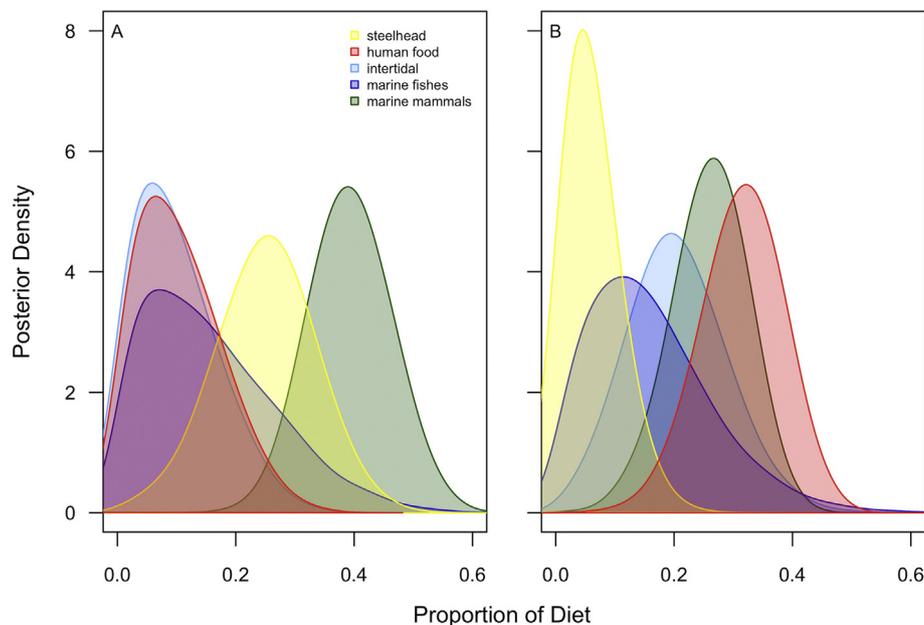


Fig. 2. Proportion of diet sources that contribute to Suess-corrected historical (A) and modern (B) Western Gull stable isotope signatures. Data are represented as posterior densities from the mixing model output from MixSIAR, using potential prey sources and fractionation factors from Table 1.

to gull diet and presence in foraging habitat, suggesting observed location of gulls does not predict past relative diet sources of an individual (Fig. 3B). Although some individual gulls appear to frequent specific foraging locations (Frechette et al., 2015); the stable isotope data suggest most gulls forage across multiple habitat types.

3.3. Exploring shifts to steelhead predation risk

Across the vast majority of the range of realistic parameter estimates, we estimate that risk to steelhead by gull predation has increased from historic to modern time periods. The mean contribution of steelhead to gull diet has apparently decreased over time (Fig. 2); however, the relative per capita predation risk to steelhead by gulls is still likely much greater for modern gulls than for historical gulls because of increasing gull populations and declining steelhead populations (Fig. 4). Based on our best approximation of parameters, we estimate predation risk on steelhead has increased by 2.4 times (Fig. 4, red square). If we incorporate 90% confidence intervals (CI) for inferred diet change (d) into this scenario, predation risk may have increased by 0.24 to 7.7 times (Fig. 4). Further, even if we assume no change in the population of Western Gulls on Año Nuevo Island ($x = 0$), only a 24% reduction in steelhead populations would result in increased predation risk to steelhead. Similarly, if we assume no change in steelhead abundance (Fig. 4, black points), only a 4-fold increase in the gull population would result in increased predation risk to steelhead. We hypothesized both of these populations changed over time, such that the gull population on ANI has likely tripled, and steelhead populations are likely no more than 30% of their historical values (Fig. 4, red square) and result in increased predation risk over the last 100 years. There was some parameter space where we predict that steelhead predation risk has not increased, specifically those were estimates of predation from the low range of the probability distribution from the mixing models. Collectively, this exploration suggests that per capita predation risk has likely increased for steelhead over the last 100 years.

4. Discussion

We used stable isotope analysis to illuminate shifting resource baselines in the marine environment, demonstrating both modern generalist and piscivorous seabirds now feed at a lower trophic level

than they did historically. Our results also suggest anthropogenic food sources have become a larger component of modern gull diet; however, the contribution of human food to modern gull diet can vary substantially between individuals, thereby increasing the niche width of modern gulls. We previously estimated modern Western Gulls consume approximately 30% of the juvenile steelhead population each year at some central California coast watersheds (Osterback et al., 2013). Our results suggest this level of consumption may be indirectly linked to anthropogenic subsidies.

We observed a decline in $\delta^{15}\text{N}$ for Western Gulls and Brandt's Cormorants over the last 100 years suggesting modern birds are eating at a lower trophic level; however, the magnitude of decline varied between species suggesting different resource use between modern populations (Fig. 1). This has been documented in other systems, where modern seabirds feed lower in the food chain as a result of fisheries exploitation (Becker and Beissinger, 2006; Pedro et al., 2013). For example, Becker and Beissinger (2006) documented the diet of endangered Marbled Murrelets declined by 14%–38% of a trophic level (0.5–1.4‰ $\delta^{15}\text{N}$) over 100 years in Monterey Bay. Lower $\delta^{15}\text{N}$ values were attributed to eating lower trophic level prey and not due to a temporal shift in the isotope signature of the base of the food web (Rau et al., 2003). We found a similar magnitude of decline in inferred trophic level over the same temporal and spatial scale, where modern Brandt's Cormorants diet declined by ~22% of a trophic level (0.8‰ $\delta^{15}\text{N}$), providing consistent evidence for a region-wide decline in the trophic level of seabird prey. While indices of ocean conditions such as the Pacific Decadal Oscillation (PDO) may explain differences in seabird diet (Becker et al., 2007b), we did not find a significant relationship between annual PDO and $\delta^{13}\text{C}$ ($t = -0.31$; $p > 0.75$) or $\delta^{15}\text{N}$ ($t = 0.97$; $p > 0.33$) of Western Gull feathers or PDO and $\delta^{13}\text{C}$ of Brandt's Cormorant feathers ($t = -1.121$; $p > 0.27$). However, there was a positive significant relationship between annual PDO and $\delta^{15}\text{N}$ of Brandt's Cormorant feathers ($t = 2.613$; $p = 0.02$). Thus, ocean conditions may also be contributing to change in available prey and seabird diet.

Generalist gulls showed evidence of further shifts in resource use. Mixing models suggest modern gulls eat on average three times the anthropogenic resources compared to historic gulls (Fig. 2), which is likely driving the relatively larger decline in $\delta^{15}\text{N}$ in generalist gulls when compared to piscivorous Brandt's Cormorants. Increased reliance on anthropogenic sources is well-documented in seabirds, especially for

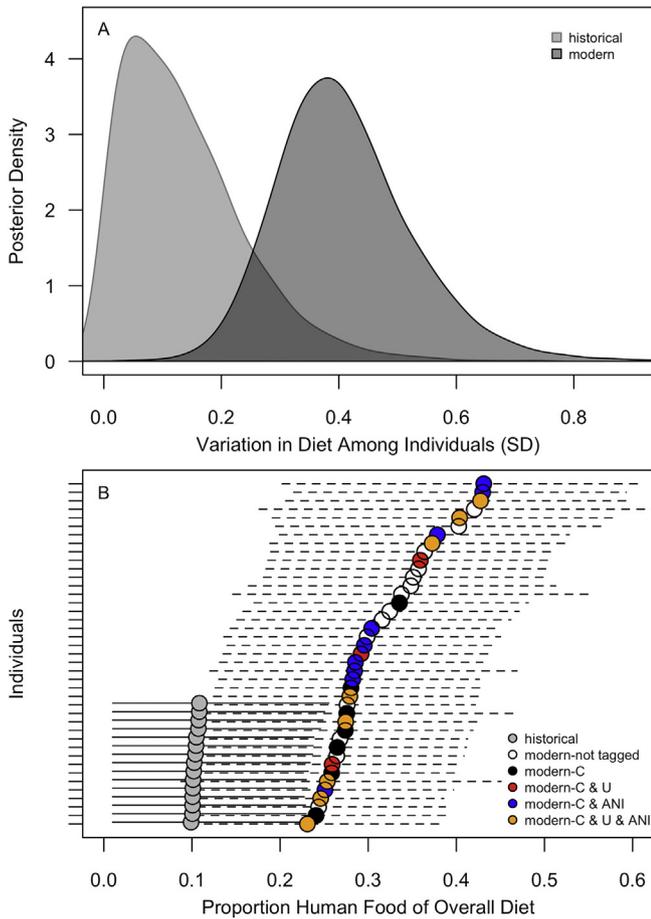


Fig. 3. Variation in isotopic signatures among individuals from Suess-corrected historical and modern Western Gulls. A) historical (light gray) and modern (dark gray) data are represented as posterior densities from the mixing model output from MixSIAR. B) The proportion of human food (points are mean posteriors and lines are 90% credible intervals) that contributes to individual gull diet for historical (light gray) and modern Western Gulls (other colors). Some modern gulls were radio-tagged and observations of those gulls in different foraging locations is indicated, including presence at creek mouths (C), urban locations such as the Santa Cruz landfill and wharf (U), and/or on Año Nuevo Island (ANI).

gulls (Duhem et al., 2008; Pedro et al., 2013). Furthermore, in a recent study on Ring-billed Gulls (*Larus delawarensis*), paired GPS tracking and stable isotope data showed individuals that forage in anthropogenic habitats exhibited depleted $\delta^{15}\text{N}$ stable isotope signatures (Caron-Beaudoin et al., 2013). On ANI, we observed 23% of Western Gull wet diet was comprised of anthropogenic resources (garbage, chicken, beef; Cassell and Shaffer, unpublished data) and recent GPS tracking data confirms that 75% of all tracked gulls from Año Nuevo Island visited the Santa Cruz landfill at least once and most visited regularly (Shaffer et al., unpublished data). These data further suggest substantial reliance on anthropogenic resources from the landfill and urban environments. The second-largest temporal change in gull diet was the 76% decrease in the contribution of steelhead to modern gull diet. A reduction in steelhead to gull inferred diet is perhaps not surprising, given steelhead populations have declined precipitously in the area (Moyle et al., 2008; Moore et al., 2011).

There was higher individual variation of inferred diets for modern gulls than historic gulls (Fig. 3A). When individuals exploit different subsets of resources the niche width of a population increases (Bolnick et al., 2007), which can promote population stability (Layman et al., 2007). One potential reason for increased niche width in modern gulls is the increased amount of anthropogenic food (e.g., landfills) available

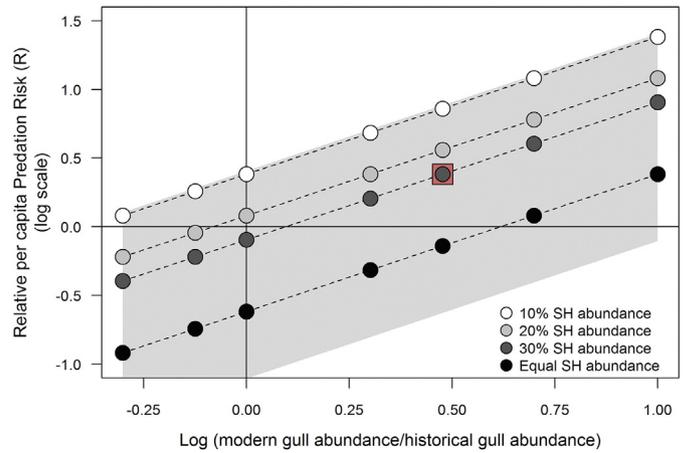


Fig. 4. The relative per capita predation risk (R) of modern versus historical juvenile steelhead (SH) based on the ratio of modern to historical proportion of steelhead to gull diet (from MixSIAR) across a suite of relative increases in gull population size and declines in SH abundance. The gray shaded region represents the 90% confidence intervals of the proportion of steelhead to gull diet assuming modern steelhead abundance is 30% of the historical abundance. The red square denotes our hypotheses of relative gull and salmonid abundance. Note data are presented on a log scale, such that where $x = 0$ denotes zero change in gull population size, and where $y = 0$ denotes zero change in relative per capita predation risk of salmonids.

to gulls now when compared to the early 1900s. Over the last 50 years the human population of Santa Cruz more than doubled (SCPL, 2000) and the total amount of waste discarded to landfills in the United States increased by 63% (USEPA, 2008). This addition of refuse may have added another axis to the gulls' niche. Our radio-tracking data only provided gull presence at foraging locations at specific snapshots in time, so it is not surprising we did not identify a relationship between the relative contribution of anthropogenic food to diet and the presence of individuals at subsidy hotspots (e.g., landfills) (Fig. 3B). Thus, while there is evidence of increased specialization, it appears different gull individuals are consuming anthropogenic subsidies as well as other food sources. Landfill management practices may be a key target for addressing subsidies to generalist predators and their potential indirect effects on native food webs.

Our study demonstrates anthropogenic sources (e.g., landfills) have become increasingly important to modern gull diet as gull populations have increased. While we cannot directly identify anthropogenic subsidies as the mechanism for gull population increase, this link has been made in other systems (Duhem et al., 2008). The effect of anthropogenic subsidies (e.g., landfills) on gull population growth may be system-dependent or influenced by the availability of alternative natural prey (discussed in Blight et al., 2015). For example, Western Gulls can successfully reproduce on a diet comprised mostly of human refuse, however they experience higher reproductive success with an increasing proportion of marine fishes to their diet (Annett and Pierotti, 1999), suggesting the relative combination of human refuse to natural resources may affect gull population growth. Other human subsidies, such as hatchery releases of juvenile salmon can also subsidize avian predators (Scheel and Hough, 1997); however, we do not believe this is the case in our system because there is only one small conservation hatchery (on Scott Creek) within the typical foraging distances of ANI Western Gulls (51 ± 28 km; Shaffer et al., unpublished data) that only produces relatively few individuals each year (Hayes et al., 2013). Although the Western Gull population on ANI has increased over the last 30 years, populations have leveled off recently and experienced declines during some years (Carle et al., 2014), providing possible evidence that other factors are starting to limit population trajectories. Furthermore, other sources of environmental change, such as the banning of DDT, could have also contributed to gull population change (Jimenez-Castro et al., 1995).

Regardless of the mechanism for growth of gull populations, the results from our model show predation risk of steelhead has likely increased over the last 100 years (Fig. 4). However, it is possible that if gulls substantially reduce predation on steelhead or switch to alternative prey altogether, relative per capita predation risk for steelhead may decline (Fig. 4). Conversely, if gulls continue to rely on anthropogenic food subsidies, their populations may stabilize or increase (Oro et al., 2013) and continue to contribute to the extinction of native prey (DeCesare et al., 2010), including steelhead. Previous research suggests Western Gull populations are dependent on availability to both natural prey and human refuse, because human refuse lacks the nutrition needed for chick development yet is an important diet item when natural prey are scarce (Pierotti and Annett, 2001). Furthermore, Western Gulls often switch from feeding on anthropogenic sources to natural prey during periods of chick rearing (Annett and Pierotti, 1989). Thus reliance of gulls on both anthropogenic sources and natural prey may be of particular concern for natural prey that are imperiled.

While stable isotope analysis provides a powerful tool to evaluate the relative contribution of diet sources to a consumer (Moore and Semmens, 2008), it is important to critically evaluate the assumptions underlying these analyses (Phillips et al., 2014). For example, temporal mismatch between prey and consumer tissue samples can lead to incorrect interpretation of the data (Inger and Bearhop, 2008), as can inappropriate use of fractionation factors. Due to a lack of distinct seasonal molt of the bird species evaluated in this study, we do not know the exact time period in which each sampled feather was grown. However, non-significant differences in gull feathers collected during different months and years during the modern time period suggests we captured general trends in gull diet change between historical and modern time periods. To address potential biases regarding fractionation factors, we ran a suite of alternative mixing model analyses using different fractionation values and potential prey stable isotope signatures and found results were qualitatively similar (see online Appendix). Although sample sizes of gull feathers differed between modern and historical time periods, Bayesian modeling takes sample size into consideration and incorporates this uncertainty to provide robust estimates of gull diet. We acknowledge our modern samples for Western Gulls represent a shorter timeframe than our historical samples, however there were no substantial differences in the two modern years, which suggests that they capture temporally consistent patterns. Although retrospective stable isotope analysis requires assumptions, we believe the general conclusions are robust.

By altering coastal ecosystems via commercial fisheries (Pauly et al., 1998; Essington et al., 2006) and increasing the amount of anthropogenic resources at landfills (USEPA, 2008), humans have modified the resource landscape for both specialist and generalist mobile predators. We illustrate anthropogenic subsidies have increased over the last century to a generalist consumer, and the generalist consumer likely has increased predation pressure on imperiled prey. We identified indirect effects of human refuse on natural predator–prey interactions, which advance our understanding of possible management interventions such as limiting gulls access to anthropogenic food sources, restoring instream habitat to support larger steelhead populations, and deterring gulls from watersheds with native steelhead populations. We suggest anthropogenic subsidies are an underappreciated component of environmental change and, through subsidizing generalist consumers, these subsidies can have indirect food web consequences on imperiled prey.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2015.07.038>.

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