THE DISTRIBUTION, ABUNDANCE, AND HABITAT USE OF WINTERING ICELAND GULLS *LARUS GLAUCOIDES THAYERI* IN NORTHERN CALIFORNIA AND COMPARISONS WITH OTHER *LARUS* GULLS

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ABSTRACT

MOORHOUSE, S.S. 2024. The distribution, abundance, and habitat use of wintering Iceland Gulls *Larus glaucoides thayeri* in Northern California and comparisons with other *Larus* gulls. *Marine Ornithology* 52: 209–223.

Recent studies have provided significant insights, but relatively limited information is available on many aspects of the ecology and behavior of the Arctic-breeding Iceland Gull *Larus glaucoides*. In this study, the distribution, abundance, and habitat use of wintering Iceland Gulls *Larus glaucoides thayeri* in Northern California, USA, were analyzed in 30 habitat types over three winters. A total of 6012 individuals was recorded, contributing 2.3% of the total *Larus* gulls recorded. The mean number of Iceland Gulls recorded per count was highest in sanitary landfills located in the Inner Coast Range, Central Valley, Inner Coast, and San Francisco Bay Plain areas. Mean counts were lower in shoreline and intertidal flat habitats on the Inner and Outer Coasts, and low in other habitats. The relative abundance of Iceland Gulls was similar among the habitats. Habitat use was most similar to the American Herring Gull *L. smithsonianus* and most different from the Western Gull *L. occidentalis*. Most Iceland Gulls observed were adults (70%), and the percentage slightly increased from the Outer Coast to more inland areas. The availability of substantial food resources at large landfills in the region, which includes four large metropolitan areas, probably accounts for the relatively large wintering population of Iceland Gulls at the southern end of their winter range. This food source may decrease in the future as new solid-waste management requirements are implemented in California. During the breeding period, primary elements of niche segregation between the Iceland Gull and sympatric large *Larus* gull species include nesting on coastal cliffs, concentrated use of coastal shoreline and inshore habitats for feeding, and use of different food items. In the non-breeding period, elements include differences in habitat use, feeding ecology, and feeding behavior. Abundant food sources may increase overlap in certain breeding and wintering habitats.

Key words: Iceland Gull, *Larus glaucoides thayeri*, *Larus* gulls, habitat use, behavior, wintering, Northern California

INTRODUCTION

The Iceland Gull *Larus glaucoides* comprises three subspecies (*glaucoides*, *kumlieni*, and *thayeri*). It has been the subject of significant work and discussion regarding systematics and taxonomy, particularly the relationships between "Kumliens's Gull" *L. g. kumlieni* and "Thayer's Gull" *L. g. thayeri* breeding in the central and western portions of the Arctic range, respectively (e.g., Macpherson 1961, Smith 1966, Sutton 1968, Gaston & Decker 1985, Snell 1989, Snell 1991, Chesser *et al.* 2017, Browning 2022). General information on winter distribution and abundance indicates that the core winter range of *thayeri* includes coastal areas of southern Alaska (USA), British Columbia (Canada), and northern Washington state (USA), with mostly lower numbers southward to Northern California (USA; Gilligan *et al.* 1994, Vermeer & Morgan 1997, Snell 2002, Marshall *et al.* 2003, Wahl *et al.* 2005, Campbell *et al.* 2007, Snell *et al.* 2020). The Iceland Gull in California has been described (Cogswell 1977, Garrett & Dunn 1981, Unitt 1984, Stallcup 1990, Unitt 2004, Howell & Dunn 2007, Lehman 2022) as an uncommon to locally common winter visitor in marine, coastal, and selected inland habitats in Northern California from November to March. The other large and medium-sized *Larus* gulls that winter in significant numbers in Northern California include American Herring *L. smithsonianus*, California *L. californicus*, Glaucous-winged *L. glaucescens*, Heermann's *L. heermanni*, Ring-billed *L. delawarensis*, Short-billed *L. brachyrhynchus*, and Western *L. occidentalis* gulls (Cogswell 1977, Stallcup 1990, Howell & Dunn 2007). Hybrid American Herring × Glaucous-winged gulls and Glaucous-winged × Western gulls also occur in significant numbers.

Much less information is available on the ecology and behavior of this species, including all three subspecies (Snell *et al.* 2020). Ingolfsson (1967) described the feeding ecology and behavior of wintering Iceland (*glaucoides*), European Herring *L. argentatus*, Glaucous *L. hyperboreus*, Great Black-backed *L. marinus*, and Lesser Black-backed *L. fuscus* gulls in Iceland. Moorhouse (2021) studied the feeding ecology and behavior of breeding *kumlieni* on southwestern Baffin Island in the Canadian territory of Nunavut, including habitat use and comparisons with sympatric Glaucous and American Herring gulls. Gaston *et al.* (2007) described the feeding behavior of breeding *thayeri* in Lyon Inlet on the Melville Peninsula in Nunavut, and Allard *et al.* (2010) made observations of the feeding behavior of breeding *thayeri* on St. Helena Island in Nunavut. Gutowsky *et al.* (2020) recently provided significant information on the broad-scale migration, winter distribution, and habitat use of *thayeri* on the Pacific coast of North America.

Differences in habitat use and feeding ecology by *Larus* gulls occurring together have been reported in a wide range of studies.

Ingolfsson (1967) documented significant differences in feeding habitat use, feeding techniques, and food use by five wintering *Larus* gull species in Iceland, including the Iceland Gull (*glaucoides*). Burger (1988) demonstrated differences in habitat use, foraging techniques, and food use by many *Larus* gulls. Habitat segregation has also been reported in breeding *Larus* gull species in a variety of locations (Hunt & Hunt 1973, Kubetzki & Garthe 2003, Rome & Ellis 2004, Lato *et al.* 2021).

No studies or descriptions have presented a detailed analysis of the distribution, abundance, and habitat use of wintering Iceland Gulls in Northern California or elsewhere in their winter range on the Pacific coast of North America based on direct observations of large numbers of individuals. In addition, no detailed information is available on the age-class distribution of wintering Iceland Gulls in this region as it might relate to distribution, abundance, and habitat use, or on the use of food waste at landfills for feeding, a common behavior shown by many other gull species. This information is needed to expand our understanding of the ecology and behavior of this poorly known species (Snell *et al.* 2020). Additional information is also needed to address both potential differences between *glaucoides*, *kumlieni*, and *thayeri* and related questions about the systematic relationships among these subspecies.

Objectives

The objectives of this study were to conduct detailed field studies to analyze the distribution, abundance, and habitat use of wintering Iceland Gulls (*thayeri*) in Northern California, which is at the southern end of the winter range, including comparisons with other large and medium-sized *Larus* gull species and potential variations based on age class. A specific component of this work was to evaluate the use of landfills for feeding by *thayeri* and other gull species. The availability of this food source may decrease in the future resulting from the implementation of Senate Bill (SB) 1383 in California, which was enacted in January 2022 to reduce the volume of food waste in landfills by increasing diversion and composting of food waste (CalRecycle 2023). An overall objective of the study was to provide information on the ecological niche of this species as compared to other closely related *Larus* gulls.

METHODS

Field observations were completed in the winters (November–March) of 2020/21, 2021/22, and 2022/23. A total of 667 counts were conducted over 212 days over the three winters.

Study region, geographic areas, habitats, and study sites

The study region included the San Francisco Bay area and adjacent areas in the Central Valley and along the coast, from the mouth of Russian River to Monterey Bay (Fig. 1). The region was divided into six geographic areas and 30 habitats.

The geographic areas included all the major physiographic areas that support significant wintering gull populations (Table 1 and Fig. 2): Pacific Ocean, Outer Coast (adjacent to the Pacific Ocean), Inner Coast (around the edges of San Francisco Bay), Bay Plain (area surrounding San Francisco Bay between the Outer Coast Range and Inner Coast Range), Inner Coast Range (between the Bay Plain and Central Valley), and Central Valley (between the Inner Coast Range and Sierra Nevada mountains).

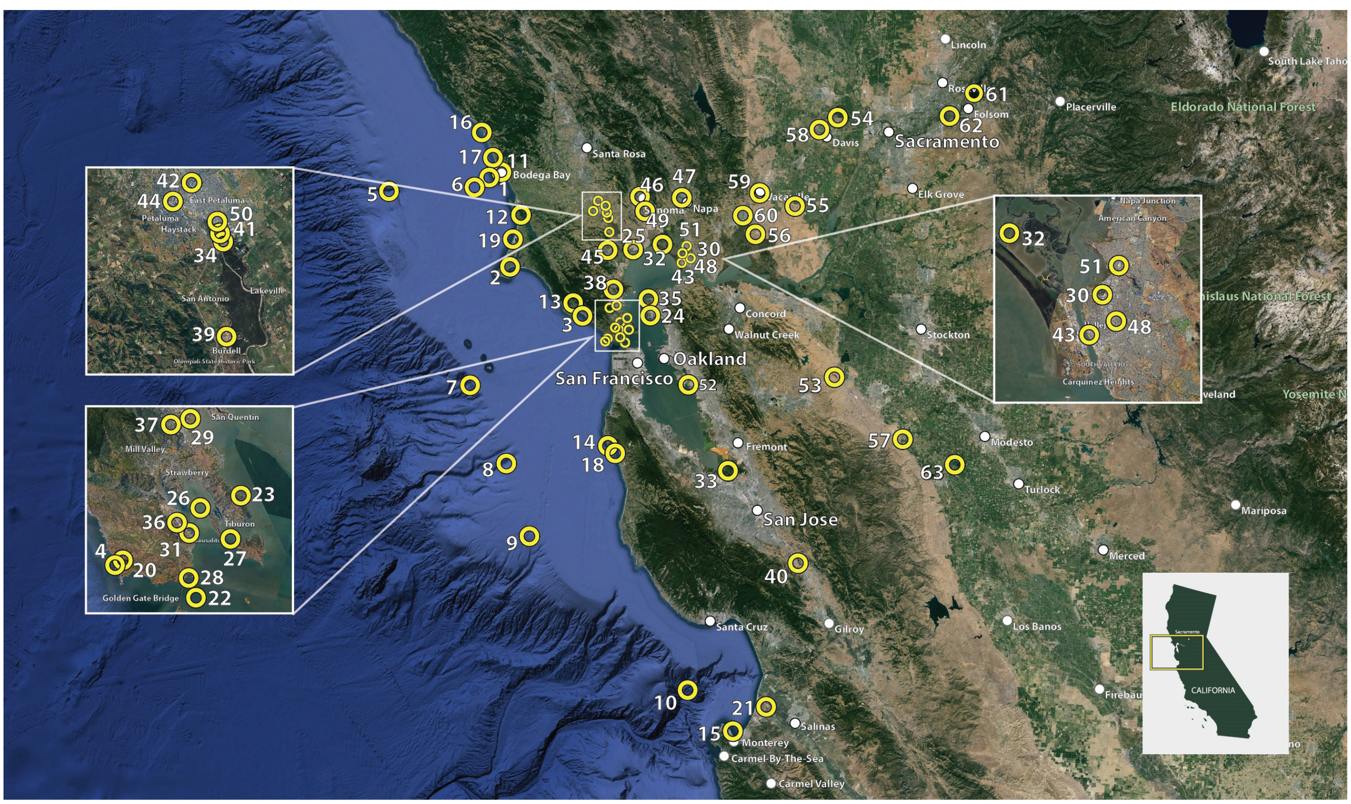

Fig. 1. Map of the study region assessed for the distribution, abundance, and habitat use of wintering Iceland Gulls *Larus glaucoides thayeri* in Northern California, USA, including numbered study sites. Study site numbers and names are included in Table 1.

TABLE 1
Geographic areas, habitats, and study sites selected to assess the distribution, abundance, and habitat use of wintering Iceland Gulls *Larus glaucoides thayeri* in Northern California, USA

Geographic area & habitat	Code	Study sites[a]	Area of coverage
Pacific Ocean			
Inshore (50–1000 m from shore)	PO1	Bodega Head/Sonoma Coast State Park (1), Pt. Reyes/Drakes Beach (2), Stinson Beach (3), Pt. Diablo/Bird Island (4)	1.6 km of shoreline to limit of observability
Offshore (pelagic trips over 1000 m from shore)	PO2	Bodega Canyon (5), Bodega Bay pelagic nearshore (6), pelagic offshore continental shelf SW of Southeast Farallon Island (7), Pioneer Sea Canyon (8), pelagic offshore continental shelf in San Mateo County (9), Monterey Bay (10)	Area to limit of observability
Outer Coast			
Main shoreline (includes areas within 50 m)	OC1	Bodega Head/Sonoma Coast State Park (1), Pt. Reyes/Drakes Beach (2), Stinson Beach (3), Pt. Diablo/Bird Island (4)	1.6 km of shoreline
Open bay	OC2	Bodega Bay (11), Tomales Bay (12), Bolinas Lagoon (13), Half Moon Bay (14), Monterey Bay (15)	1.6 km of shoreline to limit of observability
Bay shoreline (includes areas within 50 m)	OC3	Bodega Bay (11), Tomales Bay (12), Bolinas Lagoon (13), Half Moon Bay (14), Monterey Bay (15)	1.6 km of shoreline
Bay intertidal flat (includes shoreline and water within 50 m)	OC4	Bodega Bay (11), Tomales Bay (12), Bolinas Lagoon (13), Half Moon Bay (14)	1.6 km of shoreline
River/stream mouth	OC5	Russian River mouth (16), Salmon Creek mouth (17), Pilarcitos Creek mouth (18)	Mouth and 0.4 km of shoreline centered on mouth
Freshwater lake/pond	OC6	Abbott’s Lagoon (19), Rodeo Lagoon (20)	Entire waterbody
Sanitary landfill	OC7	Monterey Peninsula Landfill (21)	Entire landfill area
Inner Coast			
Main San Francisco Bay			
Open bay	IC1	Ft. Baker/Golden Gate (22), Paradise Beach County Park (23), Miller Knox Regional Park (24)	1.6 km of shoreline to limit of observability
Shoreline (includes areas within 50 m)	IC2	Ft. Baker/Golden Gate (22), Paradise Beach County Park (23), Miller Knox Regional Park (24)	1.6 km of shoreline
Intertidal flat (includes shoreline and water within 50 m)	IC3	San Pablo Bay National Wildlife Refuge (25)	1.6 km of shoreline
Small bay			
Open bay	IC4	Richardson’s Bay (26), Raccoon Strait (27), Horseshoe Bay (28)	1.6 km of shoreline to limit of observability
Shoreline (includes areas within 50 m)	IC5	Richardson’s Bay (26), Raccoon Strait (27), Horseshoe Bay (28), Corte Madera pond (29), White Slough (30)	1.6 km of shoreline
Intertidal flat (includes shoreline and water within 50 m)	IC6	Richardson’s Bay (26), Horseshoe Bay (28), Corte Madera pond (29), White Slough (30)	1.6 km of shoreline
Developed shoreline	IC7	Sausalito waterfront (31)	1.6 km of shoreline
Marsh/pond complex	IC8	Napa-Sonoma Marshes (32)	1.6 km of habitat
Marsh/pond complex-sanitary landfill	IC9	Don Edwards National Wildlife Refuge ponds A 11, 12, 13, 15, 16/Newby Island Landfill (33), Petaluma River marshes/Redwood Landfill (34)	Entire waterbody
Sanitary landfill	IC10	West Contra Costa County Landfill (35)	Entire landfill area
Developed	IC11	Cities of Sausalito (36), Corte Madera (37), San Rafael (38)	8 km driving route in each city

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Table 1 continued from previous page

Geographic area & habitat	Code	Study sites[a]	Area of coverage
Bay Plain			
Sanitary landfill	BP1	Redwood Landfill (39), Kirby Canyon Landfill/Ogier Ponds (40)	Entire landfill area
Freshwater lake/pond-sanitary landfill	BP2	Shollenberger Park pond (41), Lucchesi Park pond (42)	Entire waterbody
Park/lawn	BP3	Vallejo Independence Park (43)	Entire park area
Developed	BP4	Cities of Petaluma (44), Novato (45), Sonoma (46), Napa (47), Vallejo (48)	8 km driving route in each city
Animal feedlot	BP5	Sonoma dairy cattle feedlot (49)	Entire feedlot area
Food processing plant	BP6	Petaluma chicken processing plant (50)	Entire plant area
Waste recycling facility	BP7	Vallejo Recology Waste Recycling Facility (51), Davis Street Waste Recycling Facility (52)	Entire facility area
Inner Coast Range			
Freshwater lake/pond-sanitary landfill	ICR1	Bethany Reservoir/Altamont Landfill (53)	Entire waterbody
Central Valley			
Sanitary landfill	CV1	Yolo County Landfill (54), Hay Road Landfill (55), Potrero Hills Landfill (56), Tracy Landfill (57)	Entire landfill area
Developed	CV2	Cities of Davis (58), Vacaville (59), Fairfield (60)	8 km driving route in each city

[a] Numbers in parentheses are the study site identification numbers shown in Fig. 1. eBird data were used to cover the following study sites: all Offshore sites (27 counts) except Monterey Bay, Monterey Peninsula Landfill (all counts), and Don Edwards National Wildlife Refuge ponds/Newby Island Landfill (8 counts).

The habitats included those used by *Larus* gulls in the region, ranging from marine to coastal to inland habitats. The Outer Coast Range (between the Outer Coast and Bay Plain and other areas) was not included because only a few habitats for gulls were identified. Habitats included in the analysis were selected based on two criteria: types that covered the largest surface area in the region and types that were known to support significant numbers of at least one species of wintering *Larus* gull. Habitats such as cropland and wet grassland were extensive and used by certain gull species in some of the six geographic areas, but the sporadic and ephemeral use of these made survey coverage difficult and they were not included. Water bodies such as ponds and lakes/reservoirs were not included for the same reason, except for water bodies located adjacent to sanitary landfills that were used for loafing.

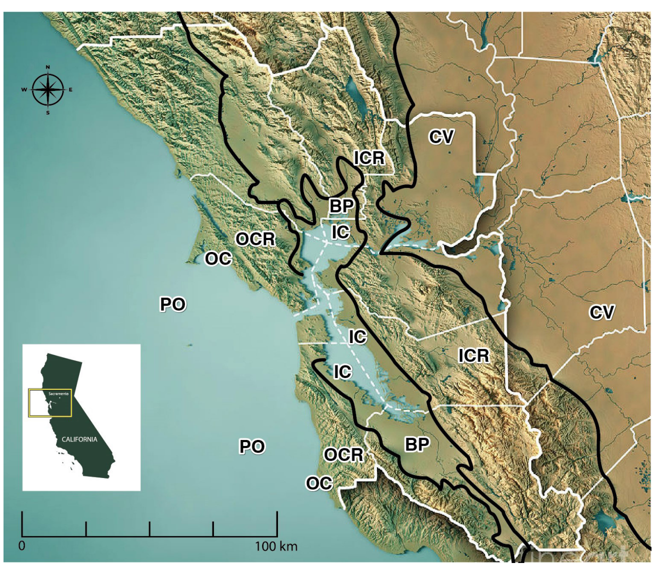

Fig. 2. Map of the study region showing the geographic regions covered, including the Pacific Ocean (PO), Outer Coast (OC), Outer Coast Range (OCR), Bay Plain (BP), Inner Coast (IC), Inner Coast Range (ICR), and Central Valley (CV). White lines show county boundaries and the thicker white line shows the San Francisco Bay area.

Study sites were selected based on the following criteria: (1) the degree to which the site was representative of the habitat, (2) researcher accessibility, and (3) how well gulls could be observed. A total of 60 study sites were covered in the 30 habitats (Table 1 and Fig. 1), and there were typically 1–5 study sites in each habitat.

Data collection

Count methods

Each study site included either the entire habitat if sufficiently small (e.g., a small bay or lake) or a portion thereof (e.g., Outer Coast main shoreline, Main San Francisco Bay shoreline). If a site comprised a portion of the total area of the habitat at the location, the linear area covered in the count included was 1.6 km in length along the shoreline (Table 1), a distance that was feasible to cover in the field while providing a representative sample. The distance was measured on a map and then confirmed in the field. Observations were completed from one or more locations at each study site, depending on the number of locations needed to cover the entire site. The area covered at each location was that in which all gulls could be identified to species and age class with certainty. This did not significantly vary among study sites. For habitats with more than one study site, data were pooled in the analysis, with a total linear coverage area of 1.6 km that included all the sites. If more than one site was covered for a habitat, the number of counts conducted at each site was similar. Certain study sites included more than one habitat (e.g., bay shoreline, bay intertidal flat, and open bay at Bodega Bay; Outer Coast main shoreline and inshore ocean at Pt. Diablo/Bird Island; Table 1).

The same locations were used for each count. Count duration at all study sites was 1–2 hours, depending on the complexity of observations at the site, which was a function of the number of gulls present and their movements. Gulls were counted in continuous scans of the area of coverage, using 10×50 binoculars and a 30× spotting telescope.

At most study sites, complete counts of all Iceland Gulls in each age class and of other gull species present were conducted. However, very large numbers of gulls were present at some sites (e.g., landfills). In these cases, large subgroups that could be observed in detail were assessed for the number of gulls in each age class based on counts or estimated percentages. These values were then extrapolated to estimate both the total number of Iceland Gulls and the number of Iceland Gulls in each age class for the entire site. The same approach was used to estimate total numbers of other gull species present. When such extrapolations were made, at least 50% of the gulls present in the entire area were observed in detail. The number of individuals counted or estimated was established as the number recorded. At least 15 counts were completed in each habitat and the number of counts ranged from 15–68 (Table 2). Counts were conducted at various times of day, although counts at landfills were not completed late in the day because many gulls typically departed the landfills for roosting areas in mid-afternoon. All counts in intertidal flat habitats were conducted at low tide.

Data collection and analysis

Each individual gull or group of gulls observed in each count was assigned to one habitat category. When more than one habitat was used by the individual or group, the observation was assigned to the category used for the longest period.

Data were also collected on the age/plumage class of each Iceland Gull observed, including the following classes: (1) juvenal/first basic-first winter, (2) second basic-second winter, (3) third basic-third winter, and (4) adult/fourth basic-fourth winter (Dwight 1925).

Data on the behavior of Iceland Gulls and other gull species were also recorded. Each individual gull or group of gulls was assigned to one of two behavior categories, based on the behavior observed for the longest period. The two behavior categories were feeding and loafing (i.e., sleeping, resting, bathing, or preening) on land or water. Birds observed flying high overhead in long-distance movements were not recorded as occurring in the habitat, but they were recorded separately. In addition, observations of concentrated groups of gulls flying over the study region but away from the study sites were recorded.

Use of eBird data

eBird is an online citizen-science program developed by the Cornell Lab of Ornithology for the collection and analysis of field observations by birders and field ornithologists (eBird 2021). The eBird database was used in the present study to provide information in three categories: (1) additional data for certain habitats and study sites that were covered in surveys, (2) additional selected age-class data for certain habitats that were covered in surveys, and (3) an overview of Iceland Gull distribution and abundance in the study region and on the Pacific coast. Fifty-three eBird counts in category 1 were included in the detailed analysis of the numbers of individuals recorded in each habitat. The observations in categories 2 and 3 were not included in the detailed analyses of the numbers of gulls recorded in each habitat, but they were used to provide supplementary information. eBird counts included in category 1 are described in Table 1, and a summary of the eBird data sources is presented in the Appendix (available on the website). All eBird data in categories 1 and 2 were raw counts collected by expert birders and field ornithologists (see Appendix). The data in category 3 are from the *Status and Trends Summary* analyses, which include all available observations, and are modeled results based on normalized data. All eBird data used were collected in the winter period (November–March) covered in this study.

RESULTS

A total of 5543 Iceland Gulls was recorded over the study period: 1716 in the winter of 2020/21, 1839 in 2021/22, and 1988 in 2022/23. When eBird counts are included, the total number of Iceland Gulls recorded was 6012 (Table 2). Individual counts in the habitats ranged from 0 to 258. In most habitats, fewer than 20 Iceland Gulls were recorded per count.

Habitat use and behavior

Absolute abundance

The mean number of Iceland Gulls recorded per count varied by habitat and geographic area (Table 2, see Table 1 for the habitat codes used below). The mean number was highest in the Inner Coast Range freshwater lake/pond-sanitary landfill habitat (ICR1, 56.6 birds), followed by the Central Valley sanitary landfill (CV1, 49.2), Inner Coast marsh/pond complex-sanitary landfill (IC9, 19.1), Inner Coast sanitary landfill (IC10, 17.6), Bay Plain sanitary landfill (BP1, 14.8), Outer Coast river/stream mouth (OC5, 12.8), and Outer Coast sanitary landfill (OC7, 10.7) habitats. The highest individual counts were recorded in the CV1 (258), Inner Coast small bay shoreline (IC5, 226), and ICR1 (210) habitats.

To simplify comparing counts among habitats, the counts were combined for IC9 and IC10 and for ICR1 and CV1, based on habitat similarities, geographic proximity, and observed interchange of gulls. Analysis of variance indicated significant differences among the mean counts in the five habitats ($n = 183$, $F = 9.84$, $P < 0.001$). Pairwise comparisons of these habitats indicated the following significant differences in mean counts: OC5 < ICR1/CV1 ($\bar{x} = 50.9$) ($Q = 5.60$, $P = 0.001$); OC7 < ICR1/CV1 ($Q = 5.92$, $P < 0.001$); IC9/IC10 ($\bar{x} = 18.3$) < ICR1/CV1 ($Q = 4.79$, $P < 0.01$); and BP1 < ICR1/CV1 ($Q = 5.31$, $P < 0.01$). This analysis shows that mean counts of Iceland Gulls in the combined habitats of ICR1 and CV1 were significantly higher than in the other four habitats.

TABLE 2
Numbers of Iceland Gulls *Larus glaucoides thayeri* and other *Larus* gull species recorded in major habitats in Northern California, USA

Geographic area & habitat	Number of Iceland Gulls recorded				No. counts	Number of individuals of all gull species recorded				Iceland Gull % total gulls	Other gull species recorded (in decreasing order of abundance)[b]
	Total	Mean	SD[a]	Range		Total	Mean	SD[a]	Range		
Pacific Ocean											
Inshore	8	0.3	0.8	0–4	30	1804	60.1	62.5	5–220	0.4	California, Western
Offshore	24	0.9	1.8	0–8	28	2634	94.1	91.9	5–411	0.9	Western, California, American Herring
Total	32	0.6			58	4438				0.7	
Outer Coast											
Main shoreline	6	0.2	0.5	0–2	30	2041	68	103.5	1–485	0.3	California, Western
Open bay	2	0.1	0.5	0–2	17	1268	74.6	138	7–600	0.2	Western, California
Bay shoreline	10	0.4	1	0–4	23	5229	227.4	42.5	3–850	0.2	Western, California, Ring-billed, Heerman’s, Short-billed
Bay intertidal flat	58	3.6	4.6	0–16	16	11 777	736.1	612	38–2600	0.5	California, Short-billed, Western, Glaucous-winged
River/stream mouth	333	12.8	17.4	0–60	26	26 133	1005.1	896	2–2200	1.3	California, Western, Heerman’s
Freshwater lake/pond	1	0.1	0.3	0–1	15	156	10.4	33.9	0–132	0.6	Western, California
Sanitary landfill	192	10.7	17.9	0–75	18	30 318	1684.3	840.4	423–3687	0.6	California, Western, Glaucous-winged, American Herring
Total	602	4.2			145	76 922				0.8	
Inner Coast											
Main San Francisco Bay											
Open bay	0	0	0	0	15	421	28.1	21.7	7–85	0	Western, California, Glaucous-winged
Shoreline	1	0.1	0.3	0–1	15	264	17.6	14.5	2–54	0.4	Western, California, Glaucous-winged
Intertidal flat	0	0	0	0	15	2238	149.2	145.4	24–480	0	Ring-billed, California, Glaucous-winged
Small Bay											
Open bay	80	1.7	7	0–38	47	4010	85.3	249	0–1400	2	Western, California
Shoreline	309	9.4	39.9	0–226	33	6446	195.3	559.7	0–3000	4.8	Western, Glaucous-winged, California, Ring-billed
Intertidal flat	205	6	15.3	0–54	34	10 888	320.2	350.4	7–1600	1.9	California, Ring-billed, Short-billed, Glaucous-winged
Developed shoreline	2	0.1	0.5	0–2	15	820	54.7	56.3	13–250	0.2	Western, California
Marsh/pond complex	0	0	0	0	18	660	36.7	64	2–275	0	Ring-billed
Marsh/pond complex-sanitary landfill	286	19.1	25.5	0–90	15	8329	549.3	612.7	17–2616	3.4	American Herring, California, Glaucous-winged, Ring-billed
Sanitary landfill	264	17.6	9.1	4–38	15	24 186	1612.4	710.7	255–2594	1.1	Glaucous-winged, Western, California
Developed	0	0	0	0	16	239	14.9	9.4	0–32	0	Ring-billed, California
Total	1147	4.8			238	58 501				2	

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Table 2 continued from previous page

Geographic area & habitat	Number of Iceland Gulls recorded				No. counts	Number of individuals of all gull species recorded				Iceland Gull % total gulls	Other gull species recorded (in decreasing order of abundance)[b]
	Total	Mean	SD[a]	Range		Total	Mean	SD[a]	Range		
Bay Plain											
Sanitary landfill	680	14.8	23.1	0–120	46	18979	412.6	385.4	0–1400	3.6	California, American Herring, Glaucous-winged
Freshwater lake/ pond-sanitary landfill	340	5	4.7	0–19	68	13523	198.9	167.8	0–660	2.5	Glaucous-winged, California, Western, American Herring, Ring-billed
Park/lawn	0	0	0	0	15	1420	94.7	68.7	23–270	0	Ring-billed
Developed	0	0	0	0	15	171	11.4	7	4–26	0	Ring-billed
Animal feedlot	0	0	0	0	19	1305	68.7	91.4	0–310	0	Ring-billed
Food processing plant	0	0	0	0	21	549	26.1	17.3	4–75	0	Western, Glaucous-winged
Waste recycling facility	2	0.1	0.5	0–2	17	663	39	43.6	0–170	0.3	California, Glaucous-winged, Ring-billed
Total	1022	5.1			201	36610				2.8	
Inner Coast Range											
Freshwater lake/ pond-sanitary landfill	849	56.6	57.5	7–210	15	34760	2317.3	1641.7	540–7000	2.4	California, American Herring, Glaucous-winged
Total	849	56.6			15	34760				2.4	
Central Valley											
Sanitary landfill	2360	49.2	57.6	0–258	48	52263	1088.1	1149.4	0–3500	4.5	American Herring, California, American Herring × Glaucous-winged, Glaucous-winged
Developed	0	0	0	0	15	107	7.1	6.6	1–20	0	Ring-billed, California
Total	2360	37.5			63	52370				4.5	
Grand total	**6012**	**8.4**			**720**	**263601**				**2.3**	

[a] SD = Standard deviation.
[b] Other gull species are American Herring *Larus smithsonianus*, California *L. californicus*, Glaucous-winged *L. glaucescens*, Heermann's *L. heermanni*, Ring-billed *L. delawarensis*, Short-billed *L. brachyrhynchus*, and Western *L. occidentalis.*

Feeding and loafing were the typical behaviors shown in all the sanitary landfill habitats, and loafing was the only behavior shown in the related freshwater lake/pond-sanitary landfill habitats. Loafing was also the most common behavior in the OC5 habitat; here, gulls appear to feed at low densities in adjacent Pacific Ocean habitats. In the habitats with the highest mean counts of Iceland Gulls, the most common *Larus* gulls included California and American Herring gulls in ICR1, American Herring and California gulls in CV1 and IC9, Glaucous-winged and Western gulls in IC10, California and American Herring gulls in BP1, and California and Western gulls in OC5 and OC7 (Table 2).

Lower mean counts of Iceland Gulls (3.6–9.4 birds) were recorded in the Inner Coast small bay shoreline (IC5), Inner Coast small bay intertidal flat (IC6), Bay Plain freshwater lake/pond-sanitary landfill (BP2), and Outer Coast bay intertidal flat (OC4) habitats. The highest counts in the IC5 habitat were primarily due to large numbers of gulls, including Iceland Gulls, using shoreline habitats for feeding in Belvedere Cove and Richardson Bay during Pacific Herring *Clupea pallasii* spawning runs in mid-winter. At other times, significantly fewer individuals used this habitat. The OC4 and IC6 habitats were used by many gull species for feeding during low tides. The BP2 habitat was used by a moderate number of individuals, including Iceland Gulls, for loafing when they were not feeding at the Redwood Landfill, located 7.2 km to the south. The most common *Larus* gulls in these habitats included Western and Glaucous-winged gulls in IC5, California and Ring-billed gulls in IC6, Glaucous-winged and California gulls in BP2, and California and Short-billed gulls in OC4. Low mean counts (< 2.0) of Iceland Gulls were recorded in the other habitats. The most common gull species in these habitats varied (Table 2).

In terms of geographic areas (i.e., all habitats combined in each), the mean counts continuously increased from the Pacific Ocean to inland areas, from a low of 0.6 for the Pacific Ocean to a high of 56.6 in the Inner Coast Range and 37.5 in the Central Valley (Table 2). These results for the geographic areas are consistent with the results for the major habitats.

Relative abundance

The total number of Iceland Gulls recorded was 2.3% of the total number of all *Larus* gulls recorded (Table 2). However, the relative abundance of Iceland Gulls varied among the habitats and geographic areas. The habitats with the highest proportions (Table 2) were the Inner Coast small bay shoreline (IC5, 4.8%), Central Valley sanitary landfill (CV1, 4.5%), Bay Plain sanitary landfill (BP1, 3.6%), and Inner Coast marsh/pond complex-sanitary landfill (IC9, 3.4%). To simplify z-tests comparing proportions among habitats, values were combined for IC9 and IC10 and for ICR1 and CV1, as mentioned above. None of the pairwise comparisons of the habitats showed any significant statistical differences (at $P < 0.05$). Proportions were ≤ 2.5% in all other habitats. eBird counts completed by P. Pyle during the study period recorded 0.8% Iceland Gulls in three Outer Coast habitats at five locations on the San Francisco Peninsula, the same percentage as recorded in this study on the Outer Coast. At landfills, the relative abundance of Iceland Gulls was lowest at the Outer Coast sanitary landfill (OC7, 0.6%) and the Inner Coast sanitary landfill (IC10, 1.1%). Western and Glaucous-winged gulls were the most common species at these landfills, along with California Gulls at OC7.

The z-tests for the geographic areas indicated that none of the differences in the pairwise comparisons were significant at $P < 0.05$. The only comparison that approached statistical significance was between the Outer Coast (0.8% Iceland Gulls) and Central Valley (4.5%) ($z = -1.79$; n = 145, 63; $P = 0.073$).

Age-class distribution

The majority of Iceland Gulls recorded were adults (70%, Table 3), and the proportion was similar in each of the three years of study, ranging between 66% and 76% (Table 4). The proportions of immature gulls (first, second, and third winter) also varied somewhat, although the same pattern was evident each year, with most immature gulls being first-winter birds (20%), followed by second- (8%) and third-winter birds (3%), respectively.

The proportions of adults recorded in the habitats with the highest mean counts ranged from 52% to 84% (Table 3). Habitats with the highest mean counts and the highest proportions of adults were the Inner Coast small bay shoreline (IC5, 84%), Bay Plain sanitary landfill (BP1, 77%), Inner Coast small bay intertidal flat (IC6, 73%), Inner Coast marsh/pond complex-sanitary landfill (IC9, 73%), and Central Valley sanitary landfill (CV1, 73%). Significant associations were evident between age-class distribution and habitat ($\chi^2 = 104.4$, $df = 12$, $n = 4519$, $P < 0.001$) and between age-class distribution and geographic area ($\chi^2 = 102.1$, $df = 12$, $n = 5546$, $P < 0.001$). To simplify the analysis, only the habitats with the highest mean counts were included in the habitat comparison.

The related IC9 and IC10 habitats were combined to simplify a z-test analysis of proportions of adults in the habitats, as previously described. The Pacific Ocean habitats were excluded because of insufficient sample size. The Outer Coast river/stream mouth (OC5, 52% adults) and BP1 (77% adults) habitat comparison was the only pair with a significant difference ($z = -2.18$; n = 26, 46; $P < 0.05$). The difference between the OC5 (52%) and CV1 (73%) habitats approached significance ($z = -1.82$; n = 26, 48; $P = 0.069$). There were also significant differences between the following geographic areas: Outer Coast (50%) and Inner Coast (75%) ($z = -3.73$; n = 58, 238; $P < 0.001$), Outer Coast and Bay Plain (71%) ($z = -2.98$; n = 58, 201; $P < 0.001$), and Outer Coast and Central Valley (73%) ($z = -2.60$; n = 58, 63; $P < 0.01$). The largest differences in age-class distribution were between the Outer Coast and geographic areas that were further inland, with the proportion of adults increasing across this range. eBird age-class data for Iceland Gulls collected by P. Pyle in three Outer Coast habitats (main shoreline, river/stream mouth, and freshwater lake/pond) in 35 counts at five locations on the San Francisco Peninsula recorded 46% adults, a result very similar to the 50% in the Outer Coast habitats observed in this study.

DISCUSSION

Several Iceland Gull population estimates have been made for North America (excluding Greenland), as follows: 50 000 to 100 000 total (*kumlieni* and *thayeri*; Richards & Gaston 2018); 12 600 adult *thayeri* (Snell 2002); 25 000 breeding adult *thayeri* (Gaston *et al.* 2012); and 20 000 *thayeri* based on Christmas Bird Count data (Snell *et al.* 2020, National Audubon Society 2023). Counts of *thayeri* spring migrants in the Berner's Bay area (southeastern Alaska) have ranged from 8000 to over 12 000 (Tobish 1995, 1996). A significant portion of the total *thayeri* population probably passes through this area. The numbers of *thayeri* recorded in heavily used habitats in the current study region suggest that this wintering area is significant for this subspecies. The distribution and abundance of Iceland Gulls in the study region are most influenced by the availability of certain habitats used for feeding, as discussed below.

Habitat use and behavior

The highest counts of wintering Iceland Gulls and other *Larus* gulls were recorded in landfill and associated loafing habitats in the Central Valley, Inner Coast Range, Bay Plain, and Inner Coast areas. Included in these geographic areas are the San Francisco, Oakland, San Jose, and Sacramento metropolitan areas, which currently use many large landfills. Use of landfills for feeding by many gull species has been widely reported (e.g., Horton *et al*. 1983; Belant *et al*. 1993, 1998). In the study region, tracking studies have shown concentrated use of landfills by California Gulls breeding in colonies in the southern portion of San Francisco Bay (Ackerman *et al.* 2018). Similarly, other studies have shown use of coastal landfills and food-recycling facilities on the mainland by Western Gulls breeding at Southeast Farallon Island (43 km offshore of San Francisco) and Año Nuevo Island (1 km from shore, 47 km southeast of San Jose; Spear 1988, Shaffer *et al.* 2017). The extensive use of inland habitats by wintering Iceland Gulls in the study region is probably due primarily to the high use of landfills for feeding, as most of the largest landfills in the region are inland.

Iceland Gull distribution and abundance in the study region in the winter, based on eBird *Status and Trends Summary* data (Fink *et al.* 2022), are presented in Fig. 3. The results are very similar to the results of this study, with similar areas of highest abundance mapped on the Outer Coast, Inner Coast, and landfills on the Bay Plain and in the Central Valley. Based on eBird *Status and Trends Summary* data (Fink *et al.* 2022, Fig. 4), the core winter range on the Pacific

TABLE 3
Age-class distribution of Iceland Gulls *Larus glaucoides thayeri* in major habitats in Northern California, USA

Geographic area & habitat	Number of Iceland Gulls recorded[a]								
	First winter	% total	Second winter	% total	Third winter	% total	Adult	% total	Total
Pacific Ocean									
Inshore	0	0	0	0	0	0	8	100	8
Offshore	NA		NA		NA		NA		NA
Total	0	0	0	0	0	0	8	100	8
Outer Coast									
Main shoreline	1	25	0	0	1	25	4	50	6
Open bay	0	0	0	0	0	0	2	100	2
Bay shoreline	9	90	0	0	1	10	0	0	10
Bay intertidal flat	24	41	6	10	1	2	27	47	58
River/stream mouth	97	29	50	15	13	4	173	52	333
Freshwater lake/pond	0	0	0	0	0	0	1	100	1
Sanitary landfill	NA		NA		NA		NA		NA
Total	131	32	56	14	16	4	207	50	410
Inner Coast									
Main San Francisco Bay									
Open bay	0	0	0	0	0	0	0	0	0
Shoreline	0	0	0	0	0	0	1	100	1
Intertidal flat	0	0	0	0	0	0	0	0	0
Small bay									
Open bay	11	14	5	6	4	5	60	75	80
Shoreline	32	10	10	3	7	2	260	84	309
Intertidal flat	31	15	15	7	9	4	150	73	205
Developed shoreline	0	0	0	0	0	0	2	100	2
Marsh/pond complex	0	0	0	0	0	0	0	0	0
Marsh/pond complex-sanitary landfill	7	21	2	6	0	0	24	73	33
Sanitary landfill	57	22	24	9	7	3	176	67	264
Developed	0	0	0	0	0	0	0	0	0
Total	138	15	56	6	27	3	673	75	894
Bay Plain									
Sanitary landfill	101	15	40	6	16	2	523	77	680
Freshwater lake/pond-sanitary landfill	121	36	19	6	3	1	197	58	340
Park/lawn	0	0	0	0	0	0	0	0	0
Developed	0	0	0	0	0	0	0	0	0
Animal feedlot	0	0	0	0	0	0	0	0	0
Food processing plant	0	0	0	0	0	0	0	0	0
Waste recycling facility	0	0	0	0	0	0	2	100	2
Total	222	22	59	6	19	2	722	71	1022
Inner Coast Range									
Freshwater lake/pond-sanitary landfill	198	23	90	11	28	3	533	63	849
Total	198	23	90	11	28	3	533	63	849
Central Valley									
Sanitary landfill	413	18	163	7	56	2	1728	73	2360
Developed	0	0	0	0	0	0	0	0	0
Total	413	18	163	7	56	2	1728	73	2360
Grand total	**1102**	**20**	**424**	**8**	**146**	**3**	**3871**	**70**	**5543**

[a] NA: not available. Numbers are based on observations made during the current study and do not include the eBird counts included in other analyses in the current study for certain habitats.

TABLE 4
Age-class distribution of Iceland Gulls *Larus glaucoides thayeri* in the winters of 2020/21, 2021/22, and 2022/23 in Northern California, USA[a]

	Number of Iceland Gulls recorded								
	First winter		Second winter		Third winter		Adult		
Winter period	**Number**	**% total**	**Number**	**% total**	**Number**	**% total**	**Number**	**% total**	**Total**
2020/21	281	16	95	6	34	2	1306	76	1716
2021/22	398	22	142	8	55	3	1244	68	1839
2022/23	423	21	187	9	57	3	1321	66	1988
Total	1102	20	424	8	146	3	3871	70	5543

[a] Numbers are based on observations made during the current study and do not include the eBird counts included in other analyses in the current study for certain habitats.

coast includes coastal British Columbia and northern Washington. Relatively few areas of concentration are located on the coasts of southern Washington, Oregon, and Northern California, other than the significant concentration areas identified in this study.

As California SB 1383 is implemented, the number of *Larus* gulls, including Iceland Gulls, using landfills in California may decrease unless food at composting facilities becomes widely available. A reduction in food availability could reduce the size of the wintering gull population (Conover 1983, Horton *et al*. 1983) or change patterns of food and habitat use in the region (Weiser & Powell 2011, Osterback *et al*. 2015, Langley *et al.* 2021).

A recent satellite tracking study of Iceland Gulls provided significant new information on migration, movements, and habitat use of wintering *thayeri* on the Pacific coast of Canada and the USA (Gutowsky *et al.* 2020) that can be compared to direct observations of large numbers of individuals in the current study. The Gutowsky study included tracking four adults that wintered from Southeast Alaska to Northern California. All four gulls primarily used marine habitats, including offshore and coastal, with less use of inland habitats. One of these gulls (THGU1) wintered in the current study region and primarily occurred in marine habitats, but it also used inland habitats more than the other three tracked gulls. This individual showed large movements, traveled the furthest offshore

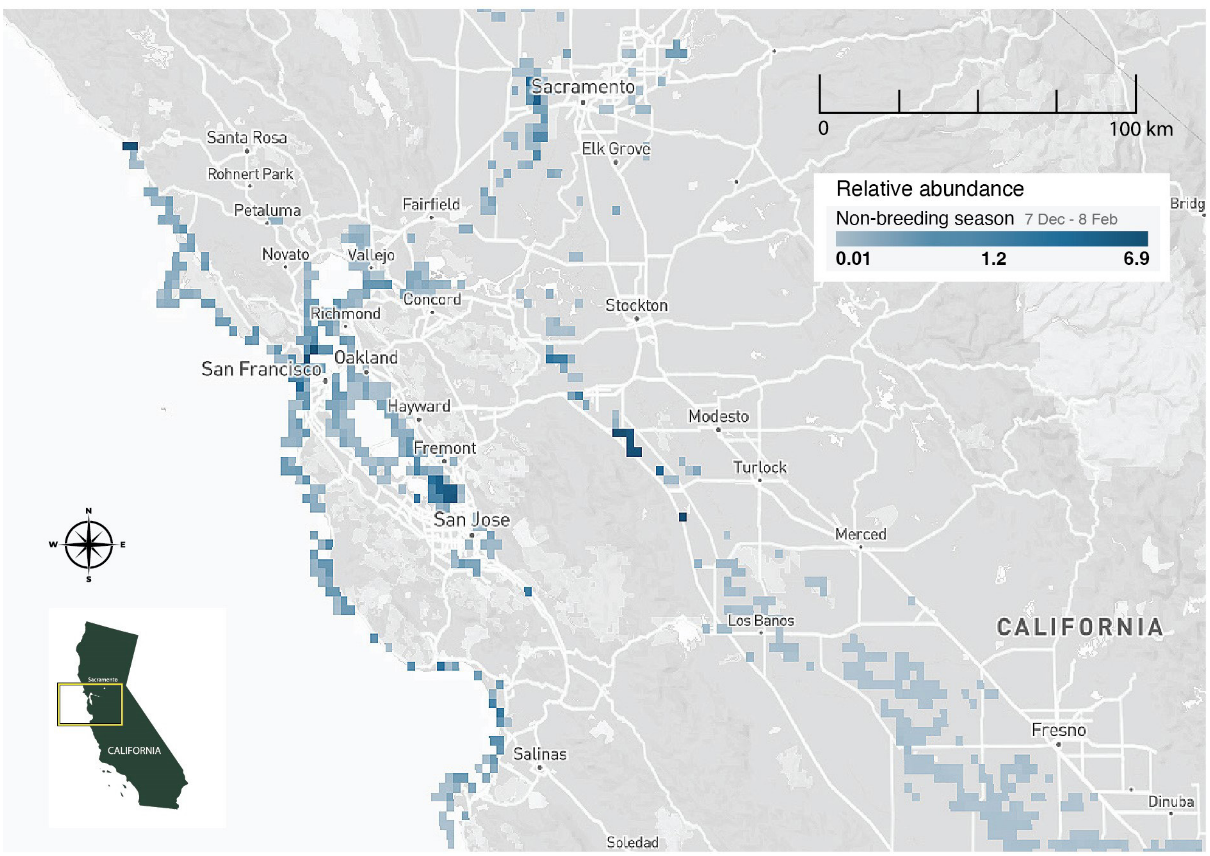

Fig. 3. Iceland Gull *Larus glaucoides thayeri* winter abundance in the study region, based on eBird data (*Status and Trends Summary*, Fink *et al.* 2022). "Relative abundance" is the estimated average count of individuals detected by an eBird observer during a one-hour, one-kilometer traveling checklist at the optimal time of day. Image credit: created on 25 July 2023 by eBird (www.eBird.org).

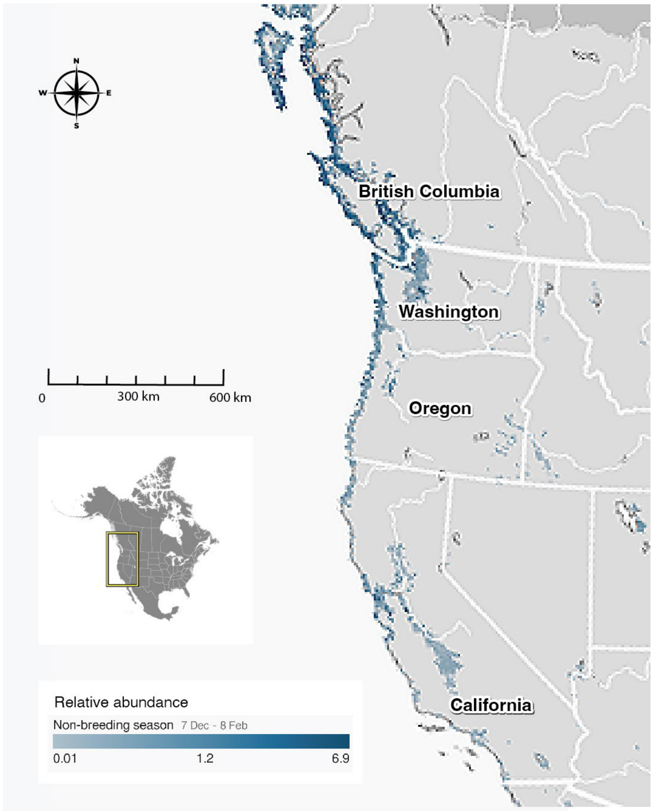

Fig. 4. Iceland Gull *Larus glaucoides thayeri* winter abundance on the Pacific coast of Canada and USA, based on eBird data (*Status and Trends Summary*, Fink *et al*. 2022). "Relative abundance" is the estimated average count of individuals detected by an eBird observer during a one-hour, one-kilometer traveling checklist at the optimal time of day. Image credit: created on 01 August 2023 by eBird (www.eBird.org).

(102 km) and inland (39 km) of all four gulls, and was the only gull in the group that used inland habitats such as cities, landfills, and agricultural areas. In another tracking study, Domalik *et al.* (2021) studied four adult Glaucous-winged Gulls equipped with satellite transmitters that nested in British Columbia. Three of the four gulls wintered in British Columbia and primarily used inshore and coastal habitats. The fourth gull wintered in Northern California and used coastal, urban, and cropland habitats, similar to THGU1.

The observations of gull movements in the current study—including mixed-species groups of 20–600 California, Herring, and Glaucous-winged gulls—coupled with observations by Gutowsky *et al.* (2020) suggest there are significant gull movements both between various landfills and between landfills and other habitats in the current study region. However, an individual adult Iceland Gull with very distinctive plumage and soft-part characteristics (approaching many *kumlieni* in terms of primary patterning, with mottled irises and a distinctively marked bill) was observed on 24 January and 01 February 2023 in this study on the bank of the Delta-Mendota Canal at the Tracy Landfill. It was observed again and photographed on 14 February 2023 at the same location (Terrill 2023). These observations suggest that there is also repeated use of the same wintering location by individual gulls. Spear (1988) observed that foraging-site fidelity in Western Gulls in the study region during the non-breeding season was most prominent among males and was significant in immatures and adults, increasing with age. Locations used by immatures were often used again when they became adults. Adults typically occurred in the same locations until the beginning of the breeding period.

Gutowsky *et al.* (2020) agreed with Snell *et al.* (2020) that *thayeri* are almost exclusively maritime or coastal in the winter and supported the conclusion of Morgan *et al.* (1991) that *thayeri* are common over the continental shelf off the coast of British Columbia and Oregon. Vermeer *et al.* (1989) also described *thayeri* as common in the winter offshore of British Columbia. Ingolfsson (1967) observed that wintering *glaucoides* in Iceland primarily fed on the ocean surface in inshore waters and did not feed at refuse dumps near the shoreline, unlike the other wintering *Larus* gulls in the region. Snell (2002) also described the species as almost exclusively maritime or coastal outside of the breeding period and less likely to feed at landfills than many other *Larus* gulls.

In contrast, Sanger (1973) and Briggs *et al.* (1987) reported only low numbers of wintering Iceland Gulls in offshore marine habitats along the California coast. eBird counts by experts included in this study include a low mean count (0.9) and 0.9% Iceland Gulls in offshore habitats, with the most common species being Western, California, and Glaucous-winged gulls. In an extensive study of marine bird populations in the fall (late September 2020–2022) in Queen Charlotte Strait and adjacent areas off the northern end of Vancouver Island in the core winter range, Gaston *et al.* (2024) recorded higher densities of Iceland Gulls in coastal areas located within 0.5 km of the shoreline around Johnstone Strait and lower densities in open-water areas. The substantially larger number of Iceland Gulls recorded in this study compared to the four tracked individuals in the Gutowsky *et al.* (2020) study may explain many of the observed differences in their use of offshore and inland habitats. Additional data collected in offshore habitats in the current study region are needed to provide more conclusive information on this topic.

Differences in habitat use by *Larus* gull species based on geography, individual, season, sex, age, food availability, competition, breeding location, and other factors have also been widely reported (Greig *et al.* 1985, Schmutz & Hobson 1998, Steenweg *et al.* 2011, Washburn *et al.* 2013, Camphuysen *et al.* 2015, Maynard & Ronconi 2018, Anderson *et al.* 2019, O'Hanlon *et al.* 2022). These differences are consistent with observed differences in habitat use by Iceland Gulls between the current study region and some other regions, including the extent of inland and offshore habitat use. Ingolfsson (1967) observed changes in habitat use by wintering *glaucoides* and other *Larus* gull species in relation to food availability in Iceland. In the current study, mid-winter Pacific Herring spawning runs concentrated Iceland Gulls and other gull species in large numbers for short time periods (usually 3–4 days) at a few sites in bay shoreline, intertidal flat, and open bay habitats in northern San Francisco Bay. These habitats supported only low numbers of Iceland Gulls at other times.

In this study, habitat use by Iceland Gulls was most similar to that of American Herring Gulls, with highest counts in habitats in the Central Valley and around the outer edges of San Francisco Bay to the north and south. However, American Herring Gulls appeared to be substantially more common in the Pacific Ocean offshore than Iceland Gulls. Habitat use was most dissimilar to that of Western and Glaucous-winged gulls, which were most common in Outer

Coast habitats and in Inner Coast habitats in the central portion of San Francisco Bay. Glaucous-winged Gulls were more widely distributed than Western Gulls in Inner Coast habitats. California Gulls were widely distributed in many habitats and geographic areas, ranging from the Pacific Ocean to the Central Valley. Ring-billed Gulls were most common in large- and small-bay intertidal flats, marsh/pond complexes, and developed habitats on the Inner Coast; parks/lawns, animal feedlots, and developed habitats on the Bay Plain; and developed habitats in the Central Valley.

Western Gulls are one of the two most common breeding species in the study region (along with the California Gull), and they are primarily permanent residents. In an extensive study involving banded gulls and direct counts, Spear (1988) found that Western Gulls breeding at the largest colony in the region on Southeast Farallon Island nested during the most productive marine period (spring and summer) and fed primarily in offshore marine habitats during this period. Using telemetry, Shaffer *et al.* (2017) also observed concentrated offshore feeding by Western Gulls breeding on Southeast Farallon Island. However, in August/September, following the completion of breeding and when marine productivity is low, these adult Western Gulls largely dispersed to coastal locations to feed at landfills and other habitats (Spear 1988). Breeding Western Gulls on Southeast Farallon Island started to return to the island in October, and many territories were re-occupied in November/December. There were some differences in habitat use by immature gulls, with more variability between years based on marine food availability. Spear (1988) attributed the observed behavior of adults to significant competition for nest sites on the island, the arrival of large numbers of wintering Glaucous-winged Gulls in the fall, slightly increased marine productivity in the winter, and completion of primary molt by Western Gulls allowing increased foraging range.

This pattern of coastal habitat use by Western Gulls in the region may affect habitat use by and abundance of other migratory gull species in the winter by increasing the availability of food and other resources in some Inner Coast habitat types in San Francisco Bay. Significant numbers of adult Western Gulls were recorded in a variety of Inner Coast and Outer Coast habitats in this study, but these counts may have included gulls nesting in smaller island colonies in central San Francisco Bay, isolated pairs nesting in urban locations around the shoreline of the central bay (Pierotti & Annett 2001), and pairs nesting in small colonies on the Outer Coast. In addition, Shaffer *et al.* (2017) showed that some individuals that nested on Southeast Farallon Island traveled directly to feeding habitats located in central San Francisco Bay, including landfills and a food-recycling facility, as well as to other habitats not used for feeding. Non-breeding adults may also show this behavior.

Age-class distribution

The overall pattern of age-class distribution observed (i.e., decreasing numbers of immatures in successive age classes) is expected based on annual mortality. However, this also suggests an annual mortality rate of more than 50% between the first and second years and between the second and third years, unless there are differences in the winter distributions of immature gulls. Kadlec & Drury (1968) recorded 68% adults, 15% first-winter birds, and 17% second- and third-winter birds in a total of 622 000 American Herring Gulls counted on the coasts of the Atlantic Ocean and Gulf of Mexico, similar to Iceland Gulls in the current study region. Estimates of annual mortality in adult American Herring, Glaucous, Western, and Iceland (*thayeri*) gulls typically range between 10%–20% (Kadlec 1976, Spear *et al.* 1987, Allard *et al.* 2006, Gaston *et al.* 2009, Allard *et al.* 2010), but less information is available for immatures. For immature Western Gulls, Spear *et al.* (1987) recorded annual mortality rates of 45% for one-year-olds, 21% for two-year-olds, and 15% for three-year-olds; higher mortality rates for immature males compared to immature females; and higher mortality rates for breeding adult females compared to males. American Herring Gull band recoveries for 12 681 gulls included 55% juveniles, 15% one-year-olds, 7% two-year-olds, and 23% birds three or more years old (Moore 1976), suggesting that annual mortality in the first year of life and between the first and second years could be substantial. However, soft-metal band loss may contribute to over-estimates of mortality in gulls (Gaston *et al.* 2013).

The proportion of adult Iceland Gulls slightly increased from the Outer Coast to the Inner Coast and more inland areas. Adults may be more able to compete for food at landfills and other habitats in Inner Coast and inland areas when large numbers of gulls are present. Other studies have indicated that adult European Herring Gulls use landfills more than immatures, and that adult males dominate adult females and immatures in feeding areas at landfills (Monaghan 1980). Numerous studies have also shown that immature *Larus* gulls of a wide range of species are less efficient foragers at landfills and other habitats than adults (Verbeek 1977, Searcy 1978, Greig *et al.* 1983, MacLean 1986, Monaghan *et al.* 1986, Burger 1987).

Ecological niche of the Iceland Gull

Niche segregation between breeding Iceland Gulls (*kumlieni*) and sympatric Glaucous and American Herring gulls on southwestern Baffin Island includes coastal cliff nesting, along with concentrated use of coastal shoreline and inshore habitats for feeding by Iceland Gulls (Moorhouse 2021). Although Glaucous Gulls also nest on cliffs, niche separation in the breeding period is probably increased by American Herring and Glaucous gulls using a wider range of inland and terrestrial habitats for nesting and feeding, consuming a wider range of foods, and exhibiting different feeding behaviors (Richards & Gaston 2018). Differences in habitat and food use in the winter have also been documented between *glaucoides* and other species that winter in Iceland (Ingolfsson 1967). Wintering *thayeri* in this study showed differences in habitat use compared to Western and Glaucous-winged gulls, but were similar to American Herring Gulls, at least in inland and Inner Coast habitats. However, it is also clear that Iceland Gulls and other *Larus* gull species are opportunistic generalists that take advantage of abundant food sources in a variety of habitats, including long-term sources such as food waste at landfills and short-term sources such as Pacific Herring eggs during winter spawning runs in Inner Coast habitats. The availability of such food sources can significantly affect habitat use. Potential differences between *thayeri*, *kumlieni*, and *glaucoides* have not been studied in detail and may also exist during the breeding and wintering periods.

Additional studies of the Iceland Gull are needed to provide important information on this relatively poorly known species and complement the work of this study, Gutowsky (2020), and Moorhouse (2021). These include analyses of habitat use and of feeding ecology and behavior of wintering *thayeri* and *kumlieni* in their core winter ranges, as well as the same aspects for breeding and wintering *glaucoides,* and breeding *thayeri.* In all these analyses, comparisons with other *Larus* gull species that occur in the same areas as the three subspecies would be important. This information could also help address continuing questions about the systematics of this complex species, including relationships among these currently recognized subspecies (Snell *et al.* 2020). Additional information concerning the breeding period could also help address issues related to potential adverse impacts from climate change in the Arctic (Bush & Lemmen 2019) and resource extraction, tourism, pollution, and commercial fishing bycatch (Richards & Gaston 2018). Future studies of wintering Iceland Gulls and other *Larus* gull species could also provide valuable information on the potential effects of reducing the volume of food waste disposed in sanitary landfills in California and other wintering areas.

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