GLAUCOUS-WINGED GULLS *LARUS GLAUCESCENS* AS SENTINELS FOR A CENTURY OF ECOSYSTEM CHANGE – LONG-TERM TRENDS IN POPULATION, DIET, AND EGG PRODUCTION IN NORTH AMERICA'S SALISH SEA

by

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Abstract

Ecological studies characterising population trends over decades or centuries can help to describe the range of variability in a study system, with well-studied species being strong candidates for providing the long-term data required for retrospective studies. Seabirds represent useful real-time monitors of marine systems and may also play this role in studies characterizing historical ecological change. The glaucous-winged gull *L. glaucescens* is a generalist marine bird occurring in the Salish Sea, an urbanized coastal area of southwestern British Columbia and northwestern Washington, where it has been studied or collected since the mid-1800s. Its twentieth-century populations experienced dramatic growth followed by a steep decline, with recent trajectories unclear. I used multiple methods to characterise long-term trends in gull number, diet, and egg production, and to test hypotheses about causes of population change. My approach combined meta-analysis of historical reproductive traits, statistical modeling of population trend, and stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) of historical and modern gull feathers and forage fish, with modeled population trend showing a continued decline in gull numbers from the 1970s to the present. Meta-analytical results pointed to decreasing egg and clutch size and a delayed lay date over the twentieth century to the present, while stable isotope analysis showed declining feather $\delta^{13}C$ and $\delta^{15}N$ since 1860, all of which was consistent with a growing reliance by gulls on non-fish foods. Demographic modeling showed that declining clutch size and productivity were largely sufficient to account for the gull population decline, and pointed to recovery from cessation of nineteenth-century egging as being an important contributor to the increase phase. These modeling results implied that

declining consumption of forage fish affected gull productivity. Additional results from stable isotope analysis also supported a hypothesis of dietary change; namely, declining forage fish C:N ratios over time indicated a decrease in fish lipid content, and thus a decline in prey quality. Overall, my results highlight the value of compiling multiple retrospective studies to better understand the complex factors affecting long-term trends in animal populations.

Preface

The field research component of my dissertation was carried out under Permit No. A07-0309 from the University of British Columbia's Animal Care Committee, Scientific Permits Nos. BC-10-0057, BC-09-0290 and 10596 P from Environment Canada, and Research Permit No. 102098 from the BC Ministry of Environment (BC Parks). Collection of author-generated data was carried out using protocols that explicitly minimised disturbance to breeding birds.

I wrote this dissertation as a series of publishable manuscripts. A version of Chapter 2 was published as Blight, L.K. 2011. Egg production in a coastal seabird, the glaucous-winged gull (*Larus glaucescens*), declines during the last century. PLoS ONE 6(7):e22027.doi:10.1371/journal.pone.0022027. I conceived of the research (with the assistance of my supervisory committee), conducted or supervised the data collection, analysed the data, and wrote the manuscript.

I wrote Chapter 3 as a draft manuscript for publication in collaboration with Drs. Mark Drever (Environment Canada) and Peter Arcese (UBC), under the proposed title "Generalist foragers affected by multiple factors over time: a century-long population trend of glaucous-winged gulls in the Georgia Basin, Canada". I was responsible for determining the research questions and approach, collecting the data and supervising its compilation, and writing most of the manuscript. Mark Drever and I collaborated in determining the questions to be addressed by the chapter's population trends model and the secondary analyses of those results. Mark also wrote the *R* code for analysing the data, and contributed the relevant text for those sections of

the Methods and Results sections. Peter Arcese suggested the use of balance models (following Walters and Martell 2004) to test hypotheses about causes of population trends, and developed the prototype demographic models to do so, while I compiled the data that parameterised the models, and revised model parameters. I also revised the manuscript based on comments by these two co-authors.

I also wrote Chapter 4 as a draft manuscript for publication, in collaboration with Drs. Keith Hobson (Environment Canada) and Peter Arcese (UBC). Its working title is "Changing gull diets in a changing world: a 150-year feather isotope record from a northeast Pacific coastal zone". I designed the study, collected or coordinated the collection of feather samples and forage fish muscle tissue from museums, prepared 50% of museum samples for isotopic analysis and supervised the preparation of the remaining 50%, analysed the data, and wrote the manuscript. Keith Hobson provided input on interpretation of results, and suggested the use of C:N ratios in order to compare results with other studies. The sourcing of feathers from museum specimens was carried out using an international database of museum-held marine birds compiled by Drs. Peter Arcese and Ryan Norris, with additional specimens located by me via museums' online databases. As co-authors, Drs. Arcese and Hobson provided editorial comments, and I incorporated these into the manuscript.

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A wildlife study investigating 150-year trends in population and diet must draw upon data compiled from a multitude of sources. For my dissertation I not only collected my own data but also utilised museum specimens, museum records, and the published and unpublished studies of several generations of researchers, with data collected and analysed using a variety of field-based, lab-based and statistical techniques. This project would not have been possible without the assistance of numerous people, and I thank them all. These many collaborators and contributors are listed in the specific chapters to which they contributed.

Discussions with friends and colleagues working on gulls, other seabirds, and related ecosystems also helped me to develop my overall research approaches. Thanks to Doug Bertram (Environment Canada), Russ Bradley (Point Reyes Bird Observatory), Carmen Cadrin (BC Ministry of Environment), Joe Galusha (Walla Walla University), Jim Hayward (Andrews University), Stephanie Hazlitt (UBC and BC Ministry of Environment), Kees Vermeer (Environment Canada, retired), Scott Pearson (Washington Department of Fish and Wildlife), and Tony Williams (Simon Fraser University). Ryan Norris provided initial comments on an early iteration of the stable isotope portion of my research proposal, and contributed his detailed template for museum sampling proposals. Moira Galbraith and her students identified invertebrates in gull food samples, and Peter Pyle engaged in useful discussions on moult patterns in glaucous-winged gulls. Our fieldwork at Mandarte Island was conducted as guests of the Tswaout and Tseycum First Nations.

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For Iain, Andréa, and the seagulls

Chapter 1: Introduction

1.1 Background

One of the big questions in ecology is what constitutes a natural change in animal populations. Increasing awareness about the limitations of short-term datasets (e.g., Pauly 1995, Jackson et al. 2011) has spurred efforts to reconstruct population trends over timescales of decades, centuries, and even millennia for a host of taxa including fish, birds, marine mammals, and invertebrates (Holmgren-Urba and Baumgartner 1993, Chamberlain et al. 2005, Lotze et al. 2006, Schindler et al. 2006). Similar approaches over similar timelines have been used to reconstruct other aspects of animal biology, including diet, community composition, size-at-age, genetic diversity, and geographical range (Weber et al. 2000, McClenachan et al. 2006, Emslie and Patterson 2007, Norris et al. 2007, Ainley and Blight 2009, McClenachan 2009). In applied situations, long-term baselines are useful because ecosystems have often been shaped by human activities, and accurate historical information on the range of variability improves our estimates of accumulated changes (Wiens 1984, Arcese and Sinclair 1997), as well as our predictions about future states and our ability to manage them (Lotze et al. 2006). Additionally, identifying long-term baseline conditions contributes to our basic understanding of the mechanisms that allow ecosystems to withstand perturbations and maintain overall resilience (Pauly et al. 1998a, b, Folke et al. 2004).

Though useful, the development of such baselines over scales of more than a few decades is hindered by a paucity of relevant data (Pinnegar and Engelhard 2008). While some long-term studies are able to use the relatively straightforward approach of contrasting early surveys with

modern population records (e.g., Tingley et al. 2009), such records do not exist for the majority of species. Even when they are available, published population or occurrence records selcom extend back more than a century for any taxon. Applied historical ecology is a synoptic and sometimes multi-disciplinary approach that uses historical knowledge, broadly defined, to reconstruct long-term trends in order to inform our understanding of ecological baselines, as well as to contribute to ecosystem management (Swetnam et al. 1999, Schrope 2006, HMAP 2008). Due to the seminal work of prominent ecologists (e.g., Pauly 1995, Pauly et al. 1998a, Jackson et al. 2001, Schrope 2006, Lotze and Worm 2009, Jackson et al. 2011), efforts to reconstruct historical trends are now particularly advanced for marine systems, with some reconstructions dating back to the early days of European exploitation of the seas.

The study of causes of changes in marine ecosystems through time, marine historical ecology uses diverse sources of early biological information that often pre-date modern collection methods such as population surveys. These may include more conventional historical sources (e.g., archived data or unpublished museum records), but also less traditional ones such as old logbooks and other historical documents, and genetic or stable isotope analysis of museum or archaeological specimens (e.g., Sáenz-Arroyo et al. 2006, Pinnegar and Engelhard 2008, Gutowsky et al. 2009). For example, McClenachan et al. (2006) used explorers' accounts and trade records to map historical nesting beaches of Caribbean sea turtles back to the 1600s, concluding that current populations are currently at <1% of their pre-exploitation abundance. Ferretti et al. (2008) utilised multiple historical sources and extracted data from fisheries landings, sightings records and scientific surveys to reconstruct the population trends of large Mediterranean sharks for the nineteenth and twentieth centuries, revealing similarly steep

declines. Even studies that are primarily archaeological in nature may provide a context against which to measure current states, such as the changing nesting or migratory distribution of seabirds over hundreds to thousands of years (e.g., Causey et al. 2005, Bovy 2007).

Although the unconventional nature of these and other data sources can complicate comparisons with data collected in modern times, this problem can be addressed by application of robust methods such as Bayesian statistics or meta-analysis, with the resulting output providing credible information on long-term trends (e.g., Ferretti et al. 2008 and in prep, Blight 2011). Oral histories are less frequently used (Claesson et al. 2010), but present their own particular set of issues regarding validation of potential data and are not discussed further here.

Many historical reconstructions focus on species thought to be indicative of broader ecosystem trends by virtue of their links to essential system processes or trophic levels. The concept of indicator or sentinel species is well established as a way to monitor current or emerging ecosystem conditions, but the same approach, used retrospectively, can also provide insight into past ecological states or long-term changes. “Sentinel” species have been described as those that provide “early warning in the case of unsustainable harvesting practices” (Grémillet and Charmantier 2010: 1499), or sound “an alarm that may indicate an unknown pollution or food supply problem” (Furness and Camphuysen 1997: 727); similarly, an indicator species can be “a species that reflects the effects of a disturbance regime” (Lindenmayer et al. 2000: 943), or, more broadly, something that is used as a “surrogate measure” (Landres et al. 1988: 317). Colonial seabird species are seen as ideal environmental indicators as they are easily monitored, and frequently consume prey species that are also consumed by humans (i.e., birds

can help to monitor fish stocks; Montevecchi 1993, Furness and Camphuysen 1997, Piatt et al. 2007), sampling marine environments at a nested hierarchy of spatial and temporal scales (Woehler 2012). In addition, a number of seabird species are common, or occur in high numbers at relatively few breeding locations. This coloniality facilitates sampling by researchers, and commonly occurring species can allow for study designs that provide greater statistical power (Koch et al. 2011).

With their reduced predictive power, short-term studies can limit the reliability of seabirds as indicators (Woehler 2012), but there are now a number of datasets in existence that track seabird populations over multiple decades (e.g., Coulson and Thomas 1985, Ainley 2002, Mills et al. 2008, Cury et al. 2011). However, fewer studies have taken a synoptic approach and provided a detailed overview of changes in seabird biology over a century or more, thus capturing the effects of early exploitation, rare stochastic events, or multi-generational environmental change (for examples see Thompson et al. 1995, Rauzon 2001, Lotze 2005, Bovy 2007, Emslie and Patterson 2007, Garthe and Flore 2007, Grandgeorge et al. 2008). These long-term studies are of interest not only for the general scientific reasons mentioned above, but because the very traits that have made seabirds reliable indicators – their coloniality, competition with humans for fish prey, and sensitivity to environmental changes – have also made them vulnerable to human impacts (cf. Croxall et al. 2012). Because of this, many seabird species now occur at only a fraction of their former abundance, in habitats as diverse as the North Sea coast and the uninhabited archipelagos of the tropical Pacific Ocean (Lotze 2005, Blight et al. 2006). Studies that promote a greater understanding of these declines and their causes are of considerable value for purposes of conservation.

A wealth of research worldwide has shown quantitatively how seabird survival and reproductive output (as well as other traits such as behaviour, phenology, and physiology) are linked with the availability of prey at sea, and how natural or anthropogenic crashes in fish stocks or changes in prey phenology can dramatically affect the population trajectories of seabird predators (reviewed in Piatt et al. 2007). For example, Crawford et al. (2007) suggested that by the latter part of the twentieth century, the carrying capacity of the Benguela Current for African penguins *Spheniscus demersus* was reduced to 10 –20% of that of the 1920s, as a result of environmental variability and competition for forage fish with humans and with growing populations of fur seals *Arctocephalus pusillus*. Similarly, effects of both climate change and the harvesting of fish and krill have been linked to declines in certain seabird populations breeding in Antarctic waters (Ainley and Blight 2009, Trivelpiece et al. 2010). In the California Current system, breeding behaviour and success of auk species have been correlated with both prey declines and changes to the timing of prey availability, linked to sea surface temperature shifts (Bertram et al. 2001, 2005, Blight et al. 2010). Mechanisms linking seabird population trends with declining availability of their prey include breeding propensity (Schreiber and Schreiber 1984, Murphy et al. 1992), decreased egg production and number of chicks fledged (Hiom et al. 1991, Bertram et al. 2001, 2005, Wanless et al. 2005, 2007), and even survival of adults when conditions are particularly poor (Barber and Chavez 1983).

Seabird population changes related to food or other stressors may occur system-wide, as in the examples above, or may take place at a more local level. In the inshore waters of the Salish Sea

Figure 1.1: The Georgia Basin and Salish Sea. Grey line showing Canada/US border denotes boundary between Georgia Basin (Canada) and Puget Sound (USA) regions, which together approximately form the Salish Sea. © The SeaDoc Society / Norman Maher, with permission.

(coastal Washington (WA) and British Columbia (BC); Fig. 1.1; described in Study Area, below), the by-products of a rapidly growing human population (e.g., pollution, habitat and species loss, and overfishing) have affected coastal and marine ecosystems since at least the advent of

European colonisation (Province of British Columbia 1915, Fraser et al. 2006, Johannessen and Macdonald 2009), with seabirds being among the wildlife species affected by these changes (Norris et al. 2007, Blight in prep.). The goal of my dissertation research was to reconstruct long-term trends in population size, diet, and breeding biology of the glaucous-winged gull *Larus glaucescens*, a Salish Sea marine bird, and to use this information to infer aspects of past ecological conditions in my study system. This species underwent population declines in the region in the late twentieth century, and prior to my research this decline appeared to have continued into the 2000s (Sullivan et al. 2002).

The glaucous-winged gull is a widespread and abundant mesopredator of North Pacific marine and nearshore ecosystems, and its presence near human habitations means it has been the subject of a number of studies since Europeans settled in the region. Gulls are a tractable species for studies of environmental change because their dietary plasticity means they are highly adaptable to anthropogenic effects on their environment; as with other trophic generalists, they may track such changes without being extirpated by them (Purvis et al. 2000, Layman et al. 2007). The specific objectives of my research were to:

- Compile approximately 100 years of historical population data for glaucous-winged gulls in the Canadian portion of the Salish Sea (the Georgia Basin; see Study area, below), and conduct the first comprehensive population inventory in the study region in 25 years;

- Use this updated dataset to provide the first quantitative estimates of long-term population trend within the region;

- Use stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis of feathers from modern birds and museum specimens to track long-term (150 y) dietary changes in glaucous-winged gulls in the study area;

- Assess historical trends in reproductive output of glaucous-winged gulls in the region, and test for relationships of these trends to changes in gull diet;

- Test competing hypotheses about the potential drivers of glaucous-winged gull population trends over the past century; and

- Conduct this work in a way that would facilitate the development of methods using gulls for long-term monitoring strategies in coastal marine ecosystems.

Despite the examples cited herein, marine birds in general are poorly represented in the historical ecology literature (HMAP 2008), so this work represented a potential expansion of existing approaches in this field. In the remainder of this chapter, I (i) describe the study system (the biology of the study species and its known history of population change; the study area); (ii) introduce a set of hypotheses to explain these changes, and their related predictions; (iii) describe the data I used to test these predictions; and (iv) provide a general overview of each subsequent chapter. Details of data collection methods and analyses are outlined in the specific chapters to which they apply.

1.2 Study System

1.2.1 Study Species and Historical Population Trends

The glaucous-winged gull has a global breeding range that extends around the northern coastal Pacific from northwest Oregon to the islands of the western Bering Sea and the Kamchatka Peninsula (Hayward and Verbeek 2008). A conspicuous species with accessible nesting colonies, it has been studied by ecologists and naturalists in North America for the last 100+ years, with periodic surveys carried out at nesting colonies in the Salish Sea since at least 1900 (Anonymous 1908, Drent and Guiguet 1961, Hayward and Verbeek 2008; Appendix 2) and eggs and skins collected from 1860 on (Carter and Sealy 2011; Chapters 2 and 4).

Early twentieth century trends had not been described in detail prior to my research, but various partial reports from the Georgia Basin show that the glaucous-winged gull underwent a rapid and dramatic increase in population size in the early- to mid-twentieth century. Prior to the 1960s, counts of nesting gulls in the region were largely opportunistic (Anonymous 1908, Drent and Guiguet 1961, Drent et al. 1964, Campbell et al. 1990). In 1961, pre-existing count data were compiled for all Georgia Basin glaucous-winged gull colonies (Drent and Guiguet 1961), while in the 1970s and 1980s two censuses of the population (76 localities) were conducted (Campbell 1976, Vermeer and Devito 1989). These more detailed studies showed the population experiencing an overall annual growth rate of 2.9% from 1960 to 1986 (Drent and Guiguet 1961, Vermeer and Devito 1989, Vermeer 1992, Hayward and Verbeek 2008). A subset of 14 of these colonies was re-censused in 1997 and 1999 (Sullivan et al. 2002), with results indicating a decline of 31% in nesting pairs in comparison with the counts at the same

colonies in 1986. Whether similar declines had occurred at other Georgia Basin colonies, or if they had continued to the present, was unknown prior to my study. Other recent research suggested that glaucous-winged gulls breeding in the US portion of the Salish Sea were also in decline since about the 1980s (Galusha and Hayward 2002, Hayward and Verbeek 2008, Hayward et al. 2010). Glaucous-winged gulls breeding on the west coast of Vancouver Island (Fig. 1.1) decreased sharply in number in the 1960s in response to declines in herring populations, and have since stabilised at those reduced numbers (Parks Canada 2009). Trends in Alaska are poorly documented except at half a dozen sites, where they have been variable (Hayward and Verbeek 2008, Dragoo et al. 2010).

Glaucous-winged gulls nest colonially on isolated rocky islets and, relatively recently, on flat-roofed buildings in urban areas (Hayward and Verbeek 2008). Colonies range-wide are comprised of a few to several thousand pairs, though in BC the four largest colonies currently only range from about 1100 to 1900 pairs in size, down from historical highs of about 2500 pairs per colony in the 1970s and 1980s (Vermeer and Devito 1989; Appendix 2). On very small islets and some rooftops and pilings, birds nest as single pairs. Egg-laying begins in May; clutches are typically comprised of three, but frequently of two, eggs, at least in recent years (see Chapter 2). Partial incubation starts with the first egg, with full incubation commencing when the clutch is complete (LKB pers. obs.). Incubation averages about 27 d (Hayward and Verbeek 2008). A chick's first flight occurs between 37 and 53 d (Hayward and Verbeek 2008), but fledging is generally defined as survival beyond 28 d (Vermeer 1963) or 31 d (Reid 1988a), as approximately 90% of mortality occurs prior to day 30. Individuals can be long-lived, with the oldest known banded bird surviving to more than 37 years of age (Campbell 2007).

Glaucous-winged gull diet in the Salish Sea is mainly comprised of small fishes (primarily Pacific herring *Clupea pallasii* and Pacific sandlance *Ammodytes hexapterus*; Ward 1973, Vermeer 1982, Davis in prep; LKB pers. obs.), as well as intertidal invertebrates (e.g., crabs, sea stars, bivalves), carrion, spawning salmon, and trash (Hayward and Verbeek 2008, LKB unpubl. data). Garbage found in pellets regurgitated by adult glaucous-winged gulls included chicken, beef and pork bones, as well as trash such as string, paper and bottle caps. Garbage regurgitated by adults to their chicks have included French fries and raw chicken (Ward 1973, Davis in prep; LKB pers. obs.). Euphausiids are not thought to be an important prey item for glaucous-winged gulls (Hayward and Verbeek 2008) but the euphausiid (krill) *Thysanoessa spinifera* made up a substantial portion of the diet (est. 25%; LKB pers. obs.) at Mandarte Island (see Study area, below) early in the 2008 breeding season, underscoring the ability of this species to switch prey in concert with changing environmental conditions (cf. Pierotti and Annett 1990).[1]

Seabirds have evolved island nesting in part as a response to terrestrial predators (Warham 1990). Nonetheless, breeding glaucous-winged gulls (and their eggs and chicks) are taken by predatory birds and mammals in the Salish Sea, primarily bald eagles *Haliaeetus leucocephalus*, and, less frequently, by Northwestern crows *Corvus caurinus* and river otters *Lontra canadensis* (Kennedy 1968, Hayward et al. 1975, Foottit and Butler 1977, Verbeek and Morgan 1978, Verbeek 1982, Vermeer and Devito 1989, Galusha et al. 2010). Bald eagles are important apex predators in coastal marine ecosystems, and some researchers propose that eagles have driven gull population trends over recent decades (Hayward et al. 2010; see Section 1.3, Hypotheses

[1] This dietary anomaly was likely attributable to the cold waters of a La Niña year as *T. spinifera* inhabits colder waters and therefore tends to be confined to more offshore habitat in British

and predictions, below). Intraspecific predation of chicks by adults is also responsible for a proportion of chick loss in glaucous-winged gull colonies, but this factor is greatly increased by human disturbance because chicks are killed when they flee into neighbouring territories; at one colony, chick mortality was about 2.5 times higher in experimental vs. control plots, even though plots were vegetated and chicks presumably able to hide (Gillett et al. 1975). Chicks are more commonly killed by neighbouring adults at nest sites with few places for fleeing chicks to conceal themselves (e.g., rooftops, rocky sites with no vegetation cover) so that disturbance at such sites has a disproportionate effect on chick mortality (Vermeer et al. 1988, LKB pers. obs.).

1.2.2 Study Area

Based on what is known about their migratory and dispersal patterns from several banding studies (e.g., birds tend to move only 10s of kms from their colonies in winter, and birds dispersing from natal to breeding sites remain within the Salish Sea; Sprot 1937, Woodbury and Knight 1951, Pearce 1963, Butler et al. 1980, Reid 1988a, Hayward and Verbeek 2008), the glaucous-winged gulls of the Salish Sea likely represent one population. The Salish Sea is a coastal region bounded by the Coast Range and the Vancouver Island Mountains to the east and west, respectively, and includes the Strait of Georgia, Puget Sound, and the eastern Strait of Juan de Fuca (Fig. 1.1). This region's coastal marine systems have recently been ranked as being heavily altered by human activities (Halpern et al. 2008). This was the study area for Chapters 2 and 4, although for the purposes of my research I excluded Puget Sound south of the San Juan Islands. For Chapter 3, on modelling of long-term population trends, my study took place in the Canadian portion of the Salish Sea only (the Georgia Basin; Fig. 1.1), as

historical population data were less accessible for US gull colonies. Three of BC's four largest glaucous-winged gull colonies (Chain Islets, Mandarte Island, and Mitlenatch Island) are situated in the Georgia Basin. This area is occupied by approximately 50% of the Canadian population of this species (Campbell et al. 1990, Vermeer and Devito 1989, Hayward and Verbeek 2008), so that changes here represent substantive changes to the Canadian population in general. A number of smaller Georgia Basin colonies currently consisting of one to ~300 pairs are found on islets, and occasionally on cliffs and pilings. A list of Georgia Basin glaucous-winged gull colonies is provided in Appendix 2.

My colony-based fieldwork to collect reproductive data took place at Mandarte Island, BC (48.633° N, 123.283° W; Fig. 1.1). Periodic censuses (total of 23 annual counts or estimates to 2009) of glaucous-winged gulls have been conducted there since 1915, when a warden was placed on the island to regulate waterbird hunting and egg collection (Province of British Columbia 1915, 1916, Drent and Guiguet 1961). Mandarte Island has been the site of a UBC-affiliated summer research station since 1957, when studies on the behaviour, breeding biology and diet of glaucous-winged gulls were initiated (Vermeer 1963, Drent et al. 1964). Further research on Mandarte Island gulls has been conducted periodically since that time (Henderson 1972, Ward 1973, Hunt and Hunt 1976, Verbeek 1979, Vermeer 1982, Verbeek 1986, Davis in prep.), providing, in combination with data from other Salish Sea colonies (see Appendix 1), a solid source of baseline data for comparison with contemporary estimates of reproductive success (RS) and population size.

1.3 Hypotheses and Predictions

The literature suggests two primary hypotheses to explain overall glaucous-winged gull trends within the study area, and I briefly review them here:

(1) Gull populations were originally food-limited, so that survival increased in concert with human population growth and increasing availability of garbage, and subsequently decreased as waste management practices changed to burying garbage and/or shipping it out of the region (Drent and Guiguet 1961, Vermeer and Devito 1989, Vermeer 1992). The availability of garbage has been positively correlated with *Larus* gull productivity and population increases elsewhere (Spaans 1971, Pons and Migot 1995, Auman et al. 2008, Weiser and Powell 2010). However, conflicting results have been reported in other gull studies, where more successful pairs avoided garbage and fed their young on fish or other natural foods (Ward 1973, PIerotti and Annett 1990, Annett and Pierotti 1999). However, it is possible that increased garbage may only have compensated for the overfishing that greatly reduced the number of dead post-spawning salmon available during fall and winter on the BC and Washington coast in the late nineteenth century (Jewett et al. 1953, Pearse 1963, Hayward and Verbeek 2008), and for the reduction in populations of other forage fish species (see Hypothesis 3, below).

A potentially complementary hypothesis to explain centennial trends suggests that: (2) glaucous winged gull populations were originally limited by predation, i.e., gull survival increased when bald eagle populations declined from hunting and environmental contaminants such as DDT, and subsequently decreased as eagles responded to protection and reduced environmental contaminant levels (Elliott and Harris 2002, Sullivan et al. 2002, Hayward et al.

2010). Supporting this hypothesis is a study that examined prey items at Salish Sea eagle nests and found that glaucous-winged gulls were the most common prey item, comprising 35% of remains (Vermeer et al 1989). However, based on comparison with direct nest observations, studies of prey remains at eagle nests are known to strongly bias results by underestimating the contribution of fish and overestimating that of birds to eagle diet (Mersmann et al. 1992, Elliott et al. 2005a); bird are less completely ingested and their remains persist longer. Such studies also do not distinguish between depredated and scavenged items. More detailed observations have shown that Georgia Basin eagles predominantly bring fish to the nest, with some researchers suggesting birds are poor-quality prey items that are only important in winter after spawning salmon or other fish are no longer available (Elliott et al. 2005a, 2011). Eagle disturbance can also lead to nest neglect by breeding gulls, leaving their eggs and small chicks vulnerable to predation by conspecifics and other predators such as crows (Sullivan et al. 2002, Hipfner et al. 2012). However, the species' aggressive territoriality and relative tolerance to disturbance may also limit eagle-facilitated predation as nesting glaucous-winged gulls rapidly settle on their nest after disturbances, and drive away conspecifics and crows (Gillett et al. 1975; LKB pers. obs., J. Elliott pers. comm.).

Because fish-eating gulls often appear to have higher reproductive success than their conspecifics that eat garbage, and because prey fluctuations are thought to have affected other piscivorous seabirds in the Salish Sea (e.g., Norris et al. 2007, Anderson et al. 2009a, Gutowsky et al. 2009), I also hypothesized that: (3) long-term declines in fish prey availability may have contributed to glaucous-winged gull population trends, at least in the decline phase. Commercial fisheries have exerted a strong influence on Salish Sea ecosystem composition and

function over the last 100 or more years, with the level of commercial extraction of British Columbia's marine biomass similar in 1910 to that of the early 2000s (Pauly et al. 1998b). Pacific herring, for example, an important prey item for marine birds in the region, was heavily fished as early as 1910 and crashed in the 1960s due to overexploitation by a reduction fishery (Wallace 1998, Stocker et al. 2001, Stick and Lindquist 2009). For some Salish Sea herring populations the duration of spawning since the 1970s has decreased and become confined to a geographically smaller area, potentially affecting availability to birds (Therriault et al. 2009), while others exist at a fraction of their historical abundance (Stick et al. 2005, Stick and Lindquist 2009). Herring size-at-age has also declined, potentially decreasing their food value (Therriault et al. 2009). Other prey species once numerous enough to support a commercial fishery, e.g., eulachon *Thaleichthyes pacificus*, have all but disappeared from the Salish Sea (Moody and Pitcher 2010).

Given the long timelines involved in my study, it is also possible that these three factors had acted sequentially, or in concert. The first two hypotheses imply that regional gull population numbers climbed to artificially high levels in the mid-twentieth century and that the population baseline was closer to the low numbers observed at the start of the twentieth century, whereas the third hypothesis suggests that early gull numbers were suppressed. These three hypotheses are discussed in greater detail in Chapters 2 – 4.

For my research I used a common set of measurements to test several predictions derived from these hypotheses, and applied the measurements to each hypothesis as appropriate. The common measurements in my study were changes in: (a) population abundance (number of

breeding pairs); (b) $\delta^{15}N$ (from isotopic analysis of gull feathers from living and museum-archived gulls); (c) $\delta^{13}C$ (isotopic analysis of the same feathers); and (d) a suite of breeding parameters. I also wished to address the null hypothesis of no recent change to glaucous-winged gull numbers in the study area: colony counts in the study area and vicinity have not been comprehensive, and it was possible that the decline reported by Sullivan et al. (2002) was not widespread or ongoing, or that observed trends were explained by a trend toward nesting in urban areas.

My initial hypotheses and derived predictions are summarised in Table 1.1. However, my understanding of the system evolved as research progressed. For example, I learned from accounts of early naturalists and biologists that human egging likely played a greater role in determining population trends than many modern reports have suggested. Early researchers stated that systematic human egging had led to gull population declines (Province of British Columbia 1915, 1916, Pearse 1923), while subsequent research suggested that US and Canadian populations grew in the early 1900s in response to legislated protection that resulted in cessation of egging and other persecution (Drent and Guiguet 1961, Reid 1988a), as did colonial bird populations through much of North America and elsewhere (Reid 1988a, Duhem et al. 2008, Grandgeorge et al. 2008). I therefore modified my initial hypotheses and predictions, as described in the subsequent data chapters and the Conclusion to this thesis.

Table 1.1: Initial hypotheses and related predictions for changes in glaucous-winged gull populations in the Georgia Basin, British Columbia, over the study period.

Prediction (measure) – chapter where addressed	**Reproductive success (RS; various measurements, 21st vs. mid-20th C) – Chapter 2**	**Abundance (no. breeding pairs over time) – Chapter 3**	**δ^{15}N (tissue levels of sub-adult & adult ^{15}N over time) – Chapter 4**	**δ^{13}C (tissue levels of sub-adult & adult ^{13}C over time) – Chapter 4**
Hypothesis - Description *(Mechanism)*				
*H0. "**No population change in Salish Sea**" (Observed trend not real; surveys inadequate to capture real trend)*	- No change in RS parameters, 21st vs. mid-20th C	- Christmas Bird Count, Breeding Bird Survey show no decrease over time	- No correlation between δ^{15}N and population trend	- No correlation between δ^{13}C and population trend
*H1. "**Garbage (food limitation)**"* – Human food (garbage) beneficial for gull pop'ns, which increased then decreased with changing human waste management practices *(Increasing and then decreasing availability of human food acting on aspect(s) of vital rates)*	- Observed increases and then decreases in one or more of the following: clutch size; egg size; hatch success; chick mass at fledging; fledging success; reproductive output (fledglings/ female)	- Population increases with access to garbage dumps, then levels off as carrying capacity is reached or declines following waste management improvement ca. 1980	- δ^{15}N trend not predictable as terrestrial systems depleted in ^{15}N relative to marine, but agriculturally-based systems (i.e., often source of garbage in gull diet) can be enriched - δ^{15}N levels same in adults, sub-adults, as both eat easily-accessed garbage instead of fish	- Gulls from periods where population mainly feeding on garbage will show lower tissue levels of ^{13}C (less marine diet) - Tissue ^{13}C will be correlated with population increase and decrease (% garbage in diet), i.e., will show quadratic trend
*H2. "**Bald eagle predation**"* – Increasing disturbance and depredation by eagles as their pop'ns recover *(Mesopredator*	- Number of eagle days at colony (= index of predation, disturbance) correlated with gull nest survival (hatch success, fledge success, or	- Gull population trends track eagle population numbers	X	X

Prediction (measure) – chapter where addressed	Reproductive success (RS; various measurements, 21st vs. mid-20th C) – Chapter 2	Abundance (no. breeding pairs over time) – Chapter 3	$\delta^{15}N$ (tissue levels of sub-adult & adult ^{15}N over time) – Chapter 4	$\delta^{13}C$ (tissue levels of sub-adult & adult ^{13}C over time) – Chapter 4
release, followed by decreased reproductive output due to increased predation and disturbance)	reproductive output) – *Not addressed in my research, due to inadequacy of historical data*			
*H3. "**Fish prey availability**"* – Availability and quantity of forage fish prey has declined *(Declining food quality/quantity acting on aspect(s) of vital rates)*	- Observed decreases in one or more of the following: clutch size; egg size; hatch success; chick mass at fledging; fledging success; reproductive output (fledglings/ female); lay date delayed	- Overall declines in population numbers as forage fish disappear in Salish Sea	- In population decline phase, ^{15}N shows decrease over time as gulls 'forage down the food chain'	- Gulls prey-switch among different forage fish spp. over time: gull tissues show "marine" $\delta^{13}C$ values over time; or - Gulls switch from forage fish to intertidal inverts and/or garbage: tissues less enriched in ^{13}C over time

1.4 Data Collection: Methods and Rationale

Here I provide an overview of the methodological approaches I used for each part of my study, and why I selected them. Details of data collection methods and the rationales for choosing them are provided in the relevant chapters.

1.4.1 Population Trends

At the start of my study, available compilations of census data and trend estimates were decades old (Drent and Guiguet 1961, Campbell 1976, Vermeer and Devito 1989, Campbell et al. 1990) or only included a small proportion of the colonies in the study area (Sullivan et al. 2002). I compiled all historical count data available for glaucous-winged gull colonies in the Georgia Basin, and supplemented those with data from the census I conducted in 2009 – 2010. Formally testing the null hypothesis of no decline by surveying urban colonies was beyond the scope of my study (as was determining whether gulls had instead emigrated to other regions), but I reviewed data from other studies to assess indirectly whether Salish Sea glaucous-winged gulls had simply moved to new nesting habitat within or outside the region. Christmas Bird Counts (CBCs) and other regional surveys (National Audubon Society 2011, Bower 2009, Crewe et al. 2010) provided a relevant supplemental source of population information here.

1.4.2 Diet (stable isotope analysis)

Levels of stable nitrogen ($^{14}N/^{15}N$) and carbon ($^{12}C/^{13}C$) isotopes in animal tissues have often been used to explore animal diet and the structure of marine food webs (e.g., Dawson and Siegwolf 2007), with $\delta^{15}N$ values indicating relative trophic level and $\delta^{13}C$ distinguishing among terrestrial, nearshore, and pelagic prey (Hobson et al. 1994). Stable isotope analysis is considered a more powerful approach than conventional diet studies as it integrates diet over the life of the analyzed tissue. Thus, bone provides an animal's lifetime dietary values while feathers or blood reflect diet over a period of months, weeks or days. Stable isotope techniques have been widely embraced by seabird researchers and used in a wealth of studies to

investigate, among other things, diet, niche partitioning, and trophic relationships. For example, isotopic analysis has been used to examine the role of seabirds in diets of native and non-native rodent predators, enhancing our understanding of the trophic pathways of certain remote island systems (Hobson et al. 1999, Drever et al. 2000, Stapp 2002). Other studies have characterised how sympatric seabird taxa segregate diets within and among seasons (Hobson et al. 1994, Cherel et al. 2007, Davies et al. 2009) or shown how different populations of the same species may differ in the types of foods consumed (Auman et al. 2011).

While stable isotope techniques are most commonly used to study contemporary food webs, more recently researchers have turned to analysing archived specimens or ancient remains preserved *in situ* to examine historical dietary changes and answer questions about how diets of seabirds and other animals have changed over decades, centuries or even millennia (e.g., Thompson et al. 1995, Emslie and Patterson 2007, Norris et al. 2007, Hebert et al. 2008). The availability of hard tissues such as bones, eggshells and feathers in museum collections and at various archaeological deposits have proven to be valuable resources for researchers interested in reconstructing past diets, with an early foray into this technique even applied to the remains of an extinct marine bird, the great auk *Pinguinus impennis* (Hobson and Montevecchi 1991).

Apart from its well-established tradition of being used for marine birds in general, I considered a stable isotope approach to be tractable for my study system in particular as it had already been used successfully, e.g., for the congeneric herring gull *L. argentatus* in the Great Lakes (Hebert et al. 2008), and on another seabird species in coastal BC waters (marbled murrelet *Brachyramphus marmoratus*; Norris et al. 2007, Gutowsky et al. 2009). As Salish Sea glaucous-

winged gulls have been collected over approximately 150 years, I determined that museum specimens would provide an adequate source of feathers for retrospective isotopic analysis.

Decreases in diet quality likely have stronger effects during a bird's metabolically-demanding periods (e.g., breeding, winter; cf. Murphy et al. 1992). Thus, I sampled adult feather types to reflect diet during and just after the breeding period (primaries, brown-tipped winter head feathers; Verbeek 1979, P. Pyle pers. comm., LKB pers. obs.), as well as the white summer head feathers that are grown in late winter or early spring just prior to breeding (Howell and Dunn 2007, LKB pers. obs.). As sub-adult *Larus* gulls may eat different foods than adult birds (Weiser and Powell 2011), to characterise gull diet more fully I also analysed primary feathers from sub-adult birds. In general, terrestrial systems are depleted in ^{13}C and ^{15}N (though agricultural systems may be relatively enriched in ^{15}N; Hobson 2007), while marine foods are enriched, so I expected any segregation of results to be strong for the dual isotope combination.

1.4.3 Reproductive Success

Published information on breeding parameters provided comparisons with the data I collected, and a way to test whether observed changes in food supply had affected glaucous-winged gull reproductive output and thus population trends over time. For example, experimental studies show that egg size is an indicator of foods available to pre-breeding adult gulls (Hiom et al. 1991, Bolton et al. 1992, 1993), with egg size positively related to traits such as hatch success, chick survival, and chick growth in gulls (Parsons 1970, Bolton 1991) and in other seabirds (Amundsen et al. 1996, Sorensen et al. 2009) as well as in avian taxa in general (Krist 2011; meta-analysis of 283 studies). Egg production is therefore one mechanism by which changing

prey availability may mediate changes in RS and hence population trends. Key reproductive parameters I measured (at Mandarte Island) were: lay date; egg size (mass, length, width); clutch size; hatch success; fledge success; and chick mass at fledging.

Historical demographic data were available via Salish Sea studies conducted from the 1950s – 1980s (Appendix 1) and allowed me to compare key reproductive parameters from the same population in a growing phase vs. a phase of purported decline. I was unable to conduct a comparative analysis for all my demographic datasets as historical data were inadequate for comparisons with some parameters (e.g., chick mass at fledging). I also obtained measurements (length, width) of eggs collected for museums from within the study area; these had been collected in the region since at least 1902 (Carter and Sealy 2011; Chapter 2).

1.4.4 Bald Eagle Predation

I collected opportunistic data on eagle presence/absence (number of "eagle days"), disturbance frequency, age (immature or adult), and predatory events (on gull adults, eggs and chicks) for bald eagles observed at Mandarte Island and other large colonies I surveyed in the Georgia Basin. Such data are comparable with those collected for other years and localities in coastal British Columbia (Verbeek 1982, Vermeer and Devito 1986, Sullivan et al. 2002, White et al. 2006).

1.5 Overview of the Data Chapters

I organised my dissertation research into three main parts. In Chapter 2, I review the literature on egg and clutch size in seabirds, particularly gulls, and test the general prediction that these

traits would have responded to ongoing, deleterious environmental change by declining over time in my study species. To do this, I obtained historical measurements of glaucous-winged gull egg size, clutch size, and lay date from the published literature (all parameters; 1940s – 1980s), and from museum specimens (egg size; 1902 – 1946), and used meta-analyses to compare these estimates with field data I collected in 2008 – 2010. Egg and clutch size declined over time, and lay date was delayed, suggesting that long-term decreases in the availability of forage fish may have caused the changes I recorded because gulls require high-quality prey in and around the period of egg production. Delayed lay date was largely unexpected as global trends in breeding season phenology have shown advanced laying in the majority of bird species studied worldwide, with a relationship found between lay date and climate.

In Chapter 3, I compile historical colony count data for glaucous-winged gull colonies around the Georgia Basin, using records from old publications, "grey literature" (e.g., published and unpublished reports), old museum records, unpublished data provided by seabird biologists in the region, and my census data. Together these data provide a 111-year population trend for Georgia Basin glaucous-winged gulls. In this chapter I use a modelling approach to contrast potential drivers of long-term population change, testing the hypotheses outlined above. In the model, I incorporate vital rates from the literature and data on declines in clutch size from Chapter 2.

In Chapter 4, I examine whether glaucous-winged gulls had undergone a long-term change in diet by conducting stable isotope analysis of a longitudinal sample of gull feathers, from 1860 to the present, taken from birds held in museum collections in North America and the UK and

from field samples I collected. These isotope data provided evidence of a long-term decline in the trophic level and marine origins of glaucous-winged gull diet, possibly providing support for the suggestion that declining dietary quality was the mechanism driving the changes to reproductive parameters I found in Chapter 2.

In Chapter 5, the conclusion, I summarise my research on using a marine bird as an ecological sentinel or indicator species, and discuss what it may tell us about long-term ecological changes and shifting baselines in the Salish Sea. I also discuss the implications of this study for understanding effects of long-term environmental change on marine birds elsewhere: it is likely that seabirds in general are tractable indicators over historical time scales, as well as the shorter ones for which they are primarily used at present. I also address the limitations of my research, and provide management recommendations based on the major outcomes of my study.

Chapter 2: Egg Production in a Coastal Seabird, the Glaucous-Winged Gull, Declines during the Last Century[2]

2.1 Introduction

Life history theory predicts that long-lived organisms such as seabirds will maximise fitness by reducing reproductive output during periods of environmental stress, trading off between current and future reproduction. One potential way for birds to reduce reproductive investment when foraging conditions are poor early in the breeding season is by decreasing the size or number of eggs produced. Female protein and energy requirements during egg production are substantially higher than those during the non-laying period, making egg production costly (Robbins 1981, Monaghan and Nager 1997, Nager 2006; but see Williams 2005). Indeed, for many avian species there is strong evidence that under poor food conditions, egg size, number or both are reduced, though lay date responds to food supply more consistently than do egg or clutch size (Martin 1987, Meijer and Drent 1999, Christians 2002). Trade-offs reduce reproductive performance in a given year; therefore, repeated poor years, for example due to environmental factors including climatic variation and/or competition with humans for prey (Grémillet and Boulinier 2009), can mean that adult survival is traded off against a better future that never materialises, with population numbers ultimately affected. Thus, ongoing poor conditions will also have long-term population consequences, and

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understanding the mechanisms driving such changes can have important conservation implications (e.g., Bertram et al. 2001).

The world's oceans are now strongly affected by human activities, with most marine food webs simplified and impoverished by drivers such as pollution, climate change, and overfishing (Halpern et al. 2008). Like many other coastal areas over the last century or more, the inshore waters of southern British Columbia (BC) and northern Washington (WA; hereafter, the Salish Sea) have seen removal of upper trophic predators such as whales and sequential overfishing of forage fishes such as Pacific herring (Wallace 1998). This, in combination with other factors such as climate change and pollution, means that this area is now among those globally estimated to be suffering very high levels of human impacts (Halpern et al. 2008); thus, ecosystem productivity and function in the region is potentially very different than it was prior to the start of industrial activity (Wallace 1998, Johannessen and Macdonald 2009, Therriault et al. 2009). Marine systems worldwide have responded in varying ways to removal of predators and prey (Ainley and Blight 2009, Baum and Worm 2009), and as common mesopredators, marine birds are considered to be sensitive indicators of such changes in oceanic food webs, particularly given the long-term nature of some colonial seabird studies (e.g., Gill et al. 2002). The glaucous-winged gull is a conspicuous marine bird that breeds at accessible coastal nesting colonies in the northern Pacific, and as such it represents a strong potential source of indicator data: ecologists and naturalists have been researching its reproductive biology, conducting colony counts, and collecting its eggs for museums for over 100 years.

During the nesting season glaucous-winged gull diet in the study area consists of small forage fishes such as herring *Clupea pallasii* and sandlance *Ammodytes hexapterus*, garbage, and invertebrates, with diet currently (2008 – present) appearing to consist primarily of marine foods (Vermeer 1982, Gebbink et al. 2011, LKB pers. obs.). Though garbage is frequently available, it is not clear whether it is beneficial to gulls. In some parts of the world gull populations have declined in apparent response to the covering of landfills and loss of anthropogenic foods (Pons 1992); however, glaucous-winged gulls eating only herring were able to raise larger broods than were those whose diet included garbage (Ward 1973), and for congeneric Western gulls *L. occidentalis* the most successful breeders avoided eating refuse and instead fed themselves and their young mainly on fish prey (Annett and Pierotti 1999). Reduced productivity and poorer body condition was also documented in breeding female herring gulls that subsisted primarily on a terrestrial (garbage-based) diet relative to those subsisting primarily on fish foods (Hebert et al. 2002). The availability of Pacific herring, currently the primary forage fish in the Salish Sea, has likely declined in recent years, with factors such as pollution, climate change and historical overfishing believed responsible; herring were heavily exploited as early as 1910 and a stock collapse occurred in the 1960s; (Wallace 1998). Although some regional herring populations increased between about 1970 and 2002, others have decreased by up to two orders of magnitude (Stick et al. 2005, Crawford and Irvine 2009, Stick and Lindquist 2009, Therriault et al. 2009). Herring size-at-age has also declined since the 1970s at various eastern Pacific sites including the Salish Sea (Therriault et al. 2009), indicating a potential decrease in food value of individual forage fish (cf. Wanless et al. 2005). In addition, the spatial and temporal extents of spawning events in at least some parts of the study area

have been decreasing, with a contraction of locations since the late 1980s, and a loss of early (January – early February before about 1970) and late (April – May before the early 1980s) spawners (Fig. 2 in Therriault et al. 2009). In the Salish Sea, glaucous-winged gulls begin to arrive at their colonies in February and commence egg laying in May.

The purpose of this study was to assess whether hypothesised long-term food web changes in this relatively under-studied coastal ecosystem might be reflected in consumers' life history traits over time. Because large-bodied single brooded birds obtain the resources necessary for egg production in advance of the breeding season as well as during it (i.e., they are primarily "capital" breeders; Meijer and Drent 1999, Drent 2006), and as the nutritional and energetic costs of egg production seem to be relatively high in larids (Ricklefs 1974, Robbins 1981, Houston et al. 1983), I predicted that glaucous-winged gulls would be sensitive to long-term decreases in food availability prior to the breeding season as well as during egg formation, and that they would respond to this by decreasing egg or clutch size over time. To test this prediction I used a meta-analytical approach and multiple data sources, including published records and museum egg collections, to examine long-term trends in egg (108 years) and clutch (48 years) sizes. Because clutch size progressively decreases with lay date in most single-brooded species (Meijer and Drent 1999), I also tested whether clutch size was correlated with timing of breeding in the study population. Researchers often record avian clutch size and lay date, and a number of studies have used longitudinal data to report long-term trends in these traits. Egg size has been studied less often, however, with few studies reporting long-term patterns in egg size variation (Järvinen 1994, Tryjanowski et al. 2004, Potti 2008). Though avian eggs have been collected by naturalists and biologists for about 200 years, no studies have yet

used museum collections to report on long-term trends in egg size (but see Scharlemann 2001). Lastly, because food availability is believed to influence lay date in bird species more consistently than it affects egg production (Christians 2002), I also investigated changes in timing of breeding (over 52 y), predicting that if overall food availability had decreased in the Salish Sea this would result in delayed lay dates.

2.2 Study Area and Methods

2.2.1 Study Area

Field data for these analyses came from studies carried out between 1902 and 2010 at glaucous-winged gull colonies in the Salish Sea, i.e., the inshore coastal waters of the Strait of Georgia, BC, Canada, and adjacent waters, including northern Puget Sound, WA, USA and the adjacent eastern Strait of Juan de Fuca (range: 47.91° – 50.02° N, 121.95° – 125.24° W). Earlier banding studies, physical geography, and patterns of hybridization support the selection of this entire region, as does the colonies' shared history of nineteenth century exploitation and subsequent recovery (Sprot 1937, Butler et al. 1980, Reid 1988a) and their modern existence on the edge of some of the most rapidly-growing areas in Canada (Stubbs 2001). These boundaries ensured that I included all of the large colonies found in the region's inshore sea, but excluded the more westerly colonies that are strongly influenced by the open Pacific Ocean.

2.2.2 Data Sources and Inclusion Criteria

I compiled published data on glaucous-winged gull egg size, clutch size and first egg date obtained from a literature search using ISI Web of Science and keywords "glaucous-winged

gull" and "Larus glaucescens", the sources provided in the Birds of North America species account (Hayward and Verbeek 2008), and additional references cited in publications located via these searches. "Grey literature" (e.g., government reports) was included in these citations, and incorporated into the study accordingly. I applied no English-language or publication year restrictions. In the literature search, I included publications on glaucous-winged gulls that were not specifically about their reproduction because some authors (particularly in papers and reports prior to 1960, presumably as a result of older stylistic conventions) included appendices of miscellaneous biological data on the species. I supplemented published data with those I collected from 2008 to 2010 at Mandarte Island, BC (48.63° N, 123.28° W) and Arbutus Island, BC (48.70° N, 23.43° W), using methods comparable with those from earlier studies (i.e., monitoring a series of study nests through the breeding season). For egg size, I also searched museum databases (ORNIS and institutions' own records) for egg sets collected from the study area, and obtained egg length and width measurements from five museum collections (specific museums listed in Acknowledgements). To ensure that the published studies had taken place in the study area, I screened them by geographical region and then reviewed them against inclusion criteria related to research design and reporting of data (below).

In screening published studies of egg size, I only included those reporting measurements for entire clutches, (i.e., those where every egg in a nest was measured). I excluded egg measurements for 2-egg clutches, reported separately in all studies, because eggs from these clutches are smaller on average than those from the modal 3-egg clutch (Hayward and Verbeek 2008) and the proportion of 2-egg clutches reported varied by study. I only included annual egg size means (from published studies and museum specimens) derived from more than a single

clutch, and assumed that eggs collected by museums represented a random subsample of those available at a given colony because their volumes showed an approximately normal distribution, i.e., data were non-skewed. For clutch size, I required that studies had monitored their nests throughout a colony every 1 – 2 d for the duration of the laying period (i.e., I excluded studies reporting clutch sizes from opportunistic colony visits because clutch size is variable over the season). Two early studies provided no data but stated that "normal" clutch size was three (with 2-egg clutches "occasionally" found; (Schultz 1951, James-Veitch and Booth 1954); as I encountered only one actual measurement of clutch size prior to the 1980s, I retained these additional studies for comparative purposes and considered that their estimates represented a clutch size of 2.8, but did not include them in the analysis itself. Similarly, I required that published data on first egg date were collected using systematic colony monitoring protocols (study nests monitored on a regular basis throughout the breeding season) rather than opportunistic visits. All author-collected egg size, clutch size and lay date data (i.e., those I collected from 2008 – 2010; see above) were collected so as to be consistent with these literature-screening criteria.

No studies needed to be discarded due to a lack of essential meta-analytical data such as sample size. After screening of published studies and museum specimens, and addition of author-collected data, I ended up with five separate studies from which I derived seven annual means of egg size, as well as measurements from 329 eggs held in museum collections, representing an additional 14 annual means of egg size ("egg-years"; n=21); each egg-year was treated as a sample unit (Table 2.1). These egg size data spanned more than a century (1902 – 2010) and represented at least 14 glaucous-winged gull colonies in the study area. (I did not

consider study area localities that had been recorded by museum collectors as “unnamed” to be additional colonies). I retained six studies from four Salish Sea colonies reporting nine annual mean clutch sizes, and 18 estimates of first egg date from six colonies (Table 2.1). As with egg size, each clutch-year was a sample unit. For a measure of timing of breeding, I chose first egg date rather than median lay date because my nest search effort was consistent through to the late laying season, but did not continue for long enough to record the latest nests; other included studies appeared to have followed a similar protocol. While first egg date is probably more subject to stochastic variation or sampling error than is median lay date, it is nonetheless considered a reliable indicator of timing of breeding (Ainley 2002). All annual means were independent (i.e., they were not collected as repeated measures series at study sites), and as study sites were all located in or around the same inland body of water (the Salish Sea) I assumed no effect of site on vital rates, based on published inter-site comparisons of these parameters (Vermeer 1963, Verbeek 1986, Hooper 1988, Vermeer et al. 1988). Standard meta-analyses address the possibility of publication bias (publication of studies showing an effect vs. non-publication of those showing no effect) but as my study simply assessed mean measures of egg production, consideration of such bias was unnecessary.

Table 2.1: Summary of studies used in standard and meta-analyses.

Num.	Data source	Nesting colony	Location	Year(s) data collected	Response variable	*N* (effect size estimates)
1	Museum collections[1]	Various[2]	Throughout study area[3]	1902 – 1946	Egg size	14
2	Schultz 1951	San Juan Islands	Puget Sound/ Strait of Juan de Fuca, WA[4]	1948	Egg size	1
3	James-Veitch & Booth 1954	Williamson Rock	Puget Sound/ Strait of Juan de Fuca, WA	1951	Egg size	1
4	Drent et al. 1964	Mandarte Island	Haro Strait, BC[5]	1959, 1960	Lay date	2
5	Vermeer 1963	Mandarte Island	Haro Strait, BC	1961, 1962	Lay date	2
6	Vermeer 1963	Mandarte Island	Haro Strait, BC	1962	Clutch size	1
7	Hunt & Hunt 1976	Mandarte Island	Haro Strait, BC	1971, 1973	Lay date	2
8	Verbeek 1986	Mandarte Island	Haro Strait, BC	1976, 1977, 1979, 1980	Lay date	4
9	Verbeek 1986	Mandarte Island	Haro Strait, BC	1979, 1980	Clutch size	2
10	Verbeek 1986	Mandarte Island	Haro Strait, BC	1980	Egg size	1
11	Reid 1987	Protection Island	Strait of Juan de Fuca, WA	1984	Lay date	1
12	Vermeer 1988	Vancouver Harbour	Strait of Georgia, BC	1986	Lay date	2
13	Vermeer 1988	Vancouver Harbour	Strait of Georgia, BC	1986	Clutch size	2
14	Vermeer 1988	Vancouver Harbour	Strait of Georgia, BC	1986	Egg size	2

Num.	Data source	Nesting colony	Location	Year(s) data collected	Response variable	*N* (effect size estimates)
15	Hooper 1988	Victoria Harbour	Strait of Juan de Fuca, BC	1986	Lay date	1
16	Hooper 1988	Victoria Harbour	Strait of Juan de Fuca, BC	1986	Lay date	1
17	LK Blight, unpubl data	Mandarte Island	Haro Strait, BC	2008 – 2010	Lay date	3
18	LK Blight, unpubl data	Mandarte Island	Haro Strait, BC	2008, 2009	Clutch size	2
19	LK Blight, unpubl data	Mandarte Island	Haro Strait, BC	2008, 2009	Egg size	2
20	LK Blight, unpubl data	Arbutus Island	Haro Strait, BC	2010	Lay date	1

[1]See Acknowledgements for list of contributing museums. [2]See Table 2.2 for colony details. [3]See text. [4] WA – Washington, USA. [5]BC – British Columbia, Canada

2.2.3 Statistical Analyses

I used meta-analysis rather than a standard statistical approach because disparate datasets derived from a group of primary studies must be properly weighted to yield correct standard errors and *p*-values and meta-analysis has been developed specifically to perform these weightings correctly, increasing the power of significance tests while retaining robustness (Gurevitch and Hedges 1999, Borenstein et al. 2009). I used meta-regression, with fit assessed using *Q*-tests (Gurevitch and Hedges 1999, Borenstein et al. 2009), to analyse trends in glaucous-winged gull egg and clutch size over time and to examine the relationship between clutch size and first egg date. I used random-effects meta-analytical models as these assume that component studies differ not only by within-study sampling error (as fixed-effects models do), but also by a genuine difference in effect sizes among studies (Gurevitch and Hedges 1999,

Borenstein et al. 2009). Random-effects models thus incorporate among-study (here, equivalent to inter-year) variance in their estimates, and thereby generate wider confidence intervals and more conservative results than do fixed-effect models. All meta-analyses require that the results of each study be distilled to a measure of the magnitude of the effect of the measured variable – the "effect size". As I wished to ask whether egg and clutch size had decreased over time in response to declining availability of food, the effect sizes selected here for meta-analysis were mean annual egg volume and number of eggs per clutch. Variance is required to compute meta-analytical weightings and was provided in publications or calculated from raw data for all but five annual means of egg sizes, and one study reporting clutch size; for these, I imputed standard deviation (SD) from the pooled SD from all raw data for the study (Furukawa et al. 2006), using the formula

$$SD_{pooled} = \sqrt{\frac{\sum(n_i - 1)/SD^2{}_i}{\sum(n_i - 1)}}$$

and egg volume was calculated as

$$vol(cc) = \frac{length \times width^2 \times k}{1000}$$

where length and width are in mm and k is the constant 0.476, determined by Harris (1964) for another *Larus* gull.

I used the statistical software package Comprehensive Meta-Analysis v. 2.0 to perform all weightings and meta-analyses (Borenstein et al. 2005). Welch's analysis of variance (robust to

unequal sample size and variance) was used to compare mean first egg date in historical vs. current studies (1959 – 1986; 2008 – 2010).

2.3 Results

2.3.1 Egg Size

From 1902 – 2009, mean glaucous-winged gull egg volume decreased in the Salish Sea study area, with the random-effects model showing a significant negative relationship between year and egg volume (Q=7.211; p=0.007; Fig. 2.1A) and volume decreasing at an average of 0.04 cc y^{-1} (95% CI=–0.06 – –0.01; mean annual egg volume range 75.41 – 88.36 cc; See Table 2.2 for a list of effect sizes) over the study period. This equates to an overall decrease of circa 5% (4.3 cc) in mean egg volume since 1902 (108 years).

2.3.2 Clutch Size and First Egg Date

As with egg size, average clutch size decreased during the study period (Q=27.30, p<0.001; Fig. 2.1B), declining from a mean of 2.82 eggs per clutch in 1962 to 2.25 in 2009 (Table 2.2). Though not included in the analysis, qualitative descriptions of clutch size from the 1950s are consistent with these results (Fig. 2.1B). There was a negative relationship between first egg date and mean clutch size in a given year (Q=12.91, p<0.001; Fig. 2.2), with smaller clutches occurring in years where egg laying commenced later. Timing of clutch initiation also retreated over time. For historical data collected between 1959 and 1986 the mean first egg date was 15 May (range 4 – 28 May). From 2008 – 2010 the average first egg date was 22 May, 7 d later than in earlier decades (range 21 – 23 May; F=20.12, p<0.001; Fig. 2.3).

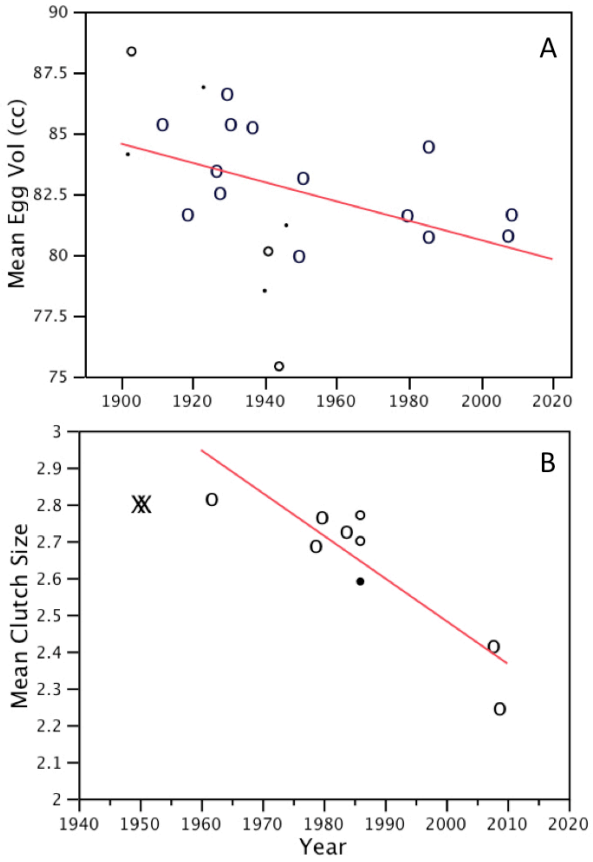

Figure 2.1: Meta-regression of glaucous-winged gull egg and clutch size vs. year, Salish Sea (SW Canada & NW USA). Symbol size represents meta-analytical weightings for each data point. Note different temporal scales on x-axes. (A) Egg volume decreased over the study period (1902 – 2009; Q=7.211, p<0.01), with eggs now 5% smaller on average than at the turn of the twentieth century. (B) Clutch size decreased between 1962 and 2009 (Q=27.30, p<0.001). Two data points from the 1940s – 1950s (represented by ✕) are not included in the meta-analysis due to inadequate reporting criteria (see text), but are plotted here to further illustrate robustness of trend.

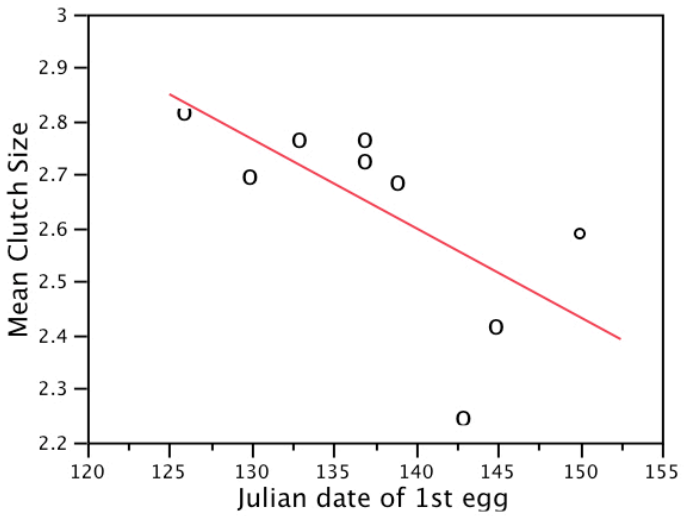

Figure 2.2: Meta-regression of glaucous-winged gull clutch size vs. date of first egg. Clutch size decreased with delayed onset of breeding (first egg date; Q=12.91, p<0.001; 1962 – 2009 data). Symbol size represents meta-analytical weightings for each data point.

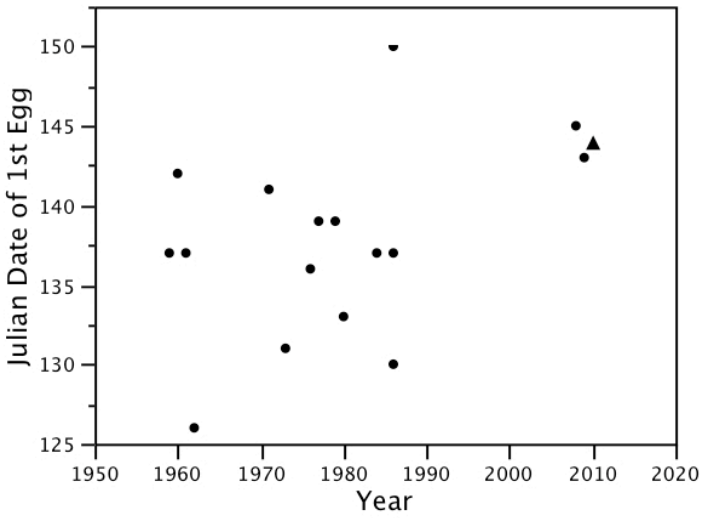

Figure 2.3: Date of first egg retreated significantly from 1959 – 2010 (p=0.03, ▲: n=2 observations), with mean commencement date 7 d later in 2008 – 2010 than in earlier decades (F=20.12, p<0.001).

Table 2.2: Summary of all effect sizes used in meta-analyses of changes in egg and clutch size over time.

Data ID	Data source	Study location	Study year	Variable	Effect size (mean egg or clutch size)	SD	*N* (samples per study or year)
Mus1902	Museum collections	Mandarte I, BC*	1902	Egg size	84.13	2.07	6
Mus1903	Museum collections	Mandarte I, BC	1903	Egg size	88.36	7.20	13
Mus1912	Museum collections	Island County, WA;* Whidbey I, WA; Williamson Rock, WA	1912	Egg size	85.44	6.41	39
Mus1919	Museum collections	Bird Rock, WA; Flattop I, WA; White Rock, WA	1919	Egg size	81.73	6.23	24
Mus1923	Museum collections	Orcas I, WA; Peapod I, WA	1923	Egg size	86.89	6.6	6
Mus1927	Museum collections	Gull Rock, WA; Viti Rocks, WA	1927	Egg size	83.54	7.27	50
Mus1928	Museum collections	San Juan Islands, USA;	1928	Egg size	82.62	8.28	23
Mus1930	Museum collections	Viti Rocks, WA; Williamson Rock, WA	1930	Egg size	86.67	5.48	38
Mus1931	Museum collections	Viti Rocks, WA	1931	Egg size	85.42	6.32	42

Data ID	Data source	Study location	Study year	Variable	Effect size (mean egg or clutch size)	SD	*N* (samples per study or year)
Mus1937	Museum collections	Colville Rock, WA; Williamson Rock, WA	1937	Egg size	85.32	7.96	59
Mus1940	Museum collections	Gulf of Georgia, BC; Howe Sound, BC	1940	Egg size	78.52	6.88	6
Mus1941	Museum collections	Howe Sound, BC	1941	Egg size	80.14	6.64	12
Mus1944	Museum collections	Howe Sound, BC	1944	Egg size	75.41	4.17	6
Mus1946	Museum collections	Howe Sound, BC	1946	Egg size	81.21	6.36	6
Schultz	Schultz 1951	San Juan Is, WA	1948	Egg size	80.03	7.64	43
J-V&Booth	James-Veitch & Booth 1954	Williamson Rock, WA	1951	Egg size	83.23	7.64	30
Verbeek	Verbeek 1986	Mandarte I, BC	1980	Egg size	81.69	7.64	144
VermeerCol	Vermeer 1988	Vancouver Harbour, BC	1986	Egg size	80.81	7.64	62
VermeerSol	Vermeer 1988	Vancouver Harbour, BC	1986	Egg size	84.50	7.64	26
Mandarte08	LKB unpubl data	Mandarte I, BC	2008	Egg size	80.84	8.02	345

Data ID	Data source	Study location	Study year	Variable	Effect size (mean egg or clutch size)	SD	*N* (samples per study or year)
Mandarte09	LKB unpubl data	Mandarte I, BC	2009	Egg size	81.73	7.98	267
VermeerCS	Vermeer 1963	Mandarte I, BC	1962	Clutch size	2.82	0.40	479
Verbeek1986a	Verbeek 1986	Mandarte I, BC	1979	Clutch size	2.69	0.59	297
Verbeek1986b	Verbeek 1986	Mandarte I, BC	1980	Clutch size	2.77	0.47	417
Reid	Reid 1987	Protection I, WA	1984	Clutch size	2.73	0.78	704
Vermeer1988a	Vermeer 1988	Vancouver Harbour, BC	1986	Clutch size	2.70	0.60	80
Vermeer1988b	Vermeer 1988	Vancouver Harbour, BC	1986	Clutch size	2.77	0.51	52
Hooper	Hooper 1988	Victoria Harbour, BC	1986	Clutch size	2.59	0.79	22
Mandarte2008	LKB unpubl data	Mandarte I, BC	2008	Clutch size	2.42	0.73	210
Mandarte2009	LKB unpubl data	Mandarte I, BC	2009	Clutch size	2.25	0.84	175

* BC – British Columbia, Canada ; WA – Washington, USA;

2.4 Discussion

2.4.1 Egg Size, Clutch Size and Lay Date

These results reveal long-term declines in egg and clutch sizes of glaucous-winged gulls in the Salish Sea, likely as a result of reductions in availability of food. Mean egg size decreased by circa 5% from 1902 – 2009. Similarly, mean clutch size has declined to the lowest ever recorded for the region. Five of nine studies reporting clutch size took place at a single site (Mandarte Island), including twenty-first century clutch sizes, so that the Mandarte data may have had a large influence on the results. However, opportunistically-collected data from other Salish Sea colonies appear to support the hypothesis of a regional clutch size decline over time: population counts at 17 colonies recorded a mean clutch size of 2.29 in 2010 (LKB unpubl. data). Though these additional data represent only a snapshot of the number of eggs per nest (and were thus not incorporated into the analysis), they provide a good proxy for mean annual clutch size as they were collected immediately prior to peak hatch, when most gulls should be incubating an entire clutch. These concurrent egg and clutch size declines are noteworthy because although gulls lack an obligate clutch size, a mode of three is a well-known feature of most *Larus* gulls' biology, and egg size reduction is a flexible mechanism that allows birds to accommodate limited decreases in energy availability while maintaining offspring number (Martin 1987). I suggest this study's results are consistent with a decline in availability of high-quality fish prey pre- and during the breeding season. The actual cost of egg production to breeding birds in general is controversial (Williams 2005) but for gulls at least there is good evidence that food input, particularly in the form of protein, affects egg size and clutch number

(Houston et al. 1983, Bolton et al. 1992, Bolton et al. 1993, Meijer and Drent 1999, Hebert et al. 2002, Nager 2006). California gulls *L. californicus* breeding at Mono Lake, California have been reduced to laying 2-egg clutches since the early 1900s (with eggs also smaller than those from other populations); this is apparently due to regional food shortages (Winkler 1985). In red-billed gulls *L. novaehollandiae*, egg and clutch size over 41 years were positively correlated with the availability of their preferred prey, the euphausiid *Nyctiphanes australis* (Mills et al. 2008). Decreasing egg and clutch sizes are predictable in growing populations of birds, a response hypothesised as being due to increased competition for food (Coulson et al. 1982, Perrins and McCleery 1994, Both 1998). However, though this study population of glaucous-winged gulls grew through approximately the 1930s – 1980s (Vermeer and Devito 1989) it has subsequently been decreasing (Sullivan et al. 2002) but egg and clutch sizes have not increased in response.

Similarly, as predicted based on numerous other studies (Meijer and Drent 1999), I found a negative relationship between clutch size and first egg date, with smaller clutches produced on average in years when laying commenced later. The relationship between food supply and lay date in birds is well established, including in some gull populations (Perrins 1970, Meijer and Drent 1999, Christians 2002, Mills et al. 2008). Gulls are capital breeders that, like many waterbirds, depend partly on endogenous reserves acquired prior to initiation of breeding (Drent 2006, Sorensen et al. 2009). A primary source of late winter and early spring food for gulls as well as other waterbirds in the study region has been the considerable influx of nutrients provided by the sequential spawning of herring at sites along the north-eastern Pacific coast (Munro and Clemens 1931, Willson and Womble 2006). For example, surf *Melanitta perspicillata* and white-winged scoter *M. fusca* mass gains in March and April are related to

presence of spawning herring (Anderson et al. 2009a). However, stock declines and temporal contraction of spawning herring in the Salish Sea (most herring there now spawn in March; Stick and Lindquist 2009, Therriault et al. 2009) means that access to this prey resource has declined for pre-breeding gulls over at least the past 40 years; other forage fishes such as pilchard *Sardinops sagax* were rendered commercially extinct in the study area as early as the 1940s (Wallace 1998). A decrease in Salish Sea herring size-at-age suggests a possible decline in quality as well as availability of this favoured prey since the 1970s, and declines in forage fish food value has been shown to negatively affect seabird productivity in other systems (Wanless et al. 2005).

First egg dates of glaucous-winged gulls have become later since 1959, from a mean date of 15 May in previously published literature (1959 – 1986) to one of 22 May in my 2008 – 2010 field study. This response is largely unexpected in terms of global trends as breeding season phenology has been advancing in the majority of bird species studied worldwide, with a relationship found between lay date and climate (Crick 2004, Dunn 2004, Møller et al. 2010). While most seabirds examined in other studies also demonstrate advancing laying dates, their responses have been more variable, with some species or populations instead exhibiting significant delays in initiation of breeding over recent decades, and warming sea surface temperature (SST) invoked to explain both advancing and delaying trends (Gjerdrum et al. 2003, Møller et al. 2010). It is therefore possible that gulls' delayed lay dates are a response to changing climate. However, I found no relationship between glaucous-winged gull first egg date and local mean annual SST (from archived data recorded at Race Rocks Lighthouse Station, 48.30° W, 123.53° N; F=0.006, p=0.94) for the years over which phenological data were

available, despite a warming trend in regional SSTs since 1970 (Masson and Cummins 2007). The observed delay in laying thus supports my hypothesis of gulls responding to an overall food decline. Delayed laying has been associated with food availability in other larids, e.g., red-billed gulls also laid later when euphausiid availability was low (Mills et al. 2008).

This study shows that glaucous-winged gull egg and clutch size have decreased over time in the Salish Sea, but these changes are biologically unimportant if lifetime reproductive success is unaffected. Though I lacked the data to analyse reproductive success per se over time, my results are suggestive of biologically meaningful changes that may in part explain ongoing population declines (Sullivan et al. 2002). The most important effects of increased egg size in birds overall seem to be improved survival in the days post-hatching, allowing young chicks to weather temporary food shortages (Parsons 1970, Martin 1987, Williams 1994, Christians 2002). However, evidence from multiple studies also shows egg size to be positively related to hatching success, growth rate and chick survival (Krist 2011). The relationship between egg size and ongoing fitness seems best established in seabirds (Williams 1994) with a handful of studies demonstrating that egg size is correlated with overall reproductive success and that chick size at fledging affects future survival (Gaston 1997, Mills et al. 2008, Harris and Elliott 2011). Here I hypothesise that recent marine food web changes may be affecting gull population dynamics in the Salish Sea study area and contributing to recent population declines toward early 1900 levels, when gull numbers were locally depressed by egging and persecution (Dawson and Bowles 1909). This hints at the potential for limits to the resilience of even generalist foragers.

2.4.2 Alternative Hypotheses

While food-related explanations are the most parsimonious for trends observed here, other possible causes exist. For example, pollutants such as PCBs and PBDEs also affect avian reproduction including egg and clutch size in birds (Harris and Elliott 2011). It is unlikely that contaminants are a causative factor here, however, as DDE (the breakdown product of DDT) and other chlorinated hydrocarbons levels have mostly decreased in eggs of avian indicator species in the region since the late 1970s (Harris et al. 2003, Harris et al. 2005). Though other contaminants such as PBDEs are increasing, their occurrence is more recent (since the 1980s; Elliott et al. 2005b), and thus out of phase with observed egg and clutch declines. Two recent studies have documented body size declines and morphological changes in North American birds over the past 50 – 100 y, likely related to climate change (Desrochers 2010, Van Buskirk et al. 2010); body size changes might also affect reproductive output. I was unable to rule out this explanation and suggest it would be a fruitful direction for further study, but note that female body size explains only a small proportion of egg size variability (Christians 2002).

2.5 Conclusions

Birds should ultimately alter reproductive traits and phenology to respond to shifts in underlying features of their food webs. There is experimental evidence for supplemental food increasing gull egg and clutch size in years of poor food availability, but not in good years, indicating the ultimate limits to reproductive output as well as the potential for proximate adjustments based on diet (Hiom et al. 1991). Nutritional requirements prior to egg laying (and possibly during certain phases of chick rearing; Annett and Pierotti 1999) are likely precise and

may require birds to consume high quality fish prey at this time. Thus, glaucous-winged gulls may be unable to use alternative food sources (e.g., garbage) to buffer against consistent shortages of natural foods during certain periods of their breeding cycle, and could be undergoing an ongoing trade-off of their own survival against production of offspring. It is possible that the study population may be shifting toward a modal 2-egg clutch, as has occurred in another food-limited population of gulls in the twentieth century (Winkler 1985). Experimentally testing whether gulls in the Salish Sea respond to increased high-quality fish prey by increasing egg or clutch size would provide more conclusive evidence for or against natural food supply as a mechanism driving observed trends. Though glaucous-winged gulls are generalist feeders that are expected to buffer themselves against ecological change, the shifts in reproductive traits identified here suggest a significant impoverishment of a coastal marine ecosystem bordering one of the most rapidly growing areas in North America. Interestingly, in 2008 glaucous-winged gull egg and clutch size (and reproductive success; LKB unpubl. data) remained low despite north-eastern Pacific waters being the coolest in 50 years of records and productivity being the highest ever viewed via satellite in August (Crawford and Irvine 2009), suggesting that the study area's coastal sea may be more strongly affected by regional than by basin-wide factors (cf. Johannessen and Macdonald 2009). Future studies should investigate details of long-term trends in gull diet, possibly using a stable isotope approach. Finally, I suggest that eggs in museum collections represent an underutilised resource for observing effects of environmental change on avian demography over time.

2.6 Acknowledgements

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Chapter 3: A Century of Change in Glaucous-Winged Gull Populations in a Dynamic Coastal Environment[3]

3.1 Introduction

A key question in ecology is what constitutes a 'normal' change in animal population numbers given the fluctuations that may be observed over the course of multi-year studies (Krebs et al. 2001). Long-term data are critical to addressing this question because they are more likely to include multiple population or climate cycles and thus reveal critical underlying processes and the occurrence of rare but influential events (Wiens 1977, 1984, Ludwig 1999, Grøtan et al. 2009, Sæther et al. 2009). As a result, determining whether ongoing population declines represent a density-dependent response, an effect of short-term climate variability, or a potentially reversible response to climate change or another anthropogenic stressor (or some combination of these factors) often requires the perspective provided by several decades of data, particularly in long-lived organisms such as marine birds (cf. Ainley 2002, Blight et al. 2006, Norris et al. 2007). Applied to conservation, such long-term studies help to define the baseline or reference conditions that managers typically aim to maintain or restore, but which are often poorly articulated, with a misunderstanding of trends potentially leading to ill-advised management decisions (Arcese and Sinclair 1997). Moreover, the lack of a long-term perspective can lead to gradual acceptance of incremental species loss (Pauly 1995).

[3] This chapter is in preparation as a manuscript by L.K. Blight, P. Arcese (UBC) and M.C. Drever (Environment Canada). Proposed title: "Generalist foragers affected by multiple factors over time: a century-long population trend of glaucous-winged gulls in the Georgia Basin, Canada".

Marine birds are often identified as sensitive indicators of the status of ocean systems (Furness and Greenwood 1993, Furness and Camphuysen 1997, Boyd et al. 2006, Piatt et al. 2007, Parsons et al. 2008), with over 200 papers in the last two decades showing that seabird populations are measurably affected by changes to marine environments (Grémillet and Charmantier 2010). Here we present an analysis aimed at identifying the range of population variation for a potential sentinel species (defined in Chapter 1; Hebert et al. 1999, Hebert et al. 2009, Gebbink et al. 2011), using 111 years of count data for glaucous-winged gulls in the Georgia Basin, British Columbia, Canada. The glaucous-winged gull is a long-lived marine bird described as thriving in proximity to humans, but whose numbers currently appear to be in decline over a substantial portion of its southern range (Sullivan et al. 2002, Bower 2009, Hayward et al. 2010). This apparent decline has prompted concern about future trends (Sullivan et al. 2002), but there is also evidence to suggest that glaucous-winged gull numbers in this region were much lower at the start of the twentieth century than at present (Dawson and Bowles 1909, Drent and Guiguet 1961, Reid 1988a). Thus, it is plausible that the species responded favourably to human-induced environmental changes in the early 1900s, with these changes facilitating population growth above a baseline supported by the availability of natural foods (Vermeer 1992, Hayward et al. 2010). Under such a scenario, the recent decline would simply represent a reversal of these influences and a return to historical conditions. However, a detailed understanding of population trends to the present day has been lacking.

Larus gulls worldwide often nest colonially near human population centres (e.g., Ward 1973, Pons 1992, Oro et al. 2004). As a consequence, they have long drawn the attention of field biologists (e.g., Dutcher and Baily 1903, Anonymous 1908), who focused their initial study on

behaviour and demography (Tinbergen 1953, 1959, Vermeer 1963, Holloway and Gibbons 1996), but who incidentally recorded population numbers (e.g., Province of British Columbia 1916). To provide a definitive estimate of long-term population trends in the study region, we used colony count data for glaucous-winged gulls nesting in the Georgia Basin from 1900 to 2010, and fitted a general linear mixed model to estimate long-term changes in mean colony size over time. We also conducted a number of secondary tests to examine whether temporal trends differed by colony size or geographical location.

We next examined potential causes of population change based on hypotheses assembled from the literature to account for temporal trends in gull populations generally (Grandgeorge et al. 2008, Hayward and Verbeek 2008, Farmer and Leonard 2011) and that were appropriate to what is known about the history and ecology of glaucous-winged gulls in our study region. Specifically, we represented each of three general hypotheses as graphical scenarios in Fig. 3.1 (described in text below). We then used a simple demographic model to generate expected population trajectories, based on estimates of reproductive success and survival appropriate to each scenario, and compared these predicted trajectories to the observed population trends based on colony counts.

3.1.1 Food Limitation Hypothesis

Several lines of evidence have led to researchers hypothesising that food limitation may have driven both increases and decreases in glaucous-winged gull populations at different points during the last century. First, expanding human populations in the Georgia Basin may have increased the availability of food for gulls in the form of garbage, and by doing so facilitated

their population growth after 1920 (Vermeer and Devito 1989, Vermeer 1992, Hayward et al. 2010), as has occurred in other systems (Spaans 1971, Pons and Migot 1995), with improved garbage management practices later in the century leading to gull population declines (Hayward and Verbeek 2008).

Alternatively, decreasing food availability, in the form of forage fish population changes (Hay 1998, Wallace 1998, Stick and Lindquist 2009, Therriault et al. 2009), has also been invoked to explain recent declines in Georgia Basin glaucous-winged gull populations. This is because these declines occurred in parallel with long-term decreases in egg and clutch size (Blight 2011; Chapter 2), a pattern consistent with the idea that access to high-nutrient fish prey, as opposed to lower-quality anthropogenic garbage, appears to be critical for successful egg production in gull species generally (Houston et al. 1983, Hiom et al. 1991, Bolton et al. 1992, Bolton et al. 1993, Annett and Pierotti 1999). Under this scenario, dietary garbage might contribute to population declines rather than to increases. Forage fish depletion has also been suggested as an explanation for long-term population declines and related changes in other fish-eating birds in the Georgia Basin and elsewhere (Norris et al. 2007, Hebert et al. 2008, Ainley and Blight 2009, Hebert et al. 2009). Overall, therefore, two potential mechanisms have been proposed to link food abundance or quality to population trends in glaucous-winged gulls, and are hereafter referred to collectively as a 'food limitation' hypothesis (Fig. 3.1A).

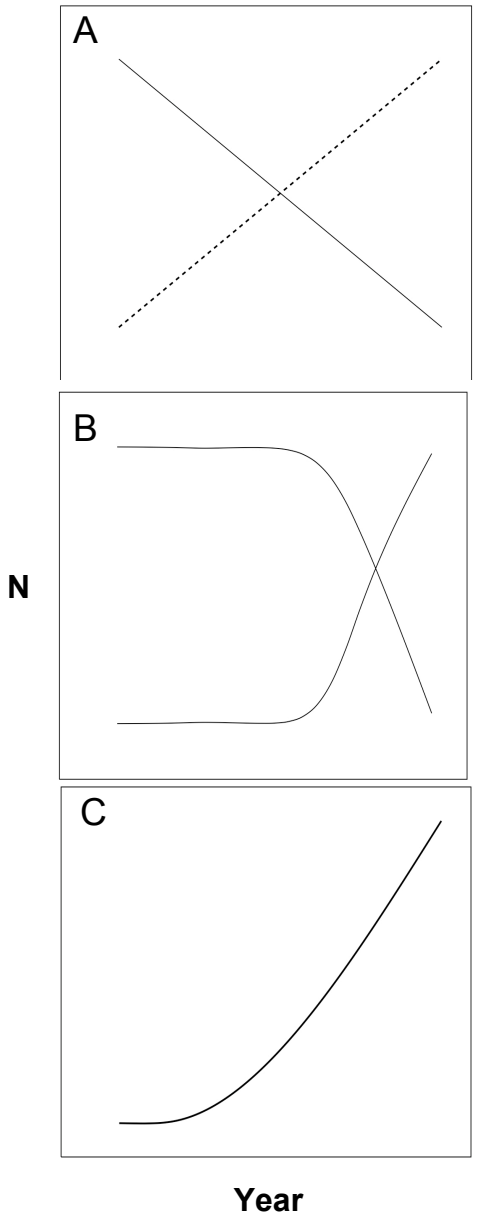

Figure 3.1: Simple graphical representation of three possible hypotheses to explain glaucous-winged gull population trends from 1900 to 2010. These mechanisms have likely acted in concert, though interactions are not depicted here. (A) Food limitation hypothesis – gull population decreases due to increased dietary garbage and/or declines in forage fish decreases productivity (solid line), or conversely, increases because increased dietary garbage increases productivity (dashed line); (B) Predation limitation hypothesis – gull population trend (upper line) shows an inverse relationship to that of eagles (lower line); (C) Egging hypothesis – egging ceases due to the ratification of the 1916 Migratory Bird Convention, and gull populations increase in response

3.1.2 Predation Limitation Hypothesis

A second hypothesis, that of 'predation limitation', might also explain long-term population trends in glaucous-winged gulls given that bald eagle populations in the region, and presumably associated predation rates, have changed over time. In the first half of the twentieth century, bald eagle numbers were suppressed by persecution and, later, exposure to chemical contaminants (DDT and PCBs; Elliott and Harris 2002). Given this, one might expect that predation by eagles on gull nests or young increased as eagles recovered in the mid to late 1900s (Sullivan et al. 2002, Environment Canada 2010, National Audubon Society 2011, Elliott et al. 2011). Under this hypothesis gull numbers should have grown or remained stable in the absence of eagles, but grown more slowly or declined as eagle populations recovered (Fig. 3.1B).

3.1.3 Egging Hypothesis

Reid (1988b) suggested that increases in the productivity of glaucous-winged gulls in the region occurred after the adoption of the Canada-US 1916 Migratory Bird Convention (Migratory Birds Treaty in the US), which reduced or eliminated human egg collecting and the killing of adults throughout our study area. Reid further suggested that the resulting increase in productivity was sufficient to explain subsequent population growth of glaucous-winged gulls on Protection Island, Washington, through to the late 1980s (Reid 1988b). Thus, the 'egging hypothesis' (Fig. 3.1C) predicts that once protected, gull populations in the Georgia Basin increased until limited by food or predators (see above). Although human egging is essentially a form of predation, it often occurred at much higher intensities than has been documented when due to eagles. For

example, at the Farallon Islands, California, nineteenth century egg hunters regularly broke all eggs found so that they could later return to collect freshly-laid second clutches (with 108,000 common murre *Uria aalge* eggs reported taken in 1886 alone; Doughty 1971). In the Georgia Basin seabird egging and shooting was common prior to legislated protection. In 1915, for example, a warden was placed at Mandarte Island to protect nesting birds as "human beings – whites, Indians, and Japanese – carry…away the birds' eggs and young" (Province of British Columbia 1916). At Mitlenatch Island, BC, Pearse (1923) noted there was poor reproductive success because "the nests are systematically robbed by Indians and fishermen" and that "the place was cleaned of eggs". On shooting, Anthony (1906) wrote that "[i]t is a common practice of a certain class of Sunday sportsmen (?) to… slaughter wantonly large numbers [of gulls] for the mere sport". When egging and hunting commenced in this region is unknown.

While each hypothesis above can be described in isolation, it seems likely that more than one mechanism influenced gull population trends over the last century (cf. Hilborn and Mangel 1997). Following methods developed by Walters (1986) and Walters and Martell (2004), we used our gull count data, published vital rates, and declines in clutch size and annual eagle numbers to test if declines in gull fecundity (as a proxy for food availability or quality – i.e., our food limitation hypothesis), predation by eagles, increased reproductive output after the banning of egging, or some combination of these factors accounted for observed population trends within our study area. Overall, the objective of our study was to use our derived glaucous-winged gull population trend and modelled effects of hypothesised causes to address five questions: 1) how has population size changed over time in the Georgia Basin; 2) is population change dependent on colony size, 3) colony location, or 4) related to temporal

variation in reproductive output and; 5) what do population trends tell us about baseline conditions in our study region?

3.2 Methods

3.2.1 Study Area and Count Data

To reconstruct population trends to the present day, we compiled published and unpublished counts of breeding gulls (number of nests or breeding pairs per colony) obtained from field studies conducted between 1900 and 2010 at glaucous-winged gull colonies in the inshore coastal waters of the Georgia Basin, Canada (Fig. 1.1; see Vermeer and Devito (1989) for gull colony locations), and supplemented those data by conducting colony censuses in 2009 and 2010. We identified historical counts via literature review and our own knowledge of local unpublished data repositories (e.g., museum archives, government records; sources detailed in Appendix 2). We also contacted seabird biologists working in the region to request their unpublished count data. Because we expected most early counts to reside in 'grey' literature, we searched all such reports cited in major reviews (e.g., Hayward and Verbeek 2008), and supplemented these sources using those found via the ISI Web of Science using the search terms "glaucous-winged gull" and "Larus glaucescens". We searched all publications related to gulls breeding in our study area (i.e., not only publications reporting on colony counts) because some authors, particularly those writing prior to ~1960, included incidental notes on gull colony sizes while reporting their focal results. Though most pre-1960 data were published in Drent and Guiguet (1961), we also encountered new records for that period in old publications by naturalists and researchers, and in museum archives. In a few cases, counts were provided as

ranges. For these we used median values as our site estimates. Most colonies sampled are located outside urban areas, and are now legally protected and rarely accessed by humans. A small portion of this population (est. <4 % of total Georgia Basin numbers in 1986; Vermeer et al. 1988) nested on city roofs, but we did not re-census these urban-nesting gulls because informal surveys (LKB pers. obs., T. Chatwin pers. comm.) suggests no marked change in urban nesting by gulls since 1986, and the cost of aerial surveys was prohibitive.

Our 2009 – 2010 counts were carried out following Vermeer and Devito (1989) and Sullivan et al. (2002; briefly, individual surveyors (smaller colonies) or survey teams of 2 – 6 people (larger colonies) walked systematically through each colony, marking nests with jellybeans to avoid recounting), who in 1986 censused all non-urban glaucous-winged gull colonies in the Georgia Basin (Vermeer and Devito 1989). Our counts replicated about 60% (49 of 83) of sites counted in 1986, but we selected these 49 sites to include most (~96%; 1986 data) of the breeding population. Of the 34 colonies we did not visit, 76% historically consisted of only ≤10 pairs. We conducted censuses from 13 – 20 June 2009 (Mandarte Island and Chain Island group) and 2010 (remaining colonies). Four colonies of 1 – 5 pairs were surveyed using binoculars on 1 July 2010. The mid-June census period was chosen to most closely replicate earlier censuses as well as to coincide with the peak of egg laying (Vermeer and Devito 1989, Sullivan et al. 2002; LKB unpubl. data). Conducting counts prior to hatching avoids disturbing gull chicks, which when frightened may flee into adjacent territories where they may be killed by neighbouring birds (Gillett et al. 1975, Hunt and Hunt 1976). To avoid disturbing nesting cormorants, we counted any gulls nesting in their vicinity using binoculars. As with previously-published studies (Vermeer & Devito 1989; also K. Vermeer pers. comm.), we counted only active nests (containing ≥1 egg, or

evidence of predation), because glaucous-winged gulls, like other larids, often build multiple nest cups prior to laying.

3.2.2 Statistical Analyses

3.2.2.1 Temporal Trends

Temporal trends in gull abundance were estimated by modelling colony counts in relation to year, from 1900 to 2010, using a mixed effects approach (Zuur et al. 2009). Colony counts were log-transformed, such that $Y_{i,t} = \log_e(Count_{i,t} + 1)$, where i = colony location and t = year, and year 1900 was set to a value of 1. We included 'Year' as a fixed effect to estimate change in colony count over time, and as a random effect to account for colony-specific variation. Thus, this model allowed trends in colony counts to vary by location, but the fixed term represented an average trend over the whole study area. In addition, the model included a random effect term for year as a categorical variable, which allowed for year-specific region-wide deviations from the overall trend, as would occur during years when data were only available from a few colonies or were driven by unusual weather events. Number of annual counts per site for the study period ranged from 1 – 22.

A model was first fit with only Year as an explanatory variable, and this model showed no significant trend in abundance over time (β_{year} = –0.077; 95% CI = [–0.006, 0.021]). However, a visual examination of a plot of residuals against year indicated the possibility of a non-linear trend, and therefore the model was refit, adding a quadratic term for year ($Year^2$) that allowed for non-linear changes over time, again as a fixed effect and as random effects that allowed effects of Year and $Year^2$ to vary with location. The quadratic effect was significant (see

Results), and we thus based our inference on this model. Residuals and random effects were normally distributed, and variance of residuals appeared constant across the range of fitted values.

Apart from providing a trend for the entire study area, this model also estimated trends at each location, and thus allowed for a series of secondary tests to examine whether trends varied with geographical location or with colony size category. For geographical location, a Pearson correlation coefficient (ρ) was calculated between the location-specific trend estimates ('early' and 'late' based on the parameter estimates for Year and $Year^2$) and latitude and longitude of the colony location. To look at relationships between trends and colony size, we divided colonies into five size class categories based on the maximum counts recorded for a given site: 1 – 10 nests ('isolates'), 11 – 50 nests ('small'), 51 – 250 nests ('medium'), 251 – 499 nests ('medium-large') and ≥500 nests ('large'), with size classes determined based on functional attributes of colony response to extrinsic variables such as predation, food supply, and weather (Furness and Monaghan 1987, Vermeer and Devito 1989). We then used an ANOVA to test whether early or late trend varied with colony size class. Because population persistence should decline with population size (due to increased vulnerability to factors regulating populations (e.g., predation) and/or to stochastic processes; (Hanski and Gilpin 1991, Courchamp et al. 1999), and because declining populations often contract in spatially non-random ways (Channell and Lomolino 2000), we predicted that smaller gull colonies would show more severe declines on average over 111 years, and that population trends may have varied geographically within the study area.

3.2.3 Testing Causes of Population Trends

We tested whether declines in gull productivity were sufficient to explain observed population changes, following the Walters (1986) and Walters and Martell (2004) method of stock reconstruction for single species assessment using a time series of abundance estimates. We created a simple, 5-stage deterministic demographic model based on available data on glaucous-winged gull age-related survival rates (Table 3.1 and text below), and a modelled decline in clutch size (CS; number of eggs laid per female) based on data from Chapter 2 (Blight 2011).

Based on our own and published data, for the first age-class (survival from egg to fledge, hereafter called reproductive success, RS) we also included a modelled decline in this parameter over time (below). For the sub-adult and adult stages we assumed that survival rates were constant, using values taken from the literature of studies in the region. Specifically, we assumed that: 2^{nd}-year survival was 0.70 (Butler et al. 1980, Reid 1988b), 3^{rd}-year survival was 0.62 (Butler et al. 1980), and adult survival was 0.87 (Reid 1988b). Where more than one value was available for a particular age-class, we took the mean of those values, except for adult survival, where we used the value of 0.87, which was the highest of the estimates provided by Hayward & Verbeek (2008; range 0.83 – 0.87), but most similar to published estimates for other adult temperate-breeding *Larus* gulls based on larger sample sizes and longer-term studies (summarised in Gaston et al. 2009). We used a female-only model, and assumed that only adult females (i.e., those entering their 4^{th} year and older) were able to breed (Hayward and Verbeek 2008). An initial exploratory model using modelled RS and CS clutch size declines alone was

inadequate to explain population trend. Therefore, because juvenile gulls are less efficient foragers than adults (Verbeek 1977, Searcy 1978, Greig et al. 1983, Skórka and Wójcik 2008) we further assumed declines in food availability might disproportionately affect the survival of 1st year gulls (fledging to 12 mo). To do so, we assumed a maximum survival rate from fledging to 12 months of age of 0.5, based on the average of published values for the region (Butler et al. 1980, Reid 1988b), and then used maximum likelihood methods implemented in Microsoft Excel (2011) to find the linear decline in 1st-year survival that resulted in the best fit to our modelled population trend (see Temporal trends, above).

Table 3.1: Survival estimates used in this study for five age classes of glaucous-winged gulls, based on published studies.

Age class	Survival estimate for this study	Published values (Salish Sea)	Source
Egg to fledging (RS)	0.83*	0.63[a], 0.50[b], 0.43[b]	Vermeer 1963[a], LKB this study[b]
1st year	0.50*	0.40, 0.61	Butler et al. 1980, Reid 1988b
2nd year	0.70	0.60, 0.80	Butler et al. 1980, Reid 1988b
3rd year	0.62	0.62	Butler et al. 1980
4th year+ (Adult)	0.87	0.83 – 0.87	Hayward and Verbeek 2008

*Initial estimate, with decline to lower values modelled over time. See text for details.

We employed a quadratic equation to model annual clutch size over time, using 10 years of field data collected in the region between 1962 and 2009 (Blight 2011; Chapter 2), and assuming an initial clutch size (intercept) of 3 in year 1900, so that

$$y_i = a + b_1 x_i + b_2 x_i^2 ,$$

where *y* is the predicted clutch size in year *i*, *a* is initial clutch size, *b* is the slope of the decline and *x* is year. As with our analysis of temporal trend (above), using a quadratic 'year'-term in the model allowed for non-linear change over time. In the absence of reliable empirical observations of clutch size in 1900, we assumed an initial clutch size of 3 because this is the modal size for the genus and early accounts describe this species as laying three eggs (Schultz 1951). We assumed that temporal declines in clutch size were similar with respect to colony size (Blight 2011; Chapter 2).

We also used a quadratic equation to model temporal trends in annual reproductive success, using values derived from three years of field data from our study area (Vermeer 1963, LKB unpubl. data), wherein *y* equalled the predicted RS in year *i*. Because egg and chick production are both positively related to food availability in gulls (e.g., Mills et al. 2008), we assumed a relatively high initial reproductive success (intercept) of 0.83 for year 1900, slightly above that reported from a relatively successful sub-population of modern-day herring gulls (~0.78; Pierotti and Annett 1990.) These annual clutch size and reproductive success values were then used in our model along with the other values above (Table 3.1).

We used the same modelling approach to explore the potential influence of predation by eagles, with the added assumption that eagle mortality would be additive to the modelled effects resulting from change in clutch size, reproductive success and 1st-year survival as described above. To keep this model simple we restricted our exploration of eagle predation to its potential effects on reproductive success. Although eagles do kill older gulls, their greatest

impact appears to occur via the predation of eggs and chicks at nesting colonies (Hipfner et al. 2012). Thus, to model eagle mortality, all other vital rates outlined above were retained in our demographic model, and we then added a term to account for predation mortality.

To do so, we assumed that the annual predation rate experienced by gulls from laying to fledging was proportional to the regional population size of bald eagles. By this method, the annual additive reduction in egg and chick production due to eagle predatrion ranged from –0.001 to –0.156; mean: –0.030; Fig. 3.2), a reduction that appears credible given our field observations (LKB pers. obs.).

For eagle population trends we used effort-adjusted Christmas Bird Count (CBC) data for British Columbia and Washington (National Audubon Society 2011). Although CBC data suffer from weakly-standardised approaches and coverage has changed over time (Dunn et al. 2005), this dataset provides the most comprehensive regional time series available for bald eagles across our study period. CBC counts started in the first decade of the twentieth century whereas regular breeding season surveys did not commence in the region until the 1980s (Elliott et al. 2011). Though the CBC provides counts of wintering individuals rather than breeding season birds, winter abundance of eagles provides a reasonable index of regional trends over time (cf. Elliott et al. 2011), and indicates that eagles occurred at low initial densities prior to 1950 but have increased rapidly over time since the 1970s. As above, we used maximium likelihood to find the best fit to our modelled population trend given additional egg and chick mortality from eagles.

To test the egging hypothesis we simply allowed the model to predict population trend based

on baseline estimates of survival and reproductive rate, and predicted that a population at equilibrium would not grow, but that populations suppressed by egg-collecting would increase.

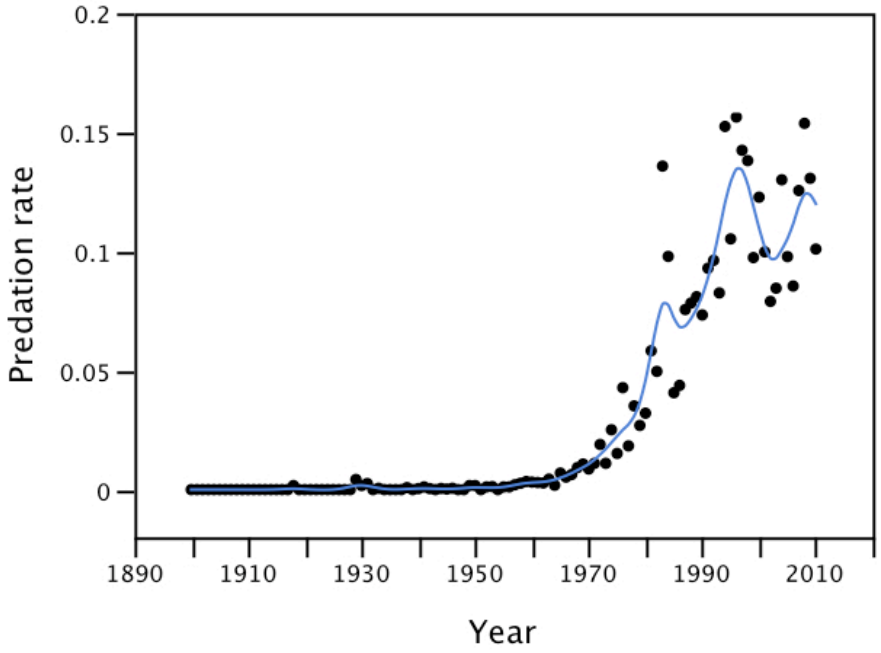

Figure 3.2: Modelled annual bald eagle predation rate on glaucous-winged gull eggs and chicks over time, with rate proportional to eagle population size. We did not correct for any effect of colony size on predation rate as most eagles occur at large gull colonies. Line tracks 10-year moving average.

3.3 Results

3.3.1 Colony Counts

We compiled 507 records of colony counts from 87 localities in the Georgia Basin over the study period (Appendix 2), with 11 colony counts available prior to 1925. Two of the Georgia Basin's largest (historically and at present) colonies were represented in these early counts, so

that our early population size estimates are likely representative of regional totals for that period. Colonies for which early count data were available were also among the most frequently censused in the region over the entire study period, and a visual inspection of the long-term trends for these sites showed agreement with our estimated population trend (Fig. 3.3).

Based on our 2009 – 2010 census, we estimate the 2010 Georgia Basin population at approximately 5600 nesting pairs, about 7400 fewer pairs (–57%) than were breeding during the regional census conducted in 1986 (13,002 pairs) but similar to the 5654 – 6654 pairs estimated in region-wide surveys during the middle of the increase phase (1959–60; Drent and Guiguet 1961, Vermeer & Devito 1989).

3.3.2 Temporal Trends

Glaucous-winged gull numbers in the Georgia Basin increased from years 1900 to 1973, reaching a maximum from 1971 – 1973 and declining thereafter (Fig. 3.3). The parameters for Year and Year^2 can broadly be interpreted as trends in first ("early") and second ("late") halves of the 111-year time series, respectively. Both these parameters were statistically significant predictors of colony count, indicating a non-linear trend over time (Table 3.2). The standard deviations (SDs) of random effects included in the model estimated how variance in log-transformed colony counts was partitioned among locations and years. These SDs indicate that most (90%) of the variation in colony counts resulted from differences among locations (Table 3.2), which underlines the strong spatial variation in colony counts over the region. The next most important source of variation was the residual SD (5%) that measured the within-location

variability in colony count, and this value was approximately double the SD attributable to region-wide swings in mean colony counts (3%; Year as categorical variable), and in trends in time among locations (2%; Year|Location).

Secondary tests indicated that the magnitude of trends did not vary with latitude or longitude, as all Pearson's correlation coefficients (ρ) had absolute values ≤0.13 and *p*-values >0.25 (Fig. 3.4A-D). In contrast, population trends did vary among colony size categories (Fig. 3.4E-F). Analysis of variance tests for comparisons of both Year and $Year^2$ effects among colony size categories were statistically significant (*F*-values >6.4 in both cases; df = 5,76, $p < 0.0001$), indicating that rates of increases and declines were unequal with respect to colony size. Specifically, regional trends were led by the largest colonies, which experienced the highest rates of increase during the early period and also the most rapid declines during the later period (Fig. 3.4E-F). Noteworthy among the declines of the larger colonies was the near-extirpation of three neighbouring colonies located near Nanaimo, BC (Five Finger Island, Snake Island, Hudson Rocks (approx. 49.14º N, 123.95º W); from 1591 nests in 1986 to 32 in 2010; Appendix 2) that together comprised a nesting aggregation of gulls comparable in size to the largest individual colonies in our study area. Another noteworthy observation at individual colonies included the extirpation or near-extirpation of at least three historically medium to large colonies (Ballenas, Chrome, and Passage Islands; Appendix 2) on islets where buildings such as lighthouses or homes had been constructed. Other than these instances, colonies tended to change in size rather than to disappear.

Table 3.2: Parameter estimates for model depicting temporal trends in colony counts of glaucous-winged gulls in the Georgia Basin, 1900-2010. Parameters with |*t*-value| > 1.96 are considered statistically significant ($P < 0.05$; bold font). Trends are based on nest or pair counts at 87 locations, and 77 years of data. $N = 507$ colony counts.

Variable	Parameter	SE	*t*-value
Fixed Effects			
Intercept	1.66	2.266	–0.73
Year	0.12	0.055	**2.25**
$Year^2$	–0.00084	0.00032	**–2.59**

Variable	SD
Random Effects	
Location	12.14
Year|Location	0.305
$Year^2$|Location	0.002
Year as categorical variable	0.335
Residual	0.676

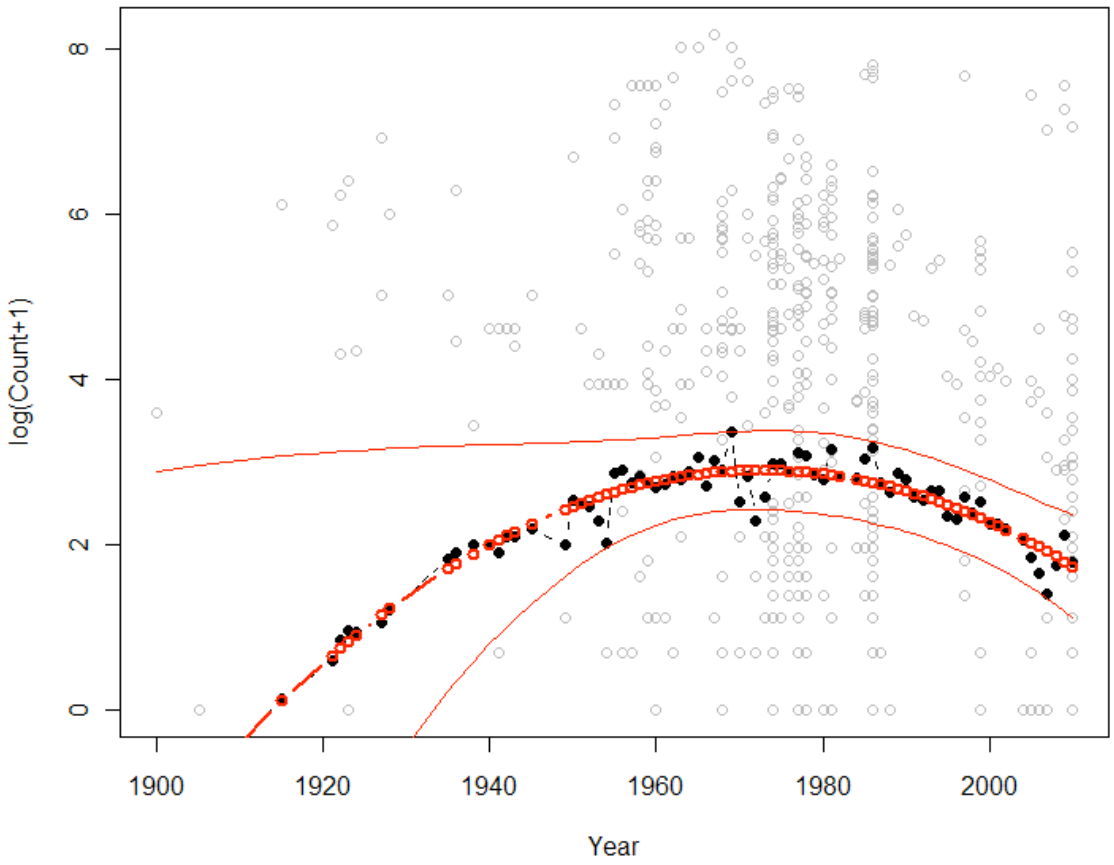

Figure 3.3: Trends in colony counts ($\log_e$) of glaucous-winged gulls in the Georgia Basin, 1900-2010. Hollow points indicate counts of pairs or nests at 87 locations. Thick hollow points along trend line indicate predicted means with 95% confidence intervals (thin lines) from quadratic trend model. Solid points indicate predicted mean incorporating a year-specific effect.

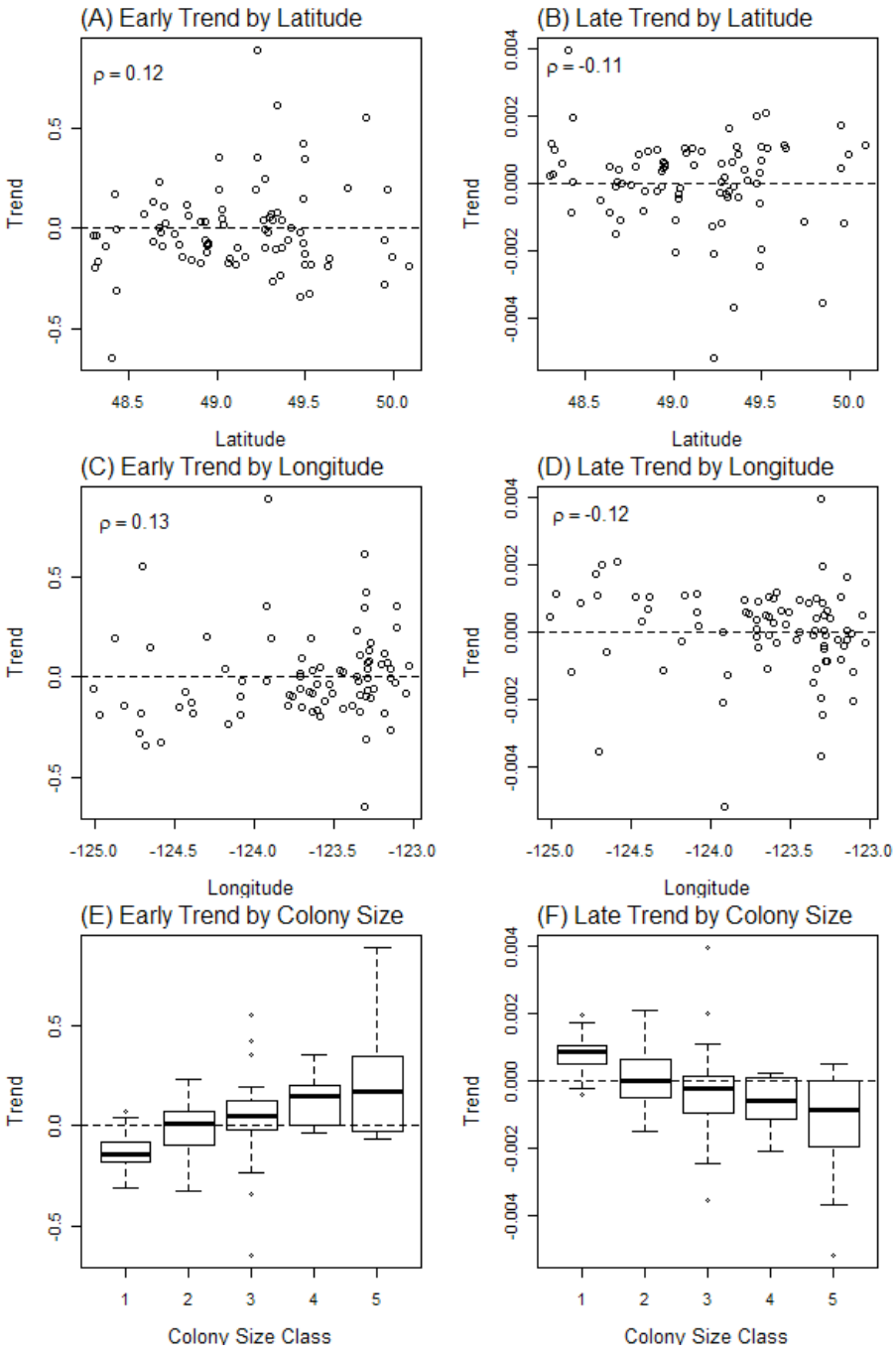

Figure 3.4: Variation in colony-specific trend estimates of gull colony counts as a function of geographical location (panels A-D) and colony size class (panels E-F; size classes defined in Methods). The study period encompassed 1900 – 2010, and was split into halves ('early' and 'late'). In the 'early' phase, larger colonies experienced the highest rate of increase and led regional trends, but experienced the most rapid declines in the 'late' phase. Pearson's correlation coefficients (ρ) for relationships between trend estimates and geographical location had $p > 0.25$.

3.3.3 Causes of Population Trends

Assuming constant adult and sub-adult survival, and trends in clutch size and reproductive success fitted to our field data and others' published values (see Methods), along with decreasing survival of 1st year birds over time, we produced a population trajectory that closely fit the population trend modelled from colony counts (Fig. 3.5A). The modelled decline of clutch size became more severe over time: overall slope for the entire study period was –0.006, while the slope for the last 50 years (since 1962) was –0.011 (Blight 2011; Chapter 2). Assuming an initial clutch size of 3 in 1900 and a subsequent decline fitted to data, our modelled clutch size began to decline below 3 (<2.95) in the 1950s.

Model fit was modestly improved by assuming that egg and chick mortality increased in proportion to bald eagle numbers, in addition to the above modelled changes. Specifically, the modelled rate of gull population decline from ~year 1974 to 2010 showed a better visual fit to our estimated gull population trend when we assumed that eagles increased egg and chick mortality as their populations grew (3.5B). This implies that food-related declines in clutch size, reproductive success and survival in 1st-year gulls, in conjunction with the addition of egg and chick loss proportional to eagle numbers, were sufficient to closely track our estimates of long-term change in glaucous-winged gull population size, without making additional assumptions about temporal variation in the survival of older age classes.

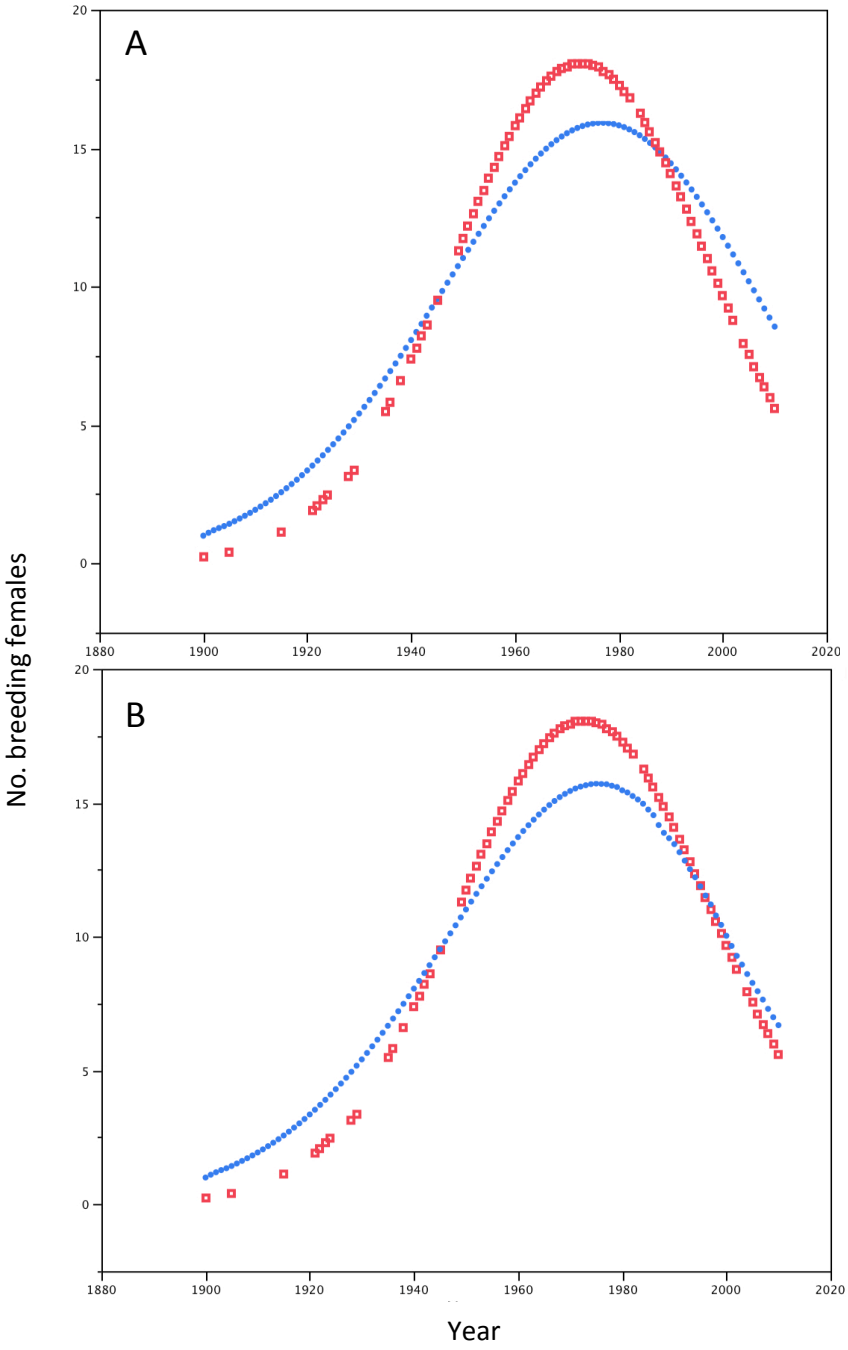

Figure 3.5: Glaucous-winged gull population trend (small solid points) with (A) modelled fit of population trajectory based on declining CS, RS and 1st year survival (large hollow points); and (B) model shown in (A) plus inclusion of additive eagle mortality on eggs and chicks, based on scaled eagle abundance.

3.4 Discussion

3.4.1 Colony Counts and Temporal Trends

During the last 111 years, the number of glaucous-winged gulls breeding in the Georgia Basin fluctuated considerably, increasing rapidly from 1900 to the mid-1970s, then declining so that 2010 levels were approximately 50% of peak recorded abundance. The timing of the population peak detected by our model is about a decade earlier than was implied in the discussion of 1986 census results, but the latter were based on fewer data (Vermeer and Devito 1989). Our study incorporated glaucous-winged gull colony count data from all available sources, and represents one of the more comprehensive sets of long-term census data available for a marine bird in Canada. Compilations of marine animal count data for time periods exceeding 100 years are generally rare, and thus are particularly valuable in studies of animal population dynamics (Pauly 1995, Pinnegar and Engelhard 2008).

Colony growth rate over time was not related to latitude or longitude, indicating that Georgia Basin gull colonies are neither contracting toward a centrum (e.g., due to changes in concentration of food availability; Therriault et al. 2009) nor shrinking toward the edge of the species' local range, as might have been expected if changing local conditions were the primary factors affecting long-term variation in colony counts. Our aggregated count data showed a relatively consistent increase and then decline in numbers at individual Georgia Basin gull colonies over the study period. In contrast, the rates of change at individual colonies varied strongly with colony size, with the largest colonies showing the highest rates of change in both the increase and the decline phases (Fig. 3.4 E-F). This result was unexpected; though more

rapid population growth at large colonies is predictable, their relatively rapid decline, compared to the relative stability and persistence of smaller colonies, ran counter to our predictions based on the common observation that extinction probability increases as population size declines (cf. Courchamp et al. 1999). This observation suggests that smaller glaucous-winged gull colonies should have been more inclined to vary widely in size, or to 'wink out,' than larger ones.

In a study contrasting small and large glaucous-winged gull colonies, Vermeer et al. (1988) found that in urban settings, solitary nesters and small colonies had significantly higher breeding success (1.10 and 1.73 vs. 0.35 chicks fledged per pair) than did a larger rooftop colony. Vermeer et al. (1988) hypothesised that gulls nesting in isolation or with few conspecifics were less likely to lose eggs or chicks to intraspecific predation. Rooftop nests were also noted to be less vulnerable to heterospecific predation (Vermeer et al. 1988). This may mean that when predators are scarce, nesting in smaller aggregations may represent a more optimal strategy for gulls (with optimal colony size for seabirds in general varying in response to adult survival and reproductive success; Brown et al. 1990). If true, the persistence and relatively low rates of decline at the smallest Georgia Basin colonies we censused may imply a recent relaxation in heterospecific predation at smaller gulls colonies. This pattern might also be expected if eagles or other predators such as river otters (Foottit and Butler 1977, Vermeer and Morgan 1978) currently focus their activities at glaucous-winged gull colonies of larger size (cf. Clode 1993). Interestingly, Ainley et al. (2005), also found that predation pressure was lower at small penguin colonies owing to these sites being less attractive to predators.

Though we did not re-visit 34 of 83 colonies censused in 1986, 76% of these historically consisted of 10 or fewer pairs, and together they accounted for only 4% of the 1986 population. We did not update census data for urban-nesting gulls in the Georgia Basin, but we suggest that this omission is unlikely to have markedly affected our results, given that no large colonies are known to exist in urban settings in our study area; nor are they known from historical records (prior to ~1950s; e.g., Bowles 1906, Eddy 1982, Hooper 1988, Vermeer et al. 1988; LKB pers. obs., T. Chatwin pers. comm.). We therefore believe that we censused all important colonies, and thus most of the glaucous-winged gulls that nest within the region. Our conclusion that the results from primarily non-urban colonies accurately reflect a region-wide trend, i.e., that glaucous-winged gulls have not simply moved to more urban habitat, is corroborated by data from regional monitoring schemes counting gulls away from their colonies, and that also show declines in recent decades (Bower 2009, Crewe et al. 2010, Environment Canada 2010, National Audubon Society 2011). It is also unlikely that gulls have emigrated to other regions because large colonies in conterminous US waters also experienced rapid declines from 1993 – 2008 (44%, Protection Island, WA; Hayward et al. 2010) or have all but disappeared (99% decline, Colville Island, WA; from ~1800 pairs in 1970s to ~20 pairs by the end of the twentieth century; Hayward and Verbeek 2008). Numbers at Canadian colonies in adjacent regions have remained relatively stable after experiencing declines in the mid-1900s (Parks Canada 2009; P. Clarkson and Y. Zharikov pers. comm.).

3.4.2 Causes of Population Trends

We used demographic models to project population trajectories over time and test alternative

hypotheses of population trend (Fig. 3.1), recognising that more than one driver would likely be required to account for multi-decadal trends. A close initial fit to estimated population trend, assuming constant adult and sub-adult survival rates estimated from the literature and declining clutch size and reproductive success trends from data, provided support for the declining productivity hypothesis (i.e., a scenario of decreasing CS, RS and survival of 1st year birds; Fig. 3.1A).

We equated declining productivity with food limitation, an assumption that is consistent with numerous findings that link limits in seabird food quality and abundance with CS and RS declines. For example, productivity of glaucous-winged gulls at colonies without access to garbage exceeded that of birds breeding near urban areas (Ward 1973) and for herring gulls, female body condition and productivity were both negatively related to blood plasma amino acid index, an indicator of dietary garbage (Hebert et al. 2002). Contrasting studies have shown that gulls respond to dietary garbage by increasing productivity, but these results may be explained by regional differences in quality and availability of garbage (Pons 1992, Pons and MIgot 1995, Weiser and Powell 2010). Our hypotheses do not discriminate between reductions in productivity due to loss of fish prey vs. increases in low-quality food (e.g., garbage), and it is possible that these two factors act in concert. However, declines in egg and clutch size and reproductive success have all been attributed to reductions in forage fish in other *Larus* gulls with similar life histories (Houston et al. 1983, Pierotti and Annett 1990, Hiom et al. 1991, Pierotti and Annett 1991, Bolton et al. 1992, Bolton et al. 1993), and each of these traits has decreased over time in our study area (Blight 2011; Chapter 2). Declines in forage fish availability and/or quality are also thought to have influenced reproduction and population

trends in other species of waterbird in our study area (Norris et al. 2007, Anderson et al. 2009a) and numerous studies have shown this to be the case in other systems (e.g., Wanless et al. 2007, Ainley and Blight 2009, Hebert et al. 2009, Grémillet and Charmantier 2010).

The close overall fit of the increase phase of our demographic models to estimated population trends (i.e., growth resulted despite constant sub-adult and adult survival) also supports the hypothesis that the observed population increase in glaucous-winged gulls during the mid-1900s was mainly the result of a cessation of egging and related human persecution. This finding is consistent with the results of Reid (1988b), who suggested that population growth rates to the early 1980s at Protection Island, Washington (~5.1% per annum), could primarily be explained by cessation of human persecution. This conclusion is also in keeping with the more generic observation that overexploitation (e.g., hunting, harvesting of propagules) is one of the leading causes of species extinctions worldwide, including common species that have been driven to extinction by human activities (Gaston 2010, Hoffmann et al. 2010).

Our modelled population increase from the early 1900s, as a result of holding sub-adult and adult survival constant, suggests a pattern typical of a rebounding animal population. Early data and anecdotes suggest that at the turn of the twentieth century, egging, and perhaps hunting, heavily affected gulls in the region, with biologists of the day consistently noting that gull populations suffered from relentless persecution (Dawson and Bowles 1909, Province of British Columbia 1915, Drent and Guiguet 1961, Pearse 1923, 1963, Drent et al. 1964). Harvest and persecution of gulls and other seabirds (e.g., tufted puffins *Fratercula cirrhata*; Blight in prep.), and resulting population effects, were not unique to the Georgia Basin but rather were globally

commonplace at the time (e.g., Falla 1937, Garthe and Flore 2007, Grandgeorge et al. 2008). A hypothesis of population limitation due to egg harvesting in the early 1900s and earlier is also consistent with the reduced reproductive success or total reproductive failure observed more recently at colonies where glaucous-winged gull eggs have been harvested, with the timing of egging sometimes resulting in birds being unable to lay replacement eggs (Vermeer et al. 1991, Zador et al. 2006). The growth of glaucous-winged gull populations in the early to middle part of the twentieth century was paralleled by rapid increases to other North American populations of waterbird species not considered to be human commensals (e.g., other gulls, terns, alcids, cormorants, cranes; Ludwig 1974, Reid 1988a, Bird Studies Canada 2010) that were also protected by the 1916 US – Canada Migratory Bird Treaty.

Modest improvement to the fit between modelled and estimated population trend with the addition of eagle predation was at least partially consistent with our predation hypothesis, i.e., that the recovery of eagle populations after the mid to late 1900s has curtailed glaucous-winged gull population growth within our study area (Fig. 3.1B) by renewing additive egg and chick mortality decades after human egging ceased to be a factor. This suggestion contrasts with the conclusions of Sullivan et al. (2002), who suggested that eagles were a primary cause of regional declines. Eagles are capable of causing large-scale disturbance at seabird colonies, including those of glaucous-winged gulls (Parrish et al. 2001, Hayward et al. 2010). However, mobbing and aggression by gulls may reduce the susceptibility of colonies to eagle attack, and also to disturbance-related predation by corvids and other gulls (Hipfner et al. 2012). Gulls do not appear frequently in the diet of nesting eagles in the Georgia Basin (Elliott et al. 2005a). Nevertheless, it is plausible that eagle predation has acted synergistically with food shortages if,

for example, food shortage increases predation risk to eggs and chicks because adults spend more time away from the nest to forage. Eagle predation is unlikely to have played a key role in driving gull population trends in the early 1900s, because early CBC data, although sparse, suggest that eagle numbers were low at that time. Human persecution of eagles and other predatory birds was also commonplace in the early 1900s, as evidenced by bounties set on eagles in Alaska from 1917 until 1952 (Zweifelhofer 2007). Thus, artificially low rates of predation by eagles may have even facilitated early population increases once humans stopped egging.

Overall, our models provide one possible set of explanations for the causes of population trends observed in Georgia Basin glaucous-winged gulls. It may be that factors not addressed by our model, such as increases in the survival of older age classes related to the availability of garbage, have also affected gull populations, but we lacked the data to test this hypothesis explicitly. Fisheries discards do not appear to have featured in the diets of the Georgia Basin's glaucous-winged gulls, at least since the 1960s (Ward 1973, Vermeer 1983), but they have been important in the population dynamics of gull species elsewhere (Tasker et al. 2000, Farmer and Leonard 2011) and could have gone undetected in our system. Detailed information on gull diet over time is therefore required to more rigorously address these hypotheses.

3.5 Conclusions

Our results indicate that glaucous-winged gull populations in the Georgia Basin have fluctuated considerably over the last 111 years. Local and other anecdotal accounts from the early twentieth century suggest that glaucous-winged gull numbers were not 'at baseline' but instead

were limited by human exploitation, something that was documented by early naturalists and researchers but that had largely disappeared from the literature after about 1960. More recently, declining availability of high-quality fish prey appears to have decreased gull productivity, perhaps making some populations more vulnerable to growing predation by recovering bald eagles. The magnitude of our documented decline surpassed that described by Sullivan et al. (2002). Our results highlight the value of long-term, retrospective studies for providing unique perspectives on causes of population change. In contrast, caution should be exercised in assuming that historical data represent 'pristine' conditions by virtue of their age. This caution is particularly relevant when baseline data are required to assess historical change in the health of ecosystems.

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Chapter 4: Changing Gull Diets in a Changing World: A 150-year Feather Isotope Record from a Northeast Pacific Coastal Zone[4]

4.1 Introduction

Marine ecosystems worldwide are responding to human-related stressors such as commercial fisheries, climate change and pollution (Halpern et al. 2008). Effects include degradation or loss of habitat, alteration of food webs, and declines in species richness and abundance, particularly in coastal areas (Roberts and Hawkins 1999, Crain et al. 2009). The complex and synergistic nature of such changes makes it important to understand how ecosystem function and composition are affected by human activities, particularly in light of the potential ecological consequences of cumulative change, and growing public concern over ocean health.

The inshore waters of southern British Columbia and northern Washington state, collectively called the Salish Sea (Fig. 1.1; previously known as the Straits of Georgia and Juan de Fuca), have been ranked among the more disturbed coastal marine systems on Earth (mean cumulative impact score for region 19.3, highest possible 19.5; Halpern et al. 2008), and as such are targets for concerted conservation and management (Fraser et al. 2006, Gaydos et al. 2008). Species recovery and ecosystem restoration require adequate baseline data to help set conservation targets, but very few long-term population trajectories exist for individual species in this region because of poor and incomplete monitoring (Pauly et al. 1998b, Gaydos and

[4] This chapter is in preparation as a manuscript of the same title by L.K. Blight, K. Hobson (Environment Canada), and P. Arcese (UBC).

Pearson 2011). Resident species for which historical population data exist stand as potential sentinel species in such systems, particularly when fluctuations in their population size or other aspects of their biology can be linked to key ecosystem states or processes. Sentinel or indicator species are particularly appropriate "when direct measurement is impossible" (Landres et al. 1988: 323), as is the case when attempting to assess past ecosystem states or the historical status of species of conservation concern. For example, Emslie and Patterson (2007) used stable isotope analysis of eggshell fragments ($\delta^{13}C$, eggshell carbonate; $\delta^{15}N$, eggshell membrane) from archaeological and modern deposits to show that penguin diet had abruptly shifted from fish to krill in the 1700s, likely due to food web shifts resulting from wide-spread removal of whales and fur seals by industrial whaling and sealing. Norris et al. (2007) and Gutowsky et al. (2009) similarly used isotopic techniques to link population declines in marbled murrelets to declines in fish prey in their diet over more than a century.

Researchers have long recognised that seabirds can be useful indicators of changes in marine food webs (Ashmole and Ashmole 1968, Furness and Greenwood 1993, Hobson et al. 1994, Furness and Camphuysen 1997, Furness 2003, Piatt et al. 2007, Woehler 2012). As long-lived animals, marine birds integrate ecosystem changes over time yet can be slow to show signs of alterations in the environment that they are sampling (Montevecchi 1993). Conducting studies spanning multiple decades overcomes this limitation, while simultaneously providing longer-term perspectives on ecological changes. Stable isotope analysis is increasingly used to measure such long-term change (Dawson and Siegwolf 2007a) because this approach is particularly suited to specimens archived in museums or deposited at archaeological sites (Hobson and Montevecchi 1991, Ainley et al. 2006, Becker and Beissinger 2006, Emslie and Patterson 2007).

Feathers are faithful indicators of diet during feather growth (Hobson 1999) and so archived collections can be used to interpret birds' past environments, particularly when combined with population trends or dietary data (Thompson et al. 1995, Norris et al. 2007).

Holarctic *Larus* gulls occur close to human populations worldwide and have been studied in detail in many parts of their range, including the Salish Sea (Howell and Dunn 2007). Gulls in other systems have shown strong responses to the availability of food and environmental change (e.g., Mills et al. 2008), and we expected them to be a similarly tractable focal species for our study region. The glaucous-winged gull is a common, marine-associated bird that has been studied and collected by naturalists and ecologists for over 150 years (Anonymous 1908, Drent and Guiguet 1961, Hayward and Verbeek 2008, Carter and Sealy 2011). We were thus able to use archived specimens to develop and apply an approach using gulls as indicators of long-term food web change in the Salish Sea, with potential applications elsewhere (cf. Hobson 2007).

As a generalist consumer, glaucous-winged gulls should be buffered against ecological fluctuations. However, their populations in the Salish Sea are known to have undergone rapid changes during the mid-twentieth century, growing at an annual rate of 2.9% from 1960 to 1986, then declining steeply thereafter so that numbers are presently at less than 50% of their peak counts from the 1970s and 80s (Galusha et al. 1987, Vermeer and Devito 1989, Sullivan et al. 2002, Hayward and Verbeek 2008; Chapter 3). It has been hypothesised that evolving human waste management practices and changing availability of garbage drove these fluctuations (Vermeer and Devito 1989, Vermeer 1992, Hayward et al. 2010) but it is not clear that diets including garbage benefit gulls at the population level. For example, glaucous-winged gulls that

fed their chicks only natural foods (~90% fish) raised offspring that were heavier, grew faster (e.g., for 2-chick broods, mean asymptotic mass of 1014 vs. 883 g; 36 vs. 29 g d^{-1}), and fledged at a higher rate (84% vs. 68%) than those feeding chicks a diet containing garbage (Ward 1973). In the congeneric Western gull *L. occidentalis*, the most successful breeders also avoided garbage and instead fed themselves and their young with fish prey (Pierotti and Annett 1990, Annett and Pierotti 1999). Thus, empirical studies imply that if glaucous-winged gulls now feed more extensively on garbage than they did historically (i.e., if access to garbage was maintained or increased), we might expect to observe declines in reproductive performance and population size. Recent results indicate that glaucous-winged gulls in the Salish Sea have experienced a long-term decline in egg volume and clutch size, with correlative evidence implicating dietary decreases in high-quality fish foods as the most likely cause (Blight 2011; Chapter 2). Conversely, for the herring gull in Europe, Spaans (1971) found a positive relationship between amount of garbage in diet and brood size, and Pons (1992) described a decrease in reproductive output after a nearby garbage disposal site closed. Weiser and Powell (2010) similarly recorded a positive relationship between dietary garbage and reproductive success for glaucous gulls *L. hyperboreas*.

In light of these conflicting observations about how dietary change over time may affect gull populations, the objective of our study was to examine and quantify long-term dietary trends in glaucous-winged gulls to test alternative hypotheses about how population trend, diet, or environmental change have been linked in this species. Specifically, we used stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of adult and sub-adult glaucous-winged gull feathers collected from 1860 to 2009 to ask whether and how gull diets changed during the rapid period of human

population increase following European colonization, and associated industrialisation of coastal marine ecosystems in the Salish Sea.

If glaucous-winged gull population trends have been driven primarily by the availability of garbage, isotopic data should reflect an increasing dietary concentration of terrestrially-based foods as human populations grew, followed by a decline after the 1980s (i.e., $\delta^{13}C$ values declining until ~1980s, and subsequently increasing) as waste management practices improved and gull numbers declined due to decreasing access to garbage (Pons 1992, Hayward and Verbeek 2008). Alternatively, if gull populations have responded primarily to declining availability of regional forage fish (Table 4.1; Wallace 1998, Therriault et al. 2009), we expected to observe the fraction of fish prey in gull diets declining over the last 150 years, with feather isotope values showing declines in both $\delta^{13}C$ and $\delta^{15}N$ over time as birds increasingly switched to feeding on marine invertebrates and/or C_3-based garbage (see below).

We further hypothesised that availability of garbage (or reduction of fish foods in the diet) might affect sub-adult birds differently than adults, given that adult gulls are known to be more proficient foragers in the marine environment (Verbeek 1977, Searcy 1978). Because of this, and because landfills are often used more by sub-adult gulls (Weiser and Powell 2011), we predicted that $\delta^{13}C$ values would indicate a more marine (i.e., more enriched in ^{13}C) adult than sub-adult diet over time, with adult $\delta^{15}N$ values likely correspondingly enriched if adults also fed at a higher trophic level.

Interpretation of past diets via isotopic data derived over decades or centuries may be con-founded by changes to baseline environmental values (via the Suess effect, i.e., the dilution

over time of $\delta^{13}C$ measurements as a result of fossil fuel-derived carbon inputs (Gruber et al. 1999) or shifts in productivity) but such changes, if predictable, may be mathematically corrected for (e.g., Sonnerup et al. 1999). Interpretation of isotopic signatures from terrestrial food webs can be further complicated by the different carbon isotope ratios of C_3 vs. C_4 plants, with C_4 plants (here, primarily corn) more enriched in ^{13}C than the majority of plants from temperate terrestrial systems (Dawson and Siegwolf 2007b). However, we judged that C_4 isotopic signatures did not affect our results because the food industry in Canada tends to be C_3 based (cf. Hebert et al. 1999), unlike the C_4, corn-based industry in the USA (Jahren and Kraft 2008, but see Chesson et al. 2009). About 98% of our feather samples were either from birds at Canadian colonies, or from the US but collected prior to 1950. It was not until the 1950s and 1960s that the economics of increased yields from new corn hybrids meant that cheap corn was available for chicken and cattle feed in the US, facilitating the growth of corn-based industrial agriculture there (Pollan 2006).

4.2 Methods

4.2.1 Study Area

Glaucous-winged gull feather samples for stable isotope analyses came from bird skins or moulted feathers collected between 1860 and 2009 at nesting colonies in the Salish Sea, i.e., the inshore waters of the Strait of Georgia, BC, Canada, and adjacent waters of northern Puget Sound, WA, USA and the eastern Strait of Juan de Fuca (approximate range: 47.91° – 50.02° N, 121.95° – 125.24° W; Fig. 1.1). These boundaries included all large colonies from the region, but excluded the more westerly colonies where diet was likely to be partially or wholly influenced

Table 4.1: Estimated years of commencement of forage fish fisheries and population declines in the Salish Sea, Canada and USA. Population trends for species other than Pacific herring are poorly documented.

Forage fish species	Common name	Timing of species' availability	Approx. year commercial/ recreational fishery began	Year of documented or suspected decline(s)	Source
Ammodytes hexapterus	Pacific sandlance	Winter, breeding season	?	?	Therriault et al. 2009
Clupea pallasii	Pacific herring	Winter/ spring (spawning), breeding season (0+)	1890s	1960s, 2000s	Therriault et al. 2009, DFO 2008
Engraulis mordax	N. anchovy	?	1890	?	Pauly et al. 1998b, Therriault et al. 2009
Mallotus villosus	Capelin	Fall spawning	1930	1970s	Hay 1998
Osmeridae	"Smelts"	Fall, year-round?	1890	Decline uncertain	Pauly et al. 1998b, Therriault et al. 2009
Sardinops sagax	Pilchard/ sardine	?	1890s	1930s, 1960s	Pauly et al. 1998b, Wallace 1998
Thaleichthyes pacificus	Eulachon	March – May	1881	1930s, 1994	Hart & McHugh 1944, Hay 1998, Hay & McCarter 2000, Therriault et al. 2009, Moody & Pitcher 2010

by the more marine regimes of the open Pacific Ocean. Banding and satellite telemetry studies indicate that most Salish Sea glaucous-winged gulls remain in or near the region year-round and that dispersal from natal to breeding sites is local (e.g., 74 – 84% of banded first year birds were recovered or re-sighted within 200 km of their natal site, 41 – 58% within 100 km, and 100% (*n*=5) of satellite-tagged adults remained in the Georgia Basin; Pearse 1963, Butler et al. 1980, Reid 1988a; J. Elliott unpubl. data), and thus primarily represent a single oceanographic region. This assumption is important for stable isotope analysis, because baseline isotope values often vary among regions (Bond and Jones 2010, Graham et al. 2010).

4.2.2 Sample Collection And Stable Isotope Analysis – Feathers

To assess long-term changes in breeding season diet in glaucous-winged gulls we examined changes in stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios for a time series of feathers grown in and around the nesting season, a physiologically demanding period when birds must ingest foods that are energetically and nutritionally conducive to courtship, egg production and other breeding activities (Robbins 1981, Meijer and Drent 1999, Williams 2005). Once grown, feathers are metabolically inert, so their isotopic values reflect diet during the period of feather generation (Mizutani et al. 1990, Hobson 1999, but see Fox et al. 2009). In situations where consumers have access only to a C_3-based food web or to marine foods, $\delta^{13}C$ values indicate the relative proportion of marine vs. terrestrial (or intertidal) foods in the diet. Stable-nitrogen isotope values are also generally higher in marine food webs than in terrestrial ones, but $\delta^{15}N$ values also reflect the trophic level at which a bird had been feeding at the time of feather growth. Enrichment in ^{15}N is typically on the order of about 3‰ per trophic level for

vertebrates (Vanderklift and Ponsard 2003, Dawson and Siegwolf 2007b).

We sampled both wing and head feathers from birds that had resided in our study area, with most specimens taken from museum collections (see below). To examine diet of breeding adults, we selected a section (~1 x 2 cm) from the tip of the innermost primary feathers as the first of these (P1) are generally moulted from mid-April to early May (Verbeek 1979), approximately 2 – 4 weeks before the lay date of first eggs (mid- to late May; Verbeek 1986, Blight 2011). Thus, isotope ratios in P1 feathers reflected breeding birds' diet choices immediately prior to and during egg production in the previous year. Innermost primaries also had the advantage of being hidden from view in standard museum specimens, so that sampling did not alter external specimen appearance. We sampled feathers from glaucous-winged gulls at eight museums in Canada, the US and the United Kingdom (see Acknowledgements for complete list of sources). We requested samples from each decade of our 1860 – 2009 study period (except the 1870s; no specimens available), targeting P1, but accepting P2 if P1 was absent. On rare occasions when P1 and P2 were missing, we sampled P3. We also collected moulted primaries (P1, P2, and possibly P3 given appearance and timing; Verbeek 1979) from the ground in the glaucous-winged gull colony at Mandarte Island, British Columbia, Canada (48.63°N, 123.28°W) in 2008 and 2009. Moulted feathers were collected from across the colony of c. 1800 breeding pairs to minimise the chance that a single individual was sampled more than once.

Adults' brown-tipped (winter) head feathers are grown during the post-breeding moult while white (summer) head feathers are grown in late winter to early spring, about the time that

birds return to nesting areas (Hayward and Verbeek 2008; LKB pers. obs.). Head feathers are moulted at the extreme ends of the breeding season and will not entirely reflect diets from critical periods such as pre-breeding mass gain, egg production or chick rearing, but they do have the advantage of causing minimal alteration to museum specimens due to the high number of head feathers per bird. We therefore sampled a subset of winter and summer adult head feathers from the same museum birds to ask if these could be used in future as a proxy indicator of long-term diet change, e.g., by showing the same trends and isotope values as primary feathers grown during breeding. As we were also interested in long-term differences in the diet of adult and sub-adult gulls we used the above protocol to sample primary feathers from sub-adult museum specimens, but did not collect contemporary field samples for these age classes due to the absence of sub-adults on Mandarte Island during the early nesting period. Sub-adult birds moult their first primaries at a similar time of year as adults, but sub-adult head feather moult patterns can be more variable (Howell and Dunn 2007, P. Pyle, pers comm.), and thus may be a poor season-specific indicator of dietary change. For this reason we did not analyse sub-adult head feathers from museum specimens.

Feather samples were prepared for analysis by soaking for 24 h in 2:1 chloroform:methanol solution, and then rinsing in clean solution. Cleaned and rinsed feathers were air dried in a fume hood for 48 h and then were weighed and from 0.25 to 0.55 mg were loaded into tin capsules. Samples were processed at the Queen's Facility for Isotope Research, Kingston, Ontario, using a ThermoFinnigan Delta Plus XP mass spectrometer interfaced to a Costech elemental analyser for C and N isotope measurements. We ran 10% (n=27) duplication on feather samples, producing a repeatability of within <0.25‰ for $\delta^{13}C$ and <0.25‰ for $\delta^{15}N$.

During analysis, we ran standards NBS-21 graphite for $\delta^{13}C$ and NIST 8548 and NIST 8550 for $\delta^{15}N$, along with an in-house standard, chicken blood (CK-1), for both $\delta^{13}C$ and $\delta^{15}N$. Within-run error (SD) associated with in-house standards was ±0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$. Stable-carbon isotope values are reported relative to Vienna Pee Dee Belemnite (VPDB) and $\delta^{15}N$ values relative to (atmospheric) Air.

4.2.3 Sample Collection and Stable Isotope Analysis – Fish

To determine whether baseline environmental values had changed and thus affected feather $\delta^{13}C$ or $\delta^{15}N$ values over time, we sampled and analysed lateral muscle tissues from forage fishes collected in the Salish Sea from 1917 – 1960. Fish were collected by earlier researchers using largely unknown methods, and deposited in the year of their collection at the Beaty Biodiversity Museum of the University of British Columbia. All specimens were initially preserved for one week in buffered formalin, then stored at the museum in isopropanol (E. Taylor, pers. comm.). Preservation techniques may deplete ^{13}C and ^{15}N values in animal tissues (Hobson et al. 1997, Arrington and Winemiller 2002, Edwards et al. 2002), but we were interested in the relative rather than the absolute values of fish tissues and assumed that any depletion that occurred would have taken place for all samples, not affecting comparability.

Collection locations were in the centre of the study area, in the vicinity of Vancouver and Nanaimo, Canada (49.28º N, 123.12º W, and 49.14º N, 123.95º W, respectively). Forage fish species (Pacific herring, Pacific sandlance and eulachon) were selected based on our own and published observations of forage fishes in modern and historical glaucous-winged gull diets (Hart and McHugh 1944, Ward 1973, Verbeek 1979, Vermeer 1983, Davis in prep; LKB pers.

obs.). Fish were sampled from the full range of decades represented in the museum's collection, with our sample size per species limited by the number and size of specimens available. We sampled only small fish (range: 43 to 97 mm in length) of the same approximate size as those currently consumed by glaucous-winged gulls (LKB pers. obs.). Fish tissue was prepared for isotope analysis by freeze-drying for 3d and then grinding each dried sample using individual capsules inside an amalgamator. As lipid extraction may affect $\delta^{15}N$ of processed tissues, and as we were interested in fishes' relative stable isotope values over time rather than in their absolute values, we elected not to include lipid extraction as part of the sample preparation process. Instead we used the C:N ratios of analysed samples to assess whether their lipid content was high and/or variable, and thus whether to correct fish $\delta^{13}C$ values for lipid effects (Post et al. 2007). Pulverised tissues were weighed (0.40 – 0.55 mg) and loaded into tin capsules and processed in the same way as feather samples, above, using tilapia (TIL-06-01) as the in-house standard. Repeatability and standards were otherwise the same as for feathers.

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

4.2.4 Statistical Analyses

To assess temporal trends in feather isotope ratios of sub-adult and adult gulls, we conducted linear regressions on the time series of $\delta^{13}C$ and $\delta^{15}N$ values of primary and head feathers. Given our prediction that a gull population driven primarily by garbage would show a pattern of

increasing terrestrial foods in diet, followed by a decrease in the 1980s, we also tested for quadratic trends in the stable-carbon isotope data from sub-adult and adult primary feathers. In marine systems, $\delta^{13}C$ vs. $\delta^{15}N$ values are typically correlated, but this relationship can break down when birds forage across biomes (Hobson and Welch 1992), or when carbon is derived from lipids and carbohydrates in addition to protein. We therefore regressed feather values of $\delta^{13}C$ on $\delta^{15}N$ to assess the relationship between these two isotopes. Given our prediction that sub-adults would be more dependent on garbage, we expected stronger coupling between the two isotopes for adults than for sub-adults, i.e., the relationship might break down with access to garbage. We used analysis of variance to test for differences among mean $\delta^{13}C$ and $\delta^{15}N$ values of each feather type (adult brown-tipped head feathers, adult white-tipped head feathers, adult primary feathers, sub-adult primary feathers). Post-hoc pairwise comparisons used Tukey-Kramer HSD tests.

We pooled isotope values for forage fishes and used the same linear modelling approach as above to assess temporal trends in $\delta^{13}C$ (herring and sandlance only; eulachon excluded due to high C:N ratios; see Results) and $\delta^{15}N$ (herring, sandlance, eulachon) values of fish muscle tissues. To assess isotopic trends in forage fish to the present day, we performed additional tests using the same model and stable-isotope data derived from non-preserved muscle tissue of forage fish collected at Mandarte Island in 2010 (regurgitated whole or near-whole fish from adult gulls; M. Davis, unpubl. data). As preservation techniques may or may not affect tissue $\delta^{13}C$ values in fish (Arrington and Winemiller 2002, Edwards et al. 2002) we did not assume modern (2011) samples were directly comparable with preserved museum specimens, and so did not pool them. We also used linear regression on C:N ratios to test for any temporal trends

in lipids in forage fish tissue (herring and sandlance only).

4.3 Results

4.3.1 Feather Samples

We analysed 270 feather samples from 216 glaucous-winged gulls collected over 150 y, from 1860 to 2009. Of these 216 birds, 194 (90%) were held in museum collections with the remainder represented by feathers collected in the field. In total, 138 feathers were adult primaries, 55 adult head feathers, and 77 sub-adult primaries, with an average of 11 adult primary feathers per decade (with the exception of the years from 1860 – 1899, when only 10 specimens were available). With one exception, analyses of $\delta^{13}C$ and $\delta^{15}N$ values showed declines over time for all feather types sampled (Table 4.2). In adult primaries, $\delta^{13}C$ values declined ~2.25‰ since 1860, i.e., they became more negative over time, indicating that the average diet of breeding birds has become less marine over the study period (Fig. 4.1A). Values of $\delta^{15}N$ in adult primary feathers also decreased, dropping ~3.75‰ from 1860 – 2009 (Fig. 4.1B). Feather $\delta^{13}C$ and $\delta^{15}N$ values for primaries of sub-adult birds showed similar trends (Figs. 4.1C & D). For adult winter head feathers, $\delta^{13}C$ values showed a non-significant decline over time, with the lack of significance probably due to sample size given that the estimated magnitude of decline was similar to that of other datasets (Table 4.2). We tested for a quadratic trend in $\delta^{13}C$ values for both sub-adult and adult primaries but were unable to fit a squared term, indicating no evidence for a curvilinear trend with respect to year.

Comparing isotopic values by feather type and specimen age-class revealed a slight but non-significant difference in mean $\delta^{13}C$ values between sub-adult and adult primaries, with sub-

adult values nominally showing a tendency toward a less marine signal (–15.36 ± –0.18‰ (sub-adult) vs. –14.92 ± –0.13‰ (adult); F=1.32, p=0.26) and the lowest mean value among all four feather types. For $\delta^{15}N$, the only among-group difference detected was between adult primaries and adult white head feathers (i.e., those grown just prior to breeding; 16.01 ± 0.14‰ vs. 15.04 ± 0.31‰; F=2.58, p=0.04). Regressing $\delta^{13}C$ on $\delta^{15}N$ revealed statistically significant relationships for all feather types. As predicted, however, $\delta^{13}C$ and $\delta^{15}N$ values were less strongly related in the breeding season diet of sub-adult birds (R^2=0.24) than in adult birds (R^2=0.41; primary feathers only).

Table 4.2: Trends in glaucous-winged gull feather $\delta^{13}C$ and $\delta^{15}N$, based on linear regression for all feather types.

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

4.3.2 Fish Samples

We obtained 37 tissue samples from forage fish collected from 1917 – 1960 (eulachon, n=7; herring, n=16; sandlance, n=14). The C:N ratios for eulachon samples were high (mean 7.8 ± 2.4 SD), indicating an elevated tissue lipid content and resulting effects on $\delta^{13}C$ values (Post et al.

2007), so we excluded these data from further analysis of $\delta^{13}C$ trends. C:N ratios of herring and sandlance were relatively low, and not variable (range 3.4 – 4.4); thus we assumed no effect of lipid content on reported $\delta^{13}C$ values for these two species, and did not mathematically correct them (as per Post et al. 2007). Unlike gull feathers, the pooled $\delta^{13}C$ and $\delta^{15}N$ values of forage fish muscle tissues showed no trend over the time period covered by preserved specimens (i.e., 1917 – 1960; $\delta^{13}C$: F=0.01, p=0.94; $\delta^{15}N$: F=0.00, p=0.99; Figs. 4.2A & B), indicating similar levels of ecosystem productivity over this portion of our study period. When analyses included stable isotope data from forage fish collected at Mandarte Island in 2010 (M. Davis, unpubl. data; n=14, sandlance and herring; C:N ratios 3.3 – 3.9), fish $\delta^{13}C$ values became less negative over time, increasing at a rate of 0.01‰ per annum (F=5.15, p=0.03). This trend is opposite to that predicted were the Suess effect altering regional stable-carbon isotope values. With the addition of these modern data, forage fish $\delta^{15}N$ values also showed a positive but non-significant trend over time (F=2.44, p=0.12). Thus, for the period 1917 – 2011, fish stable isotopes showed a trend opposite to that of feathers (if values of unpreserved fish were comparable with those of preserved ones). While all C:N ratios for herring and sandlance indicated that tissue lipid levels were not high enough to affect $\delta^{13}C$ values of preserved fish (Post et al. 2007), these ratios nonetheless declined from 1917 to 1960 (F=10.33, p<0.01). The same trend was apparent with the inclusion of 2011 data from non-preserved fish (F=58.51, p<0.0001).

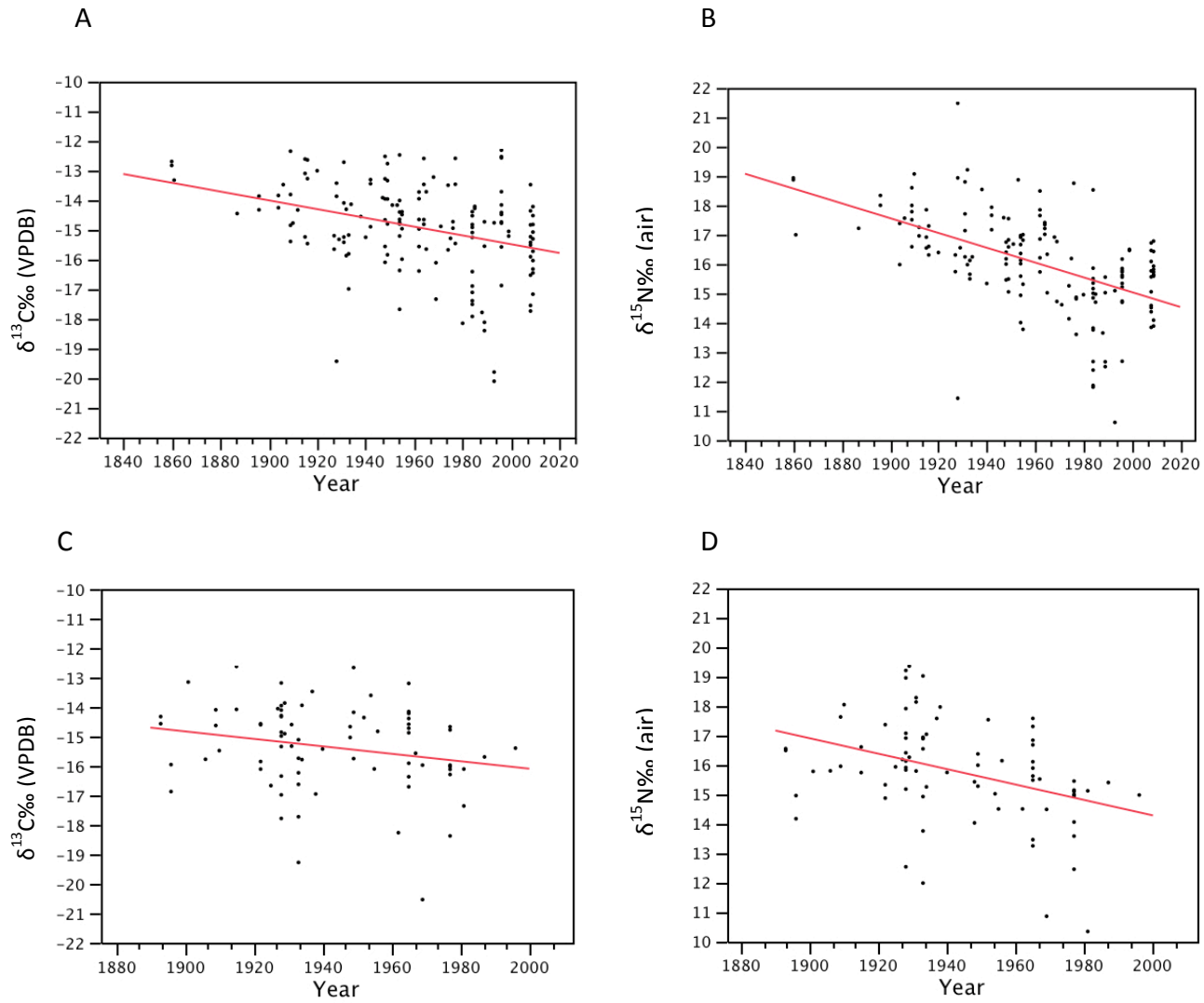

Figure 4.1: $\delta^{13}C$ and $\delta^{15}N$ of feathers from glaucous-winged gulls, 1860 – 2009 (adults) and 1893 – 2008 (sub-adults), Salish Sea region (SW British Columbia, Canada and NW Washington, USA), with $\delta^{15}N$ being the samples' ratio of $^{15}N/^{14}N$ relative to atmospheric air ("air" in y-axis label) and $\delta^{13}C$ being the samples' ratio of $^{13}C/^{12}C$ relative to Vienna Pee Dee Belemnite ("VPDB" in y-axis label). (A) $\delta^{13}C$, adult primary feathers; (B) $\delta^{15}N$, adult primary feathers; (C) $\delta^{13}C$, sub-adult primary feathers; (D) $\delta^{15}N$, sub-adult primary feathers. Note different scales for x-axes.

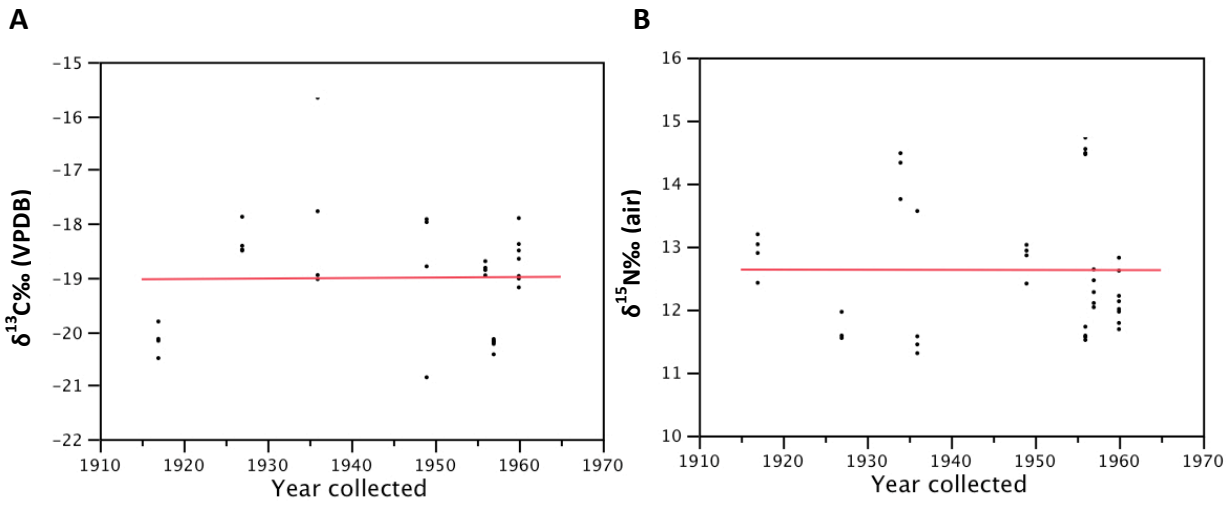

Figure 4.2: Trends in stable isotope values of preserved forage fish over time. Stable isotope analysis of preserved forage fish tissues indicate there was no change in baseline environmental values during the sampled time period (1917-1960). (A) δ13C (herring, sandlance); and (B) $\delta^{15}N$ (herring, sandlance, eulachon) of muscle tissue from forage fishes collected 1917-1960, Salish Sea region (SW British Columbia, Canada and NW Washington, USA), with $\delta^{15}N$ being the samples' ratio of $^{15}N/^{14}N$ relative to atmospheric air ("air" in y-axis label) and $\delta^{13}C$ being the samples' ratio of $^{13}C/^{12}C$ relative to Vienna Pee Dee Belemnite ("VPDB" in y-axis label).

4.4 Discussion

We found significant declines in both $\delta^{13}C$ and $\delta^{15}N$ values in gull primary and head feathers over our 150-year study period, indicating that the diets of glaucous-winged gulls in the Salish Sea have changed in both the degree of marine contribution and in trophic level over time. Because declines occurred in all feather types – adult primaries, sub-adult primaries, and adult summer and winter head feathers – our results imply that similar dietary changes occurred in all age classes, and that the shift occurred across seasons. Our interpretation of a dietary shift was supported by the invariant isotopic data from a time series of museum-archived forage fish (1917 – 1960); together, these two datasets, fish and gull, provide powerful parallel evidence

that gull diets actually changed over time, rather than that feather isotopes reflected a baseline environmental change over time. With the inclusion of contemporary stable isotope values from non-preserved fish caught in 2011, forage fish $\delta^{13}C$ and $\delta^{15}N$ became more positive over the study period, in contrast to the trend in feather values. This means that if preservation techniques did not alter fish values, the relative change in gull feather values over time was even greater than that described by our analyses.

The changes in gull feather $\delta^{13}C$ and $\delta^{15}N$ that we have documented here are similar to those described for the marbled murrelet, another coastal fish-eating seabird in the study region. Adult murrelets sampled during the pre-breeding period (~Mar – Apr) in the Georgia Basin also showed declines in feather $\delta^{15}N$ values over the 107 year period from 1889 – 1996, as did juvenile marbled murrelets sampled between 1854 and 2008, with both declines being attributed to long-term declines in the fraction of forage fish included in diets (Norris et al. 2007, Gutowsky et al. 2009). Similar patterns have also been reported for marbled murrelets in California (Becker and Beissinger 2006). Herring gulls in the Great Lakes region and greater black-backed gulls *L. marinus* in the Atlantic have also exhibited isotopic changes indicative of declines in trophic position as they tracked decreasing abundance of forage fish over time (Hebert et al. 2008, Farmer and Leonard 2011). Our results thus suggest that gulls are representative of at least one other species in the coastal northeast Pacific, and may be indicators of long-term, broad scale changes in food web composition. Our forage fish $\delta^{13}C$ values did not show the incrementally declining baseline environmental $\delta^{13}C$ values predicted by the Suess effect (i.e., declining ^{13}C values due to increases in fossil fuel burning and

deposition), indicating that during the period sampled at least, conditions in the Salish Sea meant this effect was not detectable.

The observed decline in feather stable-carbon isotopic values over time differed from the dome-shaped trend we predicted had glaucous-winged gulls tracked an increase and then a decrease in availability of garbage. Instead, the gradual declines in apparent trophic level and marine origins of diets for both sub-adult and adult gulls were more consistent with our predicted trend had glaucous-winged gulls eaten less forage fish prey over time. Whether this suggests a gradual shift to a more garbage-based diet (rather than a dietary increase in garbage, followed by a decrease) is unclear because declines in feather $\delta^{15}N$ and $\delta^{13}C$ values might also be expected with increases in intertidal invertebrates in the diet, alone or in addition to garbage. Terrestrial food webs tend to be depleted in ^{15}N relative to marine ones so that an across-biome switch could appear as a trophic decline, but agricultural systems (and hence human food waste) are generally enriched due to fertiliser input (Hobson 2007), meaning that a switch from a diet of fish to one of garbage could be less likely to show as declining $\delta^{15}N$ values.

Interestingly, the mean $\delta^{13}C$ value for primaries of adult birds collected in the 1860s (n=3, **–**12.9 ± 0.3‰ [SD]) was similar to that of ancient bone collagen from glaucous-winged gulls (~2 – 4 K yrs-old) collected from local middens (n=3, **–**13.6 ± 1.0‰; t_1=1.15, p=0.3; (Hobson 1987); adult gulls' $\delta^{13}C$ only began to shift from these apparently "ancient" values as of the late 1800s (see Fig. 4.2). Isotopic discrimination factors are different for collagen and feathers, making a direct comparison problematic. Nonetheless, these values all indicate an overwhelmingly marine diet and suggest that gulls maintained such a diet in the Salish Sea for millennia (with a

marine endpoint of –13‰ identified for bone collagen of marine consumers at these latitudes; Hobson 1987), but began to transition to a less marine diet about the time that commercial forage fish extraction commenced in the region (1880s – 1890s; Pauly et al. 1998b, Wallace 1998). Emslie and Patterson (2007) described a similar trend of sudden dietary change following commercial harvesting of marine resources – their stable isotope analysis of eggshell remains indicated that Adélie penguin diet had remained stable for thousands of years, but then switched to a lower trophic level around the time that industrial whaling and sealing commenced in Antarctica.

Little is known about long-term population trends of forage fishes that are not commercially exploited in the Salish Sea, or for those commercially fished prior to 1950 but now rare in or absent from the system (Hay 1998, Wallace 1998, Moody and Pitcher 2010; Table 4.1). However, it is quite possible that forage fishes that are now scarce or absent from the Salish Sea (e.g., pilchard *Sardinops sagax*, capelin *Mallotus villosus*) were once ecologically important in the region. Eulachon, for example, may have the highest lipid content of any marine fish species (range 15 – >50%; Payne et al. 1999, Anthony et al. 2000, Iverson et al. 2002, COSEWIC 2011), with tissue lipid levels tending to be an order of magnitude higher than in other forage fishes (Payne et al. 1999, Anthony et al. 2000, Iverson et al. 2002). Based on their C:N ratios, mean lipid levels of the locally-caught eulachon we analysed were in excess of 33% (Post et al. 2007). This species once provided gulls with high-quality food early in the breeding season: earlier researchers reported that glaucous-winged gulls fed “extensively” on eulachon in the pre-laying period (Hart and McHugh 1944, Verbeek 1979) but they not do so any longer. Commercial catches of Georgia Basin eulachon peaked in the 1950s and ‘60s (max. annual catch

~350 t; Moody and Pitcher 2010) and the population reached a historic low in 2008, with the 10-year decline rate estimated to be 98% by 2011 (COSEWIC 2011). Salish Sea and other Pacific eulachon populations have recently been listed as Endangered (Canada; COSEWIC 2011) or Threatened (US; NOAA 2010). Herring and sandlance are currently the primary fish prey of breeding glaucous-winged gulls (Ward 1973, Vermeer 1983, Davis in prep; LKB pers. obs), and trends in the C:N ratios of herring and sandlance tissues we assayed suggest that lipid levels in these two species may also have declined in the region over time. The near-extirpation of eulachon from the system, the decline and extirpation of herring and capelin, respectively, and possible decline in lipid content in currently important forage fish are all consistent with our suggestion that glaucous winged-gulls in the study area may be eating a nutritionally inferior diet compared to their ancestors. A decline in forage fish quality (i.e., reduction in size-at-age and/or lipid content of a favoured prey species) has been documented in the Salish Sea and elsewhere (Wanless et al. 2004, Therriault et al. 2009) and implicated in short-term seabird productivity fluctuations, with poor food availability for fish a likely cause (Wanless et al. 2005, Frederiksen et al. 2007). However, isotopic techniques have not yet been used to describe this phenomenon over historical time periods, and we suggest such long-term declines in food quality could be investigated further, in our study system and elsewhere.

Quantities of the forage fishes currently favoured by glaucous-winged gulls also appear to have declined over the study period. Pacific herring stocks crashed in the early 1960s and despite evidence of recovery in the region in subsequent decades (DFO 2008), their spawning aggregations have contracted substantially in time and space since approximately 1970, and now are probably much less available to seabird predators than when they spawned in higher

numbers and at more sites (Stick and Lindquist 2009, Therriault et al. 2009). Other seasonal sources of fish foods, such as roe and dead fish from spawning salmon runs in fall and winter, have also declined in their availability to gulls (Jewett et al. 1953, Hayward and Verbeek 2008). Fisheries discards have played an important role in *Larus* gull population dynamics elsewhere (Oro et al. 2004) and although discards occurred rarely in the diets of glaucous-winged gulls in the Salish Sea in the latter half of the 1900s (Ward 1973, Vermeer 1982, Vermeer 1983), they may have been more available historically. By 1930, BC fisheries were extracting more biomass than at any time after 1970 (Wallace 1998), and Salish Sea gulls presumably availed themselves of these resources at times when fisheries discards were high. Thus, our $\delta^{13}C$ and $\delta^{15}N$ data likely reflect a general loss of fish (salmon, fish offal, forage fish) from diet over time, and across seasons.

Mean stable isotope values provided only equivocal support for our prediction that the diet of sub-adult birds would be less marine than that of adults. Mean $\delta^{13}C$ of sub-adult primary feathers was slightly but not significantly depleted compared to that of breeding adults. We also found no difference in mean $\delta^{15}N$ of sub-adult vs. adult primaries, a difference that we predicted if sub-adults were feeding on a greater proportion of terrestrially-based foods (as seen in glaucous gulls; Weiser and Powell 2011). However, because modern agricultural food webs are typically enriched in ^{15}N (Hobson 2007) our ability to discriminate in detail between a marine versus a terrestrial, garbage-based diet may be limited when considering only $\delta^{13}C$ and $\delta^{15}N$ analyses (with ^{34}S potentially serving as an additional source indicator; Michener and Kaufman 2007). In contrast, the correlation between $\delta^{13}C$ and $\delta^{15}N$ values was stronger in adult than sub-adult gulls, supporting our prediction that sub-adults forage more frequently outside

the marine biome. Given the wider-ranging nature and broader food preferences of sub-adult gulls in general (Butler et al. 1980, Weiser and Powell 2011), it is likely that our results did reflect a real (albeit relatively slight) dietary difference between the two age classes. However, more detailed analyses or additional isotopes would be needed to fully characterize any differences in sub-adult and adult diets over time.

Differences in mean $\delta^{15}N$ values of adult summer head feather and adult primaries suggest that adult birds experienced a small but discernible downward trophic shift in the pre-breeding season, possibly due to being constrained by their proximity to the colony when courting and defending territories, or perhaps because egg-laying females require specific nutrients (Christians 2002) that may be provided by invertebrate prey. In contrast, similar mean isotopic values between adult primaries and winter head feathers (i.e., those grown around the end of the breeding season) suggest that adult glaucous-winged gulls tended to feed at similar trophic levels both during and immediately after breeding. Taken together, these comparisons suggest a slight difference in adult feeding habits between the pre- and early breeding period, and a potentially greater reliance on terrestrial or intertidal foods by sub-adult birds. Given the similarity between gulls' winter head feathers and primaries, the former could be a reasonable substitute for primaries in assessing historical gull diets as head feather sampling causes less obvious alteration to museum specimens.

Considering several lines of evidence, it is likely that dietary change has contributed to recent glaucous-winged gull population declines. Feathers sampled in our study integrated foods that were consumed early in the breeding season, a period when nesting gulls require high-protein

food to enhance body condition and facilitate egg production (Houston et al. 1983, Bolton et al. 1992, Bolton et al. 1993). This, and the apparent sequential loss of forage fishes from the Salish Sea during the twentieth and early twenty-first century (Table 4.1), all suggest that glaucous-winged gulls have been affected by declining access to fish prey. Though decreasing levels of high-quality food prior to the 1970s or '80s presumably did not facilitate the study population's increase phase during that period, those increases may be explained by release from human egging and persecution following the enactment of the 1916 Migratory Birds Convention, even taking into account gradually declining productivity by breeding gulls (Chapters 2 and 3; Reid 1988b, Blight 2011). Overall, the decline in gull feather $\delta^{13}C$ and $\delta^{15}N$ across age classes and time of year points to an ongoing change in the diet of glaucous-winged gulls in the Salish Sea.

4.5 Conclusions

Stable isotope analysis of feathers collected and archived over 150 years demonstrated plausible links among anthropogenic environmental change (specifically, forage fish population declines), diet, and population change in a generalist, mid-trophic predator living in an inshore sea heavily affected by human activity (Halpern et al. 2008, Johannessen and Macdonald 2009). Though we did not quantitatively correlate diet change with population trends, these results are suggestive of a species responding to ongoing environmental change or food web shifts. This isotopic study of glaucous-winged gulls in the Salish Sea highlighted long-term dietary trends similar to those documented for the marbled murrelet, another fish-eating bird whose population numbers have shown decreases region-wide (Bower 2009). Gulls and other birds collected for museums over long time periods thus have the potential to be useful sentinels for

the incremental or inter-generational ecological changes that tend to go unnoticed (cf. Pauly 1995, Hobson 2007). Population declines since the 1970s have also recently been documented for a number of other waterbird species in the Salish Sea, several of which are piscivores (Chatwin et al. 2002, Anderson et al. 2009b, Bower 2009). Causes of species declines and loss are complex, and while factors additional to the ones we identify here have presumably contributed to observed trends, we suggest that changes in diet have been important. The dietary trends identified here may assist in determining a subset of the factors that are contributing to waterbird declines, and the long-term approach we employed may also be useful for shedding light on similar changes occurring in coastal marine systems elsewhere.

4.6 Acknowledgements

The following museums and their curators provided us with feather samples: Royal British Columbia Museum, Victoria (Mike McNall and Gavin Hanke); Cowan Museum (now Beaty Biodiversity Museum, UBC; Rex Kenner); Conner Vertebrate Museum, Washington State University (Kelly Cassidy); Santa Barbara Museum of Natural History (Krista Fahy); Royal Ontario Museum, Toronto (Allan Baker, Mark Peck); Canadian Museum of Nature, Ottawa (Michel Gosselin); Burke Museum, University of Washington (Rob Faucett); Slater Museum, University of Puget Sound (Gary Shugart); University Museum of Zoology, Cambridge (Michael Brooke). Eric (Rick) Taylor facilitated sampling of archived fish tissues from the Beaty Biodiversity Museum, UBC.

Lab facilities and assistance: Kerry Klassen, April Vuletich and Kurt Kyser (Queen's Facility for Isotope Research) analysed feather samples and advised on sample prep. Alice Chang, Xanti

Larrañaga, and Gerald Singh provided advice on sample prep and mass spec use, and Tella Osler assisted with the preparation itself. John Richardson and Rob Guy provided lab facilities for feather and fish tissue sample preparation. Mikaela Davis (Simon Fraser University) generously shared her fish stable isotope data, and Craig Hebert (Environment Canada) provided unpublished data on stable isotope values of domestic animals. Comments by David Ainley and Kathy Martin improved the manuscript.

Chapter 5: Conclusion

> *[C]itizens…have reason to be proud of the gull homes in their State, and it is a civic obligation to care for and preserve them. One of the first duties of the patriotic citizen is to carefully conserve the natural objects in his locality; any one* [sic] *who would destroy them, especially for commercial purposes, is lacking in that uplifting sentiment that develops in man or woman a respect for the rights of others, and a love of country and fireside. The writer who commands and wields the most facile pen cannot fully describe the life or beauty of one of the great breeding homes of these gulls, nor can the most accurate photograph convey to the reader more than a faint picture of the bright blue sky, the sparkling sea, the graceful motion of the birds circling overhead; nor can it add the roar of the surf on the rocky shore, nor the weird and angry cries and screams of the anxious gulls.* (Dutcher & Baily, 1903, A Contribution to the Life History of the Herring Gull in the United States)

William Dutcher and William Baily wrote this call to protect the herring gull in eastern North America at a time when waterbirds and shorebirds were being systematically hunted and persecuted across the continent. The millinery industry took a tremendous toll on wild birds – up to 200 million per year (Weidensaul 2007) – and egging was carried out for personal consumption as well as commercial trade (Dawson and Bowles 1909, Pearse 1923, Pearse 1963, Doughty 1971, US Fish & Wildlife Service 2012). On weekends, shooting parties travelled to seabird colonies such as Three Arch Rocks, Oregon, where they used the birds for target practice (US Fish & Wildlife Service 2012). Early Audubon societies formed largely in response to the resulting decline in hunted species (Weidensaul 2007). Due to efforts of their members and other conservationists, the Migratory Bird Convention (Migratory Bird Treaty in the USA)

was signed in 1916 by Canada and the US, and subsequently passed into legislation. It was in this milieu that naturalists and biologists began to study and census glaucous-winged gull colonies in the vicinity of the growing cities of coastal British Columbia and Washington, providing the early data that I used in my study.

For my dissertation research I used these and more recent data, as well as archived museum specimens collected up to 150 years ago, to investigate long-term trends in diet, population numbers, and breeding biology of the glaucous-winged gull, a generalist mesopredator breeding in Pacific coastal waters. To go beyond simply extracting disparate pieces of information, studies in historical ecology (i.e., those addressing questions spanning multiple generations of researchers) must find analytical approaches that can produce robust and relevant outcomes (Ferretti et al. in prep.). I used a combination of meta-analysis, statistical modeling, and stable isotope techniques to assess multiple sources of data and ask how glaucous-winged gull population size, egg production, and diet have changed over time. Each of my chapters addressed one or more of these topics, with combined analytical methods allowing me to disentangle how multiple factors might have affected long-term population change. In this chapter I summarise the results, then provide some general conclusions drawn from the study as a whole. I also address the limitations of my research, suggest future approaches, and provide some management recommendations based on the key outcomes of my study.

5.1 Chapter 2

In Chapter 2, I reviewed the literature on egg and clutch size in gulls and other seabirds and asked whether these traits, along with lay date, had changed over time in my study species.

Birds should alter reproductive traits and phenology in response to food web shifts, with populations or individuals tracking environmental change over time (Grémillet and Charmantier 2010, Cury et al. 2011, Lewis et al. 2012). To assess any changes in the reproductive parameters I measured, I used meta-analysis to compare historical and modern data and showed that egg and clutch size had both declined, with eggs about 5% smaller than a century ago and mean clutch size tending toward two eggs. This smaller clutch contrasts with the modal clutch size of three demonstrated by large-bodied *Larus* gulls worldwide. Glaucous-winged gulls also showed a delayed lay date over time. Many studies have found a relationship between avian lay date and climate proxies such as sea surface temperature (Crick 2004, Møller et al. 2010) but I did not find this relationship in my study.

Based on the nutritional requirements of gulls prior to and during egg formation, the most plausible interpretation for the declines demonstrated here was that birds were increasingly food-limited around the period of egg formation. It is well demonstrated that nutritionally substandard foods compromise egg production in *Larus* gulls (Hiom et al. 1991, Annett and Pierotti 1999, and other references listed in Chapter 2). Thus, in Chapter 2 I inferred that the long-term changes I found in egg output for Salish Sea glaucous-winged gulls indicated a decline in forage fish availability over the study period. These changes in clutch size were incorporated into the demographic modelling employed in Chapter 3, while the hypothesis of declining forage fish in gull diet was further examined via stable isotope analysis in Chapter 4.

5.2 Chapter 3

The objectives of this chapter were to use 100+ y of compiled population count data to model population trends, and then to use demographic modelling to test potentially competing hypotheses explaining the causes of these trends. This element of my study was carried out in the Canadian portion of the Salish Sea (the Georgia Basin). The modelled population trend showed that glaucous-winged gull numbers there have changed dramatically over the last 111 years, increasing rapidly until the 1970s and then decreasing again through to the present.

Given the limited demographic data available for sub-adult and adult glaucous-winged gulls over the multi-decadal study period, the demographic models were largely heuristic in nature. They nonetheless provided useful insights into ways in which my study system may have functioned over time: invoking initial population suppression by egging in combination with long-term declines in clutch size and productivity were sufficient to explain the modelled population trends. It is likely that in the early part of the twentieth century, glaucous-winged gull numbers were not “at baseline” but were instead maintained at low numbers by human persecution. Once egging ceased, they grew as a result of (assumed) constant rates of sub-adult and adult survival. The cumulative effects of decreasing productivity from 1900 on (declining clutch size, modelled from data compiled for Chapter 2; declines in reproductive success, also modelled from historical and contemporary data; and decreasing first year survival) resulted in a population that eventually ceased to grow and began to decline in number. Results did not rule out effects of garbage on population trends (e.g., on maintaining sub-adult survival during the increase phase), but rates of modelled clutch size and reproductive success declines were

more consistent with a factor that had acted consistently from 1900 onward (e.g., overfishing) rather than one that fluctuated in intensity over time (garbage). Demographic models also provided limited support for the conclusion that recovering populations of bald eagles may have negatively affected gull numbers, as they have with other seabird species in the study area, elsewhere in North American, and in Europe (Hipfner et al. 2012).

Formally testing whether the glaucous-winged gull population decline has been caused by emigration rather that by an actual loss of breeding birds (cf. Beissinger et al. 2006) was beyond the scope of my study, but published and unpublished data from adjacent regions in Canada and the US show declining or stable populations of glaucous-winged gulls (Parks Canada 2009, Hayward et al. 2010), meaning that emigration is an unlikely explanation for observed Georgia Basin trends.

5.3 Chapter 4

Given competing hypotheses on how changing availability of garbage and/or forage fish might have limited Salish Sea glaucous-winged gull populations (Chapters 2 and 3), in Chapter 4 I used stable isotope analysis to assess gull dietary changes over the last 150 years. Museum specimens provided a time series of feathers from 1860 to 1999, and were complemented by feathers I collected in the field in 2008 and 2009. Results of this isotopic study (overall declines in feather $\delta^{13}C$ and $\delta^{15}N$ over time, for sub-adults and adults, and across all seasons sampled) showed that glaucous-winged gulls have undergone long-term dietary changes. These gull diet trends are similar to those documented for the marbled murrelet, another fish-eating bird that

has experienced population declines in the Salish Sea and further afield (Becker and Beissinger 2006, Norris et al. 2007, Bower 2009).

Stable isotope results show that glaucous-winged gulls are now eating a less marine diet than they were historically, but it is not clear whether they have switched to a more terrestrial (garbage-based) or to an intertidal (invertebrate-based) diet. For bird species that forage in both marine and non-marine biomes (primarily gulls and terns, but also some migrating anatids and shorebirds; Hobson 1999, Braune et al. 2005, Evans-Ogden et al. 2007) the use of a third stable isotope, ^{34}S, can serve as a source indicator when a combination of stable-carbon and stable-nitrogen isotopes provide ambiguous results (Michener and Kaufman 2007). Conducting this analysis for the feathers I collected for my study would provide a more detailed picture of the nature of glaucous-winged gull diet change.

It is now commonplace to correct for the Suess effect in stable isotope studies of marine food web change (something that proved unnecessary in my study). However, few isotopic studies have incorporated an additional level of stable isotope analysis to measure potentially significant changes to baseline environmental productivity (Bond and Jones 2009). I addressed this by sampling a time series of forage fish muscle tissue from specimens collected in the study area from 1917 – 1960, and subjecting these samples to their own stable isotope analysis. This was a powerful metric that allowed me to rule out the possibility that declining feather values were merely reflecting a long-term change to primary productivity (discussed in Hobson 2007), as was the case in an isotopic study of the rockhopper penguin *Eudyptes chrysocome*. There, declining $\delta^{13}C$ values from 1861 to the present were shown to reflect baseline changes to the

phytoplankton community rather than a shift in dietary items over time (Hilton et al. 2006). Also novel was my use of C:N ratios from stable isotope analysis to examine changes in forage fish quality (lipid levels) over time; this approach may prove useful in quantifying and assessing causes of food web change elsewhere.

Stable isotope analysis of feathers from museum specimens has recently emerged as a useful approach to quantifying dietary change in marine birds over centennial scales or longer (Thompson et al. 1995, Norris et al. 2007, Farmer and Leonard 2011), and my study adds to this growing body of literature. Gulls and other birds collected for museums over long time periods have the potential to be useful sentinels for the type of incremental ecological changes that tend to go unnoticed by biologists (cf. Pauly 1995). Using this isotopic approach on other waterbird species in decline in the Salish Sea (Anderson et al. 2009b, Bower 2009, Crewe et al. 2010) could help to determine if their population trends are similarly related to long-term dietary change, as is currently hypothesised about forage fish loss (SeaDoc Society 2011).

5.4 General Conclusions

Several general conclusions may be drawn from this study. Taken together, my results did not rule out the influence of garbage or eagle predation on Salish Sea glaucous-winged gulls over the last century or more, but they did suggest that an additional factor has had a larger overall influence on population growth during the population decline phase. This includes the declines in availability, and perhaps the nutritional value, of the fish prey that are likely to be essential to maximise successful reproduction in glaucous-winged gulls. Long-term declines in egg and clutch size (Chapter 2; results spanning 108 and 48 years, respectively), delayed lay date

(Chapter 2), and stable isotope analysis showing a gradual decrease in the marine contribution, trophic level and possibly lipid content of gull diet since 1860 (Chapter 4; 150 years' of data) together provide strong evidence that diets changed for these birds over the last century or more, and hint at changes to regional food webs.

These results are perhaps not surprising; a relationship between loss of fish prey and decreased productivity is well documented in marine birds (Cury et al. 2011) and other piscivorous top- and mesopredators (Ainley et al. 2007, Ainley and Blight 2009, Cury et al. 2011). Gulls, however, are extreme generalists among seabirds and are often thought to be buffered against changes in food abundance more than other marine birds (Pierotti and Annett 1990). Generalist foragers are successful precisely because of their ability to exploit redundant resources: they can prey-switch among dietary items, providing a mechanism for buffering against periodic food scarcity (Folke et al. 2004, Layman et al. 2007). Directly measuring ecological resilience (i.e., "the extent to which ecosystems can absorb recurrent natural and human perturbations and continue to regenerate without slowly degrading"; Hughes et al. 2005: 380) and its limits may not currently be possible (cf. Thrush et al. 2009), and this was not one of the goals of my research. However, my results point to reduced redundancy in Salish Sea food webs via forage fish population changes, and suggest that a loss of resilience may have resulted.

Comparing egg size measurements over time may also provide a useful metric for examining long-term ecosystem change. Trends in clutch size and lay date are often reviewed, but retrospective analyses of egg sizes in relation to environmental change are rare (Järvinen 1994, Tryjanowski et al. 2004). Museum egg collections have been used to assess long-term changes

in nesting phenology, breeding distribution, egg colour, eggshell composition and thickness, contaminant levels, stable isotope values, and clutch size (summarised in Green and Scharlemann 2003, and Kiff 2005) as well as interspecific variability in eggshell colour (Cassey et al. 2010), but to my knowledge this study was the first to use measurements from egg collections to determine long-term egg size trends. As museums around the world have extensive collections of eggs dating back to the Victorian era at least (Green and Scharlemann 2003), these specimens may provide a useful, and perhaps untapped, record of change. My study also highlighted the general importance of museum specimens and written archival material as a repository of detailed information on past ecosystem states and population numbers.

My research also revealed certain gaps in our understanding of population-level effects of top predators in the Salish Sea, where bald eagles are the primary predator of several seabird species. At some glaucous-winged gull colonies, eagles are thought to have contributed substantively to gull population declines (Vermeer and Devito 1989, Sullivan et al. 2002, Hayward et al. 2010), primarily through depredating eggs and chicks and facilitating other predators via disturbance (Verbeek 1982, Vermeer and Devito 1989, Sullivan et al. 2002, White et al. 2006, Hayward et al. 2010, Hipfner et al. 2012). However, modelling this assumption provided only limited support for eagle effects (Chapter 3). Published observations have been colony-specific and it may be that effects depend upon factors such as eagle territoriality and age class composition (Hayward et al. 2010; J. Elliott pers. comm.). Due to their aggressive behaviour, glaucous-winged gulls may also be more resilient to eagle disturbance than are other surface-nesting seabirds such as murres (*Uria* spp.) and cormorants (*Phalacrocorax* spp.;

Hipfner et al. 2012). Thus, the ways in which eagles affect their seabird prey may differ among both colonies and species. It would be fruitful to research such effects in greater detail for gulls as well as other coastal seabirds, especially given the widespread recovery of bald eagles in coastal North America and elsewhere (Hipfner et al. 2012).

Finally, my study provides an example of how shifting baselines, that is, interpretation of past ecosystem conditions through the lens provided by our present understanding (Pauly 1995), can lead to erroneous conclusions about past population states, particularly in heavily altered systems. Although review papers on glaucous-winged gull biology have generally incorporated mention of past egging or hunting as having affected populations (e.g., Hayward and Verbeek 2008), specific studies have tended to take a short-term view and focus more narrowly on limiting factors apparent to the modern researcher (garbage, eagle predation; Vermeer 1992, Sullivan et al. 2002, Hayward et al. 2010). The lack of appreciation of past literature has been described as one of the impediments to strengthening ecology as a science (Belovsky et al. 2004). While these authors were referring to a general lack of awareness about the history of ecological concepts, reliance on short-term data may similarly prevent the development of a deeper understanding of population patterns, and the complexities of how they may be regulated over time (e.g., Wiens 1977, 1984, Blight and Ainley 2008, Ainley and Blight 2009). Seabirds are underrepresented in the marine historical ecology literature (HMAP 2008) but my research adds to evidence that they are tractable subjects of studies spanning decades or centuries (Hobson 1987, Thompson et al. 1995, Bovy 2007, Emslie and Patterson 2007). By combining unrelated sources of long-term data and analytical approaches, this study provides a template for using marine birds as indicators over historical time scales.

5.5 Limitations of the Study

This study's modelling results, together with historical accounts, provide credible evidence that the low glaucous-winged gull numbers recorded at Salish Sea colonies c. 1900 were due to human impacts, and likely do not represent a population at baseline. I found only a limited number of accounts describing Salish Sea gull colonies at the start of my study, but authors of that period were unanimous in attributing the population status of glaucous-winged gulls and other seabirds to human predation (Anthony 1906, Dawson and Bowles 1909, Province of British Columbia 1915, 1916, Pearse 1923, 1963). Despite this, my study provides more of a qualitative baseline than a quantitative one, as I was unable to develop a detailed description of gull distribution and abundance for the early decades of my study period. Nonetheless, even qualitative baselines for the purposes of monitoring may be useful (Grémillet and Charmantier 2010), particularly in the context of setting general ecosystem restoration goals, where targets may be based on ecosystem function rather than on precise numbers of a given species.

Similarly, while the combined results of this study are strongly suggestive of gull reproductive success being affected by a long-term decline in forage fish availability around the early breeding period, I did not demonstrate a direct relationship between fish population change and glaucous-winged gull population trend. Historical data on forage fish are scarce to virtually non-existent for all species in the region except Pacific herring, so that a detailed examination of the relationship between specific fish species (or of the entire community of Salish Sea forage fishes over time) and gull trends was not possible within the scope of my study. Assembling long-term historical data or proxies to model detailed effects of changing Salish Sea

fish communities on their seabird predators would be a valuable exercise for purposes of future ecosystem management, as well as for understanding past trends of forage fishes and their consumers.

An important limitation of historical studies is that they necessarily provide a broad, long-term view at the expense of the fine-scale detail provided by short-term research. I was restricted in this study to data that were available over multiple decades. Because of this, I primarily focussed on data representing adult birds during the pre- and early breeding period, with egg size, clutch size and lay date only providing information on adults from the time of gaining body condition in late winter through to producing eggs in the laying period. Stable isotope data were primarily derived from adults in this same period. Thus, apart from varying the modelled survival of juvenile (1st year) birds (Chapter 3), I did not look at factors potentially affecting survival of non-adult age classes, and effects on population trends. It is likely that more complex demographic variability was at play than was input into this study's demographic model (cf. Leslie 1966, Beissinger et al. 2006). Nonetheless, the model provided a plausible, heuristic tool for conceptualising drivers of long-term population change, and was generally supported by existing data, e.g., on declining clutch size and reproductive success. Stable isotope trends in the feathers of sub-adult gulls showed the same general trends as those of adults, suggesting that at inter-decadal scales, similar dietary or food web changes were likely affecting different age classes.

5.6 Management implications

An objective of my research was to contribute to monitoring strategies for detection of future changes to coastal marine ecosystems. My results provide baseline data on egg size, clutch size and lay date and these may be useful in future monitoring efforts for the Salish Sea, because colony-based data for nesting seabirds can be collected with modest effort and budgets while providing results robust to comparisons over time and space (Bertram et al. 2002). At least some monitoring will be required to determine whether glaucous-winged gulls continue to decline in number. Monitoring should include urban gulls, because gulls breeding in proximity to humans are periodically subject to public demands for management, but any management decisions will be poorly informed in the absence of baseline data (Arcese and Sinclair 1997).

Despite currently being in decline, glaucous-winged gulls remain common within the Salish Sea and their range overall, and thus are not of conservation concern. However, as Gaston (2010) notes, common species may contribute disproportionately to ecosystem function, and I have shown that this particular species can be a rich source of long-term data. Declines in many common species reflect those in related taxa (Gaston 2010), with glaucous-winged gulls here providing information relevant to declining populations of other marine birds in the study region, and perhaps elsewhere. It is in this sense that glaucous-winged gulls may be sentinels for the Salish Sea, as may their congeners in other ecosystems. Overall, my results indicate that seabirds for which there are long-term population records, reproductive data, and museum specimens are outstanding candidates for elucidating long-term trends in species' response to environmental change.

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Appendix 1

Summary of available vital rates data for glaucous-winged gulls in the Georgia Basin. Data include those for congeneric Western gulls *L. occidentalis* from California colonies where information is lacking on glaucous-winged gulls. Data for Alaska (AK) populations are not included.

Data type	Source	Notes
Juvenile survival	Butler et al. 1980, Reid 1988a	More recent survival estimates available for Western gull (Spear and Nur 1994)
Sub-adult survival	Butler et al. 1980, Reid 1988a	More recent survival estimates available for Western gull (Spear and Nur 1994)
Adult survival	Vermeer 1963, Butler et al. 1980, Reid 1988a	More recent survival estimates available for Western gull (Spear et al. 1987, Sydeman et al. 1991)
Age at first breeding	Reid 1988a	Protection I, WA
Adult mass at breeding	Hayward and Verbeek 2008	Body mass as indication of condition of breeding adults
Clutch size	Vermeer 1963, Thoresen and Galusha 1971, Verbeek 1986, Hooper 1988, Reid 1988b, LKB unpubl. data 2008	Mandarte I, Protection I, urban roof-nesters (BC); AK data also available
Egg size	James-Veitch and Booth 1954, Verbeek and Richardson 1982, Verbeek 1986, Reid 1988b, Vermeer et al. 1988, Salzer and Larkin 1990, LKB unpubl. data 2008	May be a proxy for adult breeding condition, pre-breeding diet.
Hatch success	Vermeer 1963, Verbeek 1986, Hooper 1988, Vermeer et al. 1988, Reid 1988b, LKB unpubl. data 2008	Defined as % eggs hatched of number laid; data for Mandarte I, urban roofs, Protection I; AK data also available. May be related to egg size.

Data type	Source	Notes
Fledge success	Vermeer 1963, Reid 1988b, Vermeer and Devito 1989, Vermeer et al. 1988, Vermeer et al. 1992, LKB unpubl. data 2008	Defined as % of chicks hatched surviving to d. 28; data from Mandarte I, Protection I, urban roofs; AK data also available
Chick mass at fledge	LKB unpubl. data 2008.	
Annual reproductive success	Vermeer 1963, Vermeer et al. 1988, LKB unpubl. data 2008, Hayward and Verbeek 2008	Defined as number of young fledged divided by number of females in sample; AK data also available
Lay date	Vermeer 1963, Drent et al. 1964, Verbeek 1986, Hooper 1988, Reid 1988b, Vermeer et al. 1988, LKB unpubl. data 2008	Incl. data for urban-nesting gulls; AK data also available

Appendix 2

Colony counts of breeding glaucous-winged gulls, Georgia Basin, British Columbia, Canada, 1900 – 2010.

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Ada Island[2]		49.29	-124.08	1974	171		Campbell 1976
Ada Island		49.29	-124.08	1975	100	K Kennedy	BC Nest Record Scheme (BCNRS)[3]
Ada Island		49.29	-124.08	1978	154		BC Nest Record Scheme
Ada Island		49.29	-124.08	1980	86		Campbell et al 1990
Ada Island		49.29	-124.08	1981	155	L Giliberte, M McNall	BC Nest Record Scheme

[1] If original source reported a range of numbers, the median value is provided here

[2] Named Jelina I. until 1930

[3] Records cards filed at the Royal British Columbia Museum, Victoria, Canada

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Ada Island		49.29	-124.08	1986	124		Vermeer and Devito 1989
Ada Island		49.29	-124.08	2010	69	LK Blight, M Crombie, T Osler	LK Blight unpubl. data
Anniversary Islet		48.82	-123.18	1977	4	MS Rodway, RW Campbell	BC Nest Record Scheme
Anniversary Islet		48.82	-123.18	1978	50	HR Carter, MS Rodway	BC Nest Record Scheme
Anniversary Islet		48.82	-123.18	2005	0	P Arcese	P Arcese unpubl. data
Arbutus Island		48.71	-123.44	1976	39		Campbell et al 1990
Arbutus Island		48.71	-123.44	1985	115		Vermeer and Devito 1989
Arbutus Island		48.71	-123.44	1986	150		Vermeer and Devito 1989
Arbutus Island		48.71	-123.44	1997	97		Sullivan et al 2002,

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Arbutus Island		48.71	-123.44	1999	55	M Lemon	M Lemon unpubl. data
Arbutus Island		48.71	-123.44	2005	40		Environment Canada unpubl. data
Arbutus Island		48.71	-123.44	2007	35		Environment Canada unpubl. data
Arbutus Island		48.71	-123.44	2010	53	LK Blight, T Osler	LK Blight unpubl. data
Argyle Rocks		48.32	-123.60	1974	0	P Nott, G Seedhouse	BC Nest Record Scheme
Argyle Rocks		48.32	-123.60	1978	1	HR Carter, CD Shepard, GE Corley-Smith	BC Nest Record Scheme
Augustus Point[4]		48.95	-123.65	1974	3		Campbell 1976

[4] Kuper I

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Augustus Point		48.95	-123.65	1978	3	HR Carter, MS Rodway	BC Nest Record Scheme
Augustus Point		48.95	-123.65	1980	3	E Perkins, R Gibbs, J Goodall	BC Nest Record Scheme
Augustus Point		48.95	-123.65	1984	6	L Giliberte, M McNall	BC Nest Record Scheme
Ballenas Island[5]		49.35	-124.16	1952	50	Mrs. AG Waldon	Drent and Guiguet 1961
Ballenas Island		49.35	-124.16	1953	50	Mrs. AG Waldon	Drent and Guiguet 1961
Ballenas Island		49.35	-124.16	1954	50	Mrs. AG Waldon	Drent and Guiguet 1961
Ballenas Island		49.35	-124.16	1955	50	Mrs. AG Waldon	Drent and Guiguet 1961

[5] North cliffs of North islet

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Ballenas Island		49.35	-124.16	1956	50	Mrs. AG Waldon	Drent and Guiguet 1961
Ballenas Island		49.35	-124.16	1968	55	R Drent	BC Nest Record Scheme
Ballenas Island		49.35	-124.16	1969	120	W Campbell, RG Foottit	BC Nest Record Scheme
Ballenas Island[6]		49.35	-124.16	1986	0		Vermeer and Devito 1989
Ballenas Island		49.35	-124.16	2006	0		P Arcese unpubl. data
Ballingall Islets[7]		48.91	-123.46	1936	85	GD Sprot	BC Nest Record Scheme
Ballingall Islets		48.91	-123.46	1954	1		Campbell et al 1990

[6] In text of paper, not in data tables

[7] All counts for Ballingal Islets are for East and West islets combined

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Ballingall Islets		48.91	-123.46	1959	57	MS Rodway, RW Campbell	BC Nest Record Scheme
Ballingall Islets		48.91	-123.46	1964	50	AJ Brooks, RY Edwardds	BC Nest Record Scheme
Ballingall Islets		48.91	-123.46	1966	100	MS Rodway, RW Campbell	BC Nest Record Scheme
Ballingall Islets		48.91	-123.46	1968	155	R Best	BC Nest Record Scheme
Ballingall Islets		48.91	-123.46	1974	96		Campbell 1976
Ballingall Islets		48.91	-123.46	1976	118	MS Rodway, RW Campbell	BC Nest Record Scheme
Ballingall Islets		48.91	-123.46	1977	118	MS Rodway, RW Campbell	BC Nest Record Scheme
Ballingall Islets		48.91	-123.46	1986	145		Vermeer and Devito 1989

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Ballingall Islets		48.91	-123.46	2010	6	LK Blight, T Osler	LK Blight unpubl. data
Bare Point		48.93	-123.70	1968	1	R Drent	BC Nest Record Scheme
Bare Point		48.93	-123.70	1974	11	MS Rodway, RW Campbell	Campbell 1976
Bare Point		48.93	-123.70	1977	8	MS Rodway, RW Campbell	BC Nest Record Scheme
Bare Point		48.93	-123.70	1978	4	HR Carter, MS Rodway	BC Nest Record Scheme
Bare Point		48.93	-123.70	1980	0	E Perkins, R Gibbs, J Goodall	BC Nest Record Scheme
Bare Point		48.93	-123.70	1986	5		Vermeer and Devito 1989
Belle Chain Islets		48.83	-123.20	1966	14	RC Best	BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Belle Chain Islets		48.83	-123.20	1969	43	R Drent, J Anvik, J & J Ward	BC Nest Record Scheme
Belle Chain Islets		48.83	-123.20	1974	6		Campbell 1976
Belle Chain Islets		48.83	-123.20	1976	6		BC Nest Record Scheme
Belle Chain Islets		48.83	-123.20	1977	25	MS Rodway, RW Campbell	BC Nest Record Scheme
Belle Chain Islets		48.83	-123.20	1980	37	E Perkins, R Gibbs, J Goodall	BC Nest Record Scheme
Belle Chain Islets		48.83	-123.20	1981	78	M McNall, S Webb, L Giliberti	BC Nest Record Scheme
Belle Chain Islets		48.83	-123.20	1986	56		Vermeer and Devito 1989
Belle Chain		48.83	-123.20	2009	18	T Golumbia	T Golumbia unpubl. data

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Islets							
Bird Islet		49.36	-123.29	1974	3	M Lemon	M Lemon unpubl. data
Bird Islet		49.36	-123.29	1981	2	M Lemon	M Lemon unpubl. data
Bird Islet		49.36	-123.29	1986	38		Vermeer and Devito 1989
Bird Islet		49.36	-123.29	1999	31	M Lemon and others	Sullivan et al. 2002
Bird Islet		49.36	-123.29	2010	15	LK Blight, T Osler	LK Blight unpubl. data
Canoe Islet		49.03	-123.59	1974	67		Campbell 1976
Canoe Islet		49.03	-123.59	1976	37	MS Rodway, RW Campbell	BC Nest Record Scheme
Canoe Islet		49.03	-123.59	1977	57	MS Rodway, RW Campbell	BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Canoe Islet		49.03	-123.59	1978	50	HR Carter, MS & JA Rodway, MJ Sowden	BC Nest Record Scheme
Canoe Islet		49.03	-123.59	1986	56		Vermeer and Devito 1989
Chain Islets and Great Chain Island		48.42	-123.27	1943	80	T White	BC Nest Record Scheme
Chain Islets and Great Chain Island		48.42	-123.27	1955	1000	D Stirling	Drent and Guiguet 1961
Chain Islets and Great Chain Island		48.42	-123.27	1960	850	FA Gornall	Drent and Guiguet 1961
Chain Islets and Great Chain Island		48.42	-123.27	1968	1754	R Drent	BC Nest Record Scheme
Chain Islets and Great Chain Island		48.42	-123.27	1973	1550		BC Nest Record Scheme
Chain Islets and Great Chain Island		48.42	-123.27	1974	1764		Campbell 1976
Chain Islets and Great Chain Island		48.42	-123.27	1976	1825		BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Chain Islets and Great	Chain Island	48.42	-123.27	1977	1838		BC Nest Record Scheme
Chain Islets and Great	Chain Island	48.42	-123.27	1986	2432		Rodway 1991, Vermeer and Devito 1989
Chain Islets and Great	Chain Island	48.42	-123.27	2009	1410	LK Blight, H Carter, T Osler, A Medve, M Lambert	LK Blight unpubl. data
Channel Islands[8]		48.80	-123.38	1977	1	MS Rodway, RW Campbell	BC Nest Record Scheme
Channel Islands		48.80	-123.38	2004	0		P Arcese unupubl. data
Christie Island		49.50	-123.30	1941	1	WSM collection	Drent and Guiguet 1961
Christie Island		49.50	-123.30	1949	2	WSM collection	Drent and Guiguet 1961

[8] NE islet

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Christie Island		49.50	-123.30	1955	247	Wm Hughes, BCNRS	Drent and Guiguet 1961
Christie Island		49.50	-123.30	1956	419	Wm Hughes, BCNRS	Drent and Guiguet 1961
Christie Island		49.50	-123.30	1958	219	Wm Merilees and GM McKay, BCNRS	Drent and Guiguet 1961
Christie Island		49.50	-123.30	1959	299	Wm Merilees, GM McKay, BCNRS	Drent and Guiguet 1961
Christie Island		49.50	-123.30	1963	300		BC Nest Record Scheme
Christie Island		49.50	-123.30	1968	293	R & N Drent	BC Nest Record Scheme
Christie Island		49.50	-123.30	1971	300		BC Nest Record Scheme
Christie Island		49.50	-123.30	1974	477		Campbell 1975

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Christie Island		49.50	-123.30	1978	718	M Lemon	M Lemon unpubl. data
Christie Island		49.50	-123.30	1980	499	P Nott, M McNall	BC Nest Record Scheme
Christie Island		49.50	-123.30	1981	558	RW Campbell	BC Nest Record Scheme
Christie Island		49.50	-123.30	1986	454		Vermeer and Devito 1989
Christie Island		49.50	-123.30	1999	232		Sullivan et al 2002
Christie Island		49.50	-123.30	2010	198	LK Blight, T Osler	LK Blight unpubl. data
Chrome Island[9]		49.47	-124.68	1935	150		Munro and Cowan 1947
Chrome Island		49.47	-124.68	1974	1		Campbell 1976

[9] Previously known as Yellow Island, referred to as such in Munro and Cowan 1947

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Chrome Island		49.47	-124.68	1986	3		Vermeer and Devito 1989
Chrome Island		49.47	-124.68	2010	1	LK Blight, T Osler	LK Blight unpubl. data
Church Island		48.31	-123.59	1974	3		Campbell 1976
Church Island		48.31	-123.59	1977	0		BC Nest Record Scheme
De Courcy Island		49.11	-123.76	1977	3	MS Rodway, RW Campbell	BC Nest Record Scheme
De Courcy Island[10]		49.11	-123.76	1986	2		Vermeer and Devito 1989
De Courcy Island		49.11	-123.76	2010	0	LK Blight, T Osler	LK Blight unpubl. data
Denman Island[11]		49.49	-124.71	1986	1		Vermeer and Devito 1989

[10] De Courcy Island counts from 1986 and 2010 are for NW cliffs; area not specified for 1977

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Denman Island		49.49	-124.71	2010	1	LK Blight, T Osler	LK Blight unpubl. data
Dinner Islet		49.95	-124.72	1978	0	MG & TE Shepard, GE Colby	BC Nest Record Scheme
Dinner Islet		49.95	-124.72	1981	0	W Campbell	BC Nest Record Scheme
Dinner Islet		49.95	-124.72	2006	0	R Butler	R Butler unpubl. data
Dock Island		48.67	-123.36	1977	48		BC Nest Record Scheme
Dock Island		48.67	-123.36	2010	0	T Golumbia	T Golumbia unpubl. data

[11] Gravelly Bay Ferry Dock

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Eagle Harbour		49.35	-123.27	1974	2		Campbell 1976
Fegan Islets		49.53	-124.38	1974	2		Campbell 1976
Fegan Islets		49.53	-124.38	1986	1		Vermeer and Devito 1989
Finnerty Islands		49.50	-124.39	1974	10		Campbell 1976
Finnerty Islands		49.50	-124.39	1981	6	R W Campbell	BC Nest Record Scheme
Finnerty Islands		49.50	-124.39	1986	4		Vermeer and Devito 1989
Five Finger Island		49.23	-123.92	1959	5	Wm Merilees	Drent and Guiguet 1961
Five Finger Island		49.23	-123.92	1968	110	R & J Drent	Campbell et al 1990
Five Finger Island		49.23	-123.92	1974	559		Campbell 1976

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Five Finger Island		49.23	-123.92	1977	459	M Lemon	M Lemon unpubl. data
Five Finger Island		49.23	-123.92	1978	473	M Lemon	M Lemon unpubl. data
Five Finger Island		49.23	-123.92	1980	364	M Lemon	M Lemon unpubl. data
Five Finger Island		49.23	-123.92	1981	599	M Lemon	M Lemon unpubl. data
Five Finger Island		49.23	-123.92	1986	671		Vermeer and Devito 1989
Five Finger Island		49.23	-123.92	1999	288		Sullivan et al. 2002
Five Finger Island		49.23	-123.92	2010	2	LK Blight, M Crombie, T Osler	LK Blight unpubl. data
Gabriola Island		49.15	-123.79	1974	4	MS Rodway, RW	Campbell 1976

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
cliffs						Campbell	
Gabriola Island cliffs		49.15	-123.79	1977	5	MS Rodway, RW Campbell	BC Nest Record Scheme
Gabriola Island cliffs		49.15	-123.79	2010	4	R Butler	R Butler unpubl. data
Galiano Island cliffs[12]		48.91	-123.42	1976	4	MS Rodway, RW Campbell	BC Nest Record Scheme
Galiano Island cliffs		48.98	-123.57	1977	2	MS Rodway, RW Campbell	BC Nest Record Scheme
Galiano Island cliffs		48.91	-123.42	1977	1	MS Rodway, RW Campbell	BC Nest Record Scheme
Galiano Island		48.98	-123.57	1985	6		Vermeer and Devito 1989

[12] NW of Gray Peninsula

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
cliffs							
Galiano Island cliffs		48.98	-123.57	1986	6		Vermeer and Devito 1989
Grebe Islets[13]		49.34	-123.28	1974	7	RW Campbell	Campbell 1976
Grebe Islets		49.34	-123.28	1978	12	M Lemon	M Lemon unpubl. data
Grebe Islets		49.34	-123.28	1980	24	P Nott, M McNall	BC Nest Record Scheme
Grebe Islets		49.34	-123.28	1981	22	M Lemon	M Lemon unpubl. data
Grebe Islets		49.34	-123.28	1986	108		Vermeer and Devito 1989, Rodway 1991
Grebe Islets		49.34	-123.28	1999	257		Sullivan et al. 2002

[13] All counts for Grebe Islets are for East and West islets combined.

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Grebe Islets		49.34	-123.28	2010	33	LK Blight, T Osler	LK Blight unpubl. data
Greig Island		48.68	-123.34	1963	33	G McKay	BC Nest Record Scheme
Greig Island		48.68	-123.34	1973	35		BC Nest Record Scheme
Greig Island		48.68	-123.34	1974	40		Campbell 1976
Greig Island		48.68	-123.34	1981	53	M McNall, R Kool	BC Nest Record Scheme
Greig Island		48.68	-123.34	1985	45		Vermeer and Devito 1989
Greig Island		48.68	-123.34	1986	52		Vermeer and Devito 1989
Greig Island		48.68	-123.34	1997	5		Sullivan et al. 2002
Greig Island		48.68	-123.34	1999	14	M Lemon and others	Sullivan et al. 2002

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Greig Island		48.68	-123.34	2009	17	T Golumbia	T Golumbia unpubl. data
Harris Island		48.42	-123.29	1971	41		BC Nest Record Scheme
Harris Island		48.42	-123.29	1977	28	M G Shepard	BC Nest Record Scheme
Harris Island		48.42	-123.29	1981	19	E Taylor, L Giliberti, M McNall	BC Nest Record Scheme
Harris Island		48.42	-123.29	1986	22		Vermeer and Devito 1989
Hodgson Islands		49.63	-124.08	1986	1		Vermeer and Devito 1989
Hodgson Islands		49.63	-124.08	2006	0	R Butler	R Butler unpubl. data
Hornby Island bluffs		49.52	-124.59	1938	30		Drent and Guiguet 1961
Hornby Island		49.52	-124.59	1960	0	GE Seon	Drent and Guiguet 1961

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
bluffs							
Hornby Island bluffs		49.52	-124.59	1977	1	D Thompson	BC Nest Record Scheme
Hornby Island, St. John Point		49.52	-124.59	1968	0	GE Seon	BC Nest Record Scheme
Hornby Island, St. John Point		49.52	-124.59	1974	5		Campbell 1976
Hornby Island, St. John Point		49.52	-124.59	1986	6		Vermeer and Devito 1989
Horseshoe Bay[14]		49.40	-123.25	1956	1	A Muir	Drent and Guiguet 1961
Horseshoe Bay		49.40	-123.25	1957	1	A Muir	Drent and Guiguet 1961

[14] Actual nesting locality is cliff 2 miles N of Horseshoe Bay proper

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Horseshoe Bay		49.40	-123.25	1974	1		Campbell 1976
Hudson Rocks		49.23	-123.93	1959	80	Wm Merilees	Drent and Guiguet 1961
Hudson Rocks		49.23	-123.93	1960	38	K Vermeer	BC Nest Record Scheme
Hudson Rocks		49.23	-123.93	1968	79	R & J Drent	BC Nest Record Scheme
Hudson Rocks		49.23	-123.93	1974	248	M Lemon	M Lemon unpubl. data
Hudson Rocks		49.23	-123.93	1977	259	M Lemon	M Lemon unpubl. data
Hudson Rocks		49.23	-123.93	1978	236	M Lemon	M Lemon unpubl. data
Hudson Rocks		49.23	-123.93	1980	226	M Lemon	M Lemon unpubl. data
Hudson Rocks		49.23	-123.93	1981	308	M Lemon	M Lemon unpubl. data
Hudson Rocks		49.23	-123.93	1986	247		Vermeer and Devito 1989

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Hudson Rocks		49.23	-123.93	1999	122	M Lemon and others	Sullivan et al. 2002
Hudson Rocks		49.23	-123.93	2010	10	L Blight, T Osler	LK Blight unpubl. data
Imrie Island		48.69	-123.33	1905	0	Dawson and Edson	Drent and Guiguet 1961
Imrie Island		48.69	-123.33	1935	150	JA Munro	BC Nest Record Scheme
Imrie Island[15]		48.69	-123.33	1945	150	Meugens	Drent and Guiguet 1961
Imrie Island		48.69	-123.33	1959	200	R, JJ, & J Drent	Drent and Guiguet 1961
Imrie Island		48.69	-123.33	1960	295	MS Rodway, RW Campbell	BC Nest Record Scheme

[15] This record specified count was for “North half of island”

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Imrie Island		48.69	-123.33	1968	250	R & N Drent	BC Nest Record Scheme
Imrie Island		48.69	-123.33	1974	298		Campbell 1976
Imrie Island		48.69	-123.33	1977	315	R Hunter	BC Nest Record Scheme
Imrie Island		48.69	-123.33	1978	355		Campbell et al 1990
Imrie Island		48.69	-123.33	1985	120		Vermeer and Devito 1989
Imrie Island		48.69	-123.33	1986	216		Vermeer and Devito 1989
Imrie Island		48.69	-123.33	1997	33		Sullivan et al 2002
Imrie Island		48.69	-123.33	1999	41	M Lemon and others	Sullivan et al. 2002
Imrie Island		48.69	-123.33	2005	1		P Arcese unpubl. data

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Imrie Island		48.69	-123.33	2007	0		P Arcese unpubl. data
Inskip Rock		49.21	-123.95	1999	0	M Lemon	M Lemon unpubl. data
Java Islets[16,17]		48.76	-123.11	1900	35	H Spalding	Drent and Guiguet 1961
Java Islets		48.76	-123.11	1959	372	MS Rodway, RW Campbell	BC Nest Record Scheme
Java Islets		48.76	-123.11	1968	464	R & J Drent	BC Nest Record Scheme
Java Islets		48.76	-123.11	1969	531	R Drent, J Anvik, J & J Ward	BC Nest Record Scheme
Java Islets		48.76	-123.11	1974	372		Campbell 1976

[16] Year given as “about 1900” in original record

[17] All counts for Java Islets are for East and West islets combined

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Java Islets		48.76	-123.11	1977	374	MS Rodway, RW Campbell	BC Nest Record Scheme
Java Islets		48.76	-123.11	1980	181		Campbell et al 1990
Java Islets		48.76	-123.11	1981	384	R & C Gibb, M Hodgson	BC Nest Record Scheme
Java Islets		48.76	-123.11	1986	298		Vermeer and Devito 1989
Java Islets		48.76	-123.11	2005	52	T Golumbia	T Golumbia unpubl. data
Java Islets		48.76	-123.11	2007	20	T Golumbia	T Golumbia unpubl. data
Java Islets		48.76	-123.11	2008	17	T Golumbia	T Golumbia unpubl. data
Java Islets		48.76	-123.11	2009	25	T Golumbia	T Golumbia unpubl. data
Keefer Rock		49.97	-124.88	1970	7	R Foottit, R Butler, W	Foottit et al. 1973, BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
						Merilees	
Keefer Rock		49.97	-124.88	1973	7	R & S Butler	BC Nest Record Scheme
Keefer Rock		49.97	-124.88	1974	7		Campbell 1976
Keefer Rock		49.97	-124.88	1977	20		BC Nest Record Scheme
Keefer Rock		49.97	-124.88	1986	28		Vermeer and Devito 1989
Keefer Rock		49.97	-124.88	2006	0	R Butler	R Butler unpubl. data
Kuper Island		48.94	-123.63	1972	4	J Cooper	BC Nest Record Scheme
Kuper Island		48.94	-123.63	1974	10	MS Rodway, RW Campbell	BC Nest Record Scheme
Kuper Island		48.94	-123.63	1976	11	MS Rodway, RW Campbell	BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Kuper Island		48.94	-123.63	1977	6	MS Rodway, RW Campbell	BC Nest Record Scheme
Kuper Island		48.94	-123.63	1986	8		Vermeer and Devito 1989
Lion Islets		48.90	-123.34	1977	2	MS Rodway, RW Campbell	BC Nest Record Scheme
Lion Islets		48.90	-123.34	1986	1		Vermeer and Devito 1989
Little Group Islets		48.67	-123.36	1986	6		Vermeer and Devito 1989
Little Group Islets		48.67	-123.36	1997	3		Sullivan et al 2002
Little Group Islets		48.67	-123.36	1999	1	M Lemon	M Lemon unpubl. data
Little Group Islets		48.67	-123.36	2010	0	LK Blight, T Osler	LK Blight unpubl. data
Little Rock	Caution - see notes	50.05	-124.91	1974	1		Campbell 1976

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Little Rock	Caution - see notes	50.05	-124.91	2006	0	R Butler	R Butler unpubl. data
Little Rock[18]	Caution - see notes	50.16	-125.09	1986	1		Vermeer and Devito 1989
Major Islet		49.99	-124.82	1970	1	R Foottit, R Butler, W Merilees	Foottit et al. 1973, BC Nest Record Scheme
Major Islet		49.99	-124.82	1974	3		Campbell 1976
Major Islet		49.99	-124.82	1978	1	MG & TE Shepard	BC Nest Record Scheme
Major Islet		49.99	-124.82	2006	0	R Butler	R Butler unpubl. data
Mandarte Island		48.63	-123.29	1915	450[19]		BC Nest Record Scheme

[18] Little Rock off Read Island; different locality from above locality also named Little Rock

[19] Recorded incorrectly in Drent and Guiguet (1961) as 225 pair

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Mandarte Island		48.63	-123.29	1921	350		BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1923	600	JA Munro	BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1927	1000	Munro 1929	BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1936	534[20]		BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1955	1500		BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1957	1900	GF van Tets, and other UBC affiliates	Drent and Guiguet 1961
Mandarte Island		48.63	-123.29	1958	1900	GF van Tets, and other UBC affiliates	Drent and Guiguet 1961

[20] But 500 nests recorded in BCNRS by JA Munro for Mandarte Island, 1936

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Mandarte Island		48.63	-123.29	1959	1900	GF van Tets, and other UBC affiliates	Drent and Guiguet 1961
Mandarte Island		48.63	-123.29	1960	1900	GF van Tets, and other UBC affiliates	Drent and Guiguet 1961
Mandarte Island		48.63	-123.29	1961	1500	GC Carl	BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1962	2100	R Drent and others	BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1969	2000		BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1970	2500	I Robertson	BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1971	2000	J Ward	BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1974	1047		Campbell 1976

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Mandarte Island		48.63	-123.29	1977	1666	MS Rodway, RW Campbell	BC Nest Record Scheme
Mandarte Island		48.63	-123.29	1985	2157		Vermeer and Devito 1987
Mandarte Island		48.63	-123.29	1986	2259		Vermeer and Devito 1989
Mandarte Island		48.63	-123.29	1997	2124		Sullivan et al 2002
Mandarte Island		48.63	-123.29	2005	1700		P Arcese unpubl. data
Mandarte Island		48.63	-123.29	2007	1100		P Arcese unpubl. data
Mandarte Island		48.63	-123.29	2009	1892	LK Blight, H Carter, T Osler, A Medve	LK Blight unpubl. data
Mandarte South Islet		48.63	-123.28	1962	100		Drent et al. 1964

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Mandarte South Islet		48.63	-123.28	1974	71	BC Provincial Museum	BC Nest Record Scheme
Mandarte South Islet		48.63	-123.28	1977	71		BC Nest Record Scheme
Mandarte South Islet		48.63	-123.28	1980	106		BC Nest Record Scheme
Mandarte South Islet		48.63	-123.28	1985	100		Vermeer and Devito 1989
Mandarte South Islet		48.63	-123.28	1986	104		Vermeer and Devito 1989
Mandarte South Islet		48.63	-123.28	1997	97		Sullivan et al. 2002
Mandarte South Islet		48.63	-123.28	2007	0		P. Arcese unpubl. data
Mandarte South Islet		48.63	-123.28	2010	28	M Crombie, D Gosse	LK Blight unpubl. data
Mary Tod Island		48.43	-123.30	1986	1		Vermeer and Devito 1989

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Mary Tod Island		48.43	-123.30	2009	2	LK Blight	LK Blight unpubl. data
Maude Island		49.27	-124.08	1986	2		Vermeer and Devito 1989
Maude Island		49.27	-124.08	2010	0	LK Blight, T Osler	LK Blight unpubl. data
McRae Islet		49.74	-124.29	1969	97		Campbell et al. 1990
McRae Islet		49.74	-124.29	1974	97		Campbell 1976
McRae Islet		49.74	-124.29	1986	262		Vermeer and Devito 1989
Merry Island and Franklin Rock		49.47	-123.92	1950	800	JA Brooks, Fisheries Guardian	Drent and Guiguet 1961
Merry Island and Franklin Rock		49.47	-123.92	1960	600		BC Nest Record Scheme
Merry Island and Franklin Rock		49.47	-123.92	1968	395		BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Merry Island and Franklin Rock		49.47	-123.92	1974	1005		BC Nest Record Scheme
Merry Island and Franklin Rock		49.47	-123.92	1975	622		BC Nest Record Scheme
Merry Island and Franklin Rock		49.47	-123.92	1976	779		BC Nest Record Scheme
Merry Island and Franklin Rock		49.47	-123.92	1986	228		Vermeer and Devito 1989
Merry Island and Franklin Rock		49.47	-123.92	2006	100	R Butler	R Butler unpubl. data
Merry Island and Franklin Rock		49.47	-123.92	2010	46	LK Blight, T Osler	LK Blight unpubl. data
Miami Islet		49.04	-123.71	1968	25	R & J Drent	BC Nest Record Scheme
Miami Islet		49.04	-123.71	1974	52		Campbell 1976
Miami Islet		49.04	-123.71	1977	43	L Milnes, M Rodway	BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Miami Islet		49.04	-123.71	1980	17	E Perkins, R Gibbs, J Goodall	BC Nest Record Scheme
Miami Islet		49.04	-123.71	1981	19	G Kaiser, S Webb, L Giliberti, M McNall	BC Nest Record Scheme
Miami Islet		49.04	-123.71	1986	38		Vermeer and Devito 1989
Miami Islet		49.04	-123.71	2010	5	LK Blight, T Osler	LK Blight unpubl. data
Mitlenatch Island		49.95	-125.01	1922	500[21]	T Pearse, Taverner, HM Laing, E Jackson	BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1923	600	Mr. RM Stewart	Pearse 1923

[21] Original record reports a count of 500 pairs, differing from the number recorded in Drent and Guiguet (1961)

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Mitlenatch Island		49.95	-125.01	1927	150	T Pearse	Pearse 1929, Drent and Guiguet 1961
Mitlenatch Island		49.95	-125.01	1928	400	T Pearse	Pearse 1929, Drent and Guiguet 1961
Mitlenatch Island		49.95	-125.01	1959	600	D Stirling BCNRS	Drent and Guiguet 1961
Mitlenatch Island		49.95	-125.01	1960	1200	D Stirling	BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1960	900	R Barnes, WJ Merilees	BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1963	3000		BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1965	3000		BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Mitlenatch Island		49.95	-125.01	1967	3500	R Butler	BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1969	3000		BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1970	100	DR Drent, R Foottit	BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1973	286		BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1974	1632		Campbell 1976
Mitlenatch Island		49.95	-125.01	1977	987		BC Nest Record Scheme
Mitlenatch Island		49.95	-125.01	1986	2100		Vermeer and Devito 1989

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Mitlenatch Island		49.95	-125.01	2010	1152	LK Blight, T Chatwin, M Davis, D Scott, P Sowden, D Thomson	LK Blight unpubl. data
Mouat Islands		49.64	-124.47	1986	35		Vermeer and Devito 1989
Mouat Islands		49.64	-124.47	2006	45	R Butler	R Butler unpubl. data
Nanoose Bay Island[22]		49.26	-124.18[23]	1961	75		Environment Canada unpubl. data
Nanoose Bay Island		49.26	-124.18	1963	100		Environment Canada unpubl. data
Norris Rocks		49.48	-124.65	1960	20	R & J Drent	BC Nest Record Scheme

[22] No island of this name found, presently or historically; may be Ada Island as no other likely sites exist in Nanoose Bay.

[23] Lat and long are for Nanoose Bay

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Norris Rocks		49.48	-124.65	1968	17		Campbell et al 1990
Norris Rocks		49.48	-124.65	1974	85		BC Nest Record Scheme
Norris Rocks		49.48	-124.65	1975	170	K Kennedy	BC Nest Record Scheme
Norris Rocks		49.48	-124.65	1977	104	MG Shepard	BC Nest Record Scheme
Norris Rocks		49.48	-124.65	1978	58	MG & TE Shepard	BC Nest Record Scheme
Norris Rocks		49.48	-124.65	1981	111	M McNall, A Burger	BC Nest Record Scheme
Norris Rocks		49.48	-124.65	1986	287		Vermeer and Devito 1989
Norris Rocks		49.48	-124.65	2010	111	LK Blight, T Osler	LK Blight unpubl. data

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Pam Rocks[24]		49.49	-123.30	1956	10	JK Cooper	Drent and Guiguet 1961
Pam Rocks		49.49	-123.30	1963	7		BC Nest Record Scheme
Pam Rocks		49.49	-123.30	1968	109		BC Nest Record Scheme
Pam Rocks		49.49	-123.30	1969	99		BC Nest Record Scheme
Pam Rocks		49.49	-123.30	1971	30	GR Waters	BC Nest Record Scheme
Pam Rocks		49.49	-123.30	1974	121		Campbell 1976
Pam Rocks		49.49	-123.30	1978	151	M Lemon	M Lemon unpubl. data
Pam Rocks		49.49	-123.30	1980	105	P Nott, M McNall	BC Nest Record Scheme

[24] "Pam Rocks" consists of Pam Rock and adjacent small islet

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Pam Rocks		49.49	-123.30	1981	131	M Lemon	M Lemon unpubl. data
Pam Rocks		49.49	-123.30	1986	109		Vermeer and Devito 1989
Pam Rocks		49.49	-123.30	1999	25	M Lemon and others	Sullivan et al. 2002
Pam Rocks		49.49	-123.30	2010	7	LK Blight, T Osler	LK Blight unpubl. data
Passage Island[25]		49.34	-123.31	1958	16	A Muir, JG Sarles	Drent and Guiguet 1961
Passage Island[26]		49.34	-123.31	1959	50	J Toochin	Drent and Guiguet 1961
Passage Island		49.34	-123.31	1963	125		BC Nest Record Scheme

[25] Count was of "South tip and rock immediately south"

[26] Count was of "South rock"

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Passage Island		49.34	-123.31	1964	300	T Robertson	BC Nest Record Scheme
Passage Island		49.34	-123.31	1966	75	G Sirk	BC Nest Record Scheme
Passage Island		49.34	-123.31	1968	300	R & P Drent	BC Nest Record Scheme
Passage Island		49.34	-123.31	1971	400	GR Waters	BC Nest Record Scheme
Passage Island		49.34	-123.31	1974	496		Campbell 1976
Passage Island		49.34	-123.31	1978	798		Campbell et al 1990
Passage Island		49.34	-123.31	1986	384		Vermeer and Devito 1989
Passage Island[27]		49.34	-123.31	2010	11	LK Blight, T Osler	LK Blight unpubl. data

[27] Several houses on Passage Island, and one house of more recent construction now on rock off South point

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Point Atkinson		49.33	-123.27	1968	4		Environment Canada unpubl. data
Point Atkinson		49.33	-123.27	1974	3		Campbell 1976
Race Rocks all				1922	72		Environment Canada unpubl. data
Race Rocks[28]		48.30	-123.53	1924	75	J Munro	Munro 1925, Drent and Guiguet 1961
Race Rocks all		48.30	-123.53	1953	72	CJ Guiguet	BC Nest Record Scheme
Race Rocks all		48.30	-123.53	1958	325	GC Odlum (lightkeeper)	Drent and Guiguet 1961

[28] Assumed to be a count for all Race Rocks: original record noted that count was for "North Race Rock", but also mentions main island of Great Race without noting any records of nesting gulls

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Race Rocks all		48.30	-123.53	1981	471	BCNRS	Campbell et al. 1990, Rodway 1991
Race Rocks all		48.30	-123.53	1989	424	K Morgan, K Vermeer	Vermeer et al. 1992
Race Rocks all		48.30	-123.53	2009	115	A Harding	Lester B Pearson College unpubl. data
Ragged Islets		49.03	-123.70	1923	0		Campbell et al 1990
Ragged Islets		49.03	-123.70	1961	15		BC Nest Record Scheme
Ragged Islets		49.03	-123.70	1963	15	MS Rodway, RW Campbell	BC Nest Record Scheme
Ragged Islets		49.03	-123.70	1968	55	R Drent	BC Nest Record Scheme
Ragged Islets		49.03	-123.70	1974	103		Campbell 1976

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Ragged Islets		49.03	-123.70	1977	126	MS Rodway, RW Campbell	BC Nest Record Scheme
Ragged Islets		49.03	-123.70	1978	130		Campbell et al 1990
Ragged Islets		49.03	-123.70	1986	69		Vermeer and Devito 1989
Ragged Islets		49.03	-123.70	2010	18	LK Blight, T Osler, M Crombie	LK Blight unpubl. data
Reay Island		48.68	-123.33	1974	5		Campbell 1976
Reay Island		48.68	-123.33	1977	6		BC Nest Record Scheme
Reay Island		48.68	-123.33	1999	0	M Lemon	M Lemon unpubl. data
Reay Island		48.68	-123.33	2010	0	T Golumbia	T Golumbia unpubl. data
Reifel Refuge		49.11	-123.18	1974	3		Campbell 1976

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Reifel Refuge		49.11	-123.18	1987	1	J Perrs	BC Nest Record Scheme
Reifel Refuge		49.11	-123.18	1988	0	J Perrs	BC Nest Record Scheme
Rose Islets		49.01	-123.64	1963	50	MS Rodway, RW Campbell	BC Nest Record Scheme
Rose Islets		49.01	-123.64	1968	100		BC Nest Record Scheme
Rose Islets		49.01	-123.64	1969	100		BC Nest Record Scheme
Rose Islets		49.01	-123.64	1972	1		Campbell et al 1990
Rose Islets		49.01	-123.64	1974	208		Campbell 1976
Rose Islets		49.01	-123.64	1976	119		BC Nest Record Scheme
Rose Islets		49.01	-123.64	1977	167		BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Rose Islets		49.01	-123.64	1981	211		Campbell et al 1990
Rose Islets		49.01	-123.64	1984	41		BC Nest Record Scheme
Rose Islets		49.01	-123.64	1985	112		Vermeer and Devito 1989
Rose Islets		49.01	-123.64	1986	116		Vermeer and Devito 1989
Rose Islets		49.01	-123.64	2010	12	LK Blight, T Osler, M Crombie	LK Blight unpubl. data
Ruxton Island cliffs		49.07	-123.70	1977	2	MS Rodway, RW Campbell	BC Nest Record Scheme
Ruxton Island cliffs		49.07	-123.70	1986	2		Vermeer and Devito 1989
Sallas Rocks		48.59	-123.29	1986	29		Vermeer and Devito 1989
Sallas Rocks		48.59	-123.29	1997	13		Sullivan et al 2002

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Sallas Rocks		48.59	-123.29	2006	0	R Butler	R Butler unpubl. data
Sallas Rocks		48.59	-123.29	2009	9	T Golumbia	T Golumbia unpubl. data
Saltspring Island rock[29]		48.85	-123.44	1974	3	MS Rodway, RW Campbell	BC Nest Record Scheme
Saltspring Island rock		48.85	-123.44	1977	1	MS Rodway, RW Campbell	BC Nest Record Scheme
Saturna Island[30]		48.78	-123.04	1977	7	MS Rodway, RW Campbell	BC Nest Record Scheme
Saturna Island		48.78	-123.04	1986	7		Vermeer and Devito 1989

[29] Unnamed rock in mouth of Long Harbour

[30] South of East Point

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Sisters Islets		49.49	-124.43	1940	100	OS Dean (lightkeeper)	Drent and Guiguet 1961
Sisters Islets		49.49	-124.43	1941	100	OS Dean (lightkeeper)	Drent and Guiguet 1961
Sisters Islets		49.49	-124.43	1942	100	OS Dean (lightkeeper)	Drent and Guiguet 1961
Sisters Islets		49.49	-124.43	1943	100	OS Dean (lightkeeper)	Drent and Guiguet 1961
Sisters Islets		49.49	-124.43	1951	100	Mrs. AG Waldon	Drent and Guiguet 1961
Sisters Islets		49.49	-124.43	1968	74	R & N Drent	BC Nest Record Scheme
Sisters Islets		49.49	-124.43	1974	108		Campbell 1976
Sisters Islets		49.49	-124.43	1978	85	MG & TE Shepard	BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Sisters Islets		49.49	-124.43	1981	151	RW Campbell	Campbell et al 1990
Sisters Islets		49.49	-124.43	1986	25		Vermeer and Devito 1989
Siwash Rock		49.31	-123.16	1958	4	E Moody via J Toochin	Drent and Guiguet 1961
Siwash Rock		49.31	-123.16	1961	2		BC Nest Record Scheme
Siwash Rock		49.31	-123.16	1962	1		BC Nest Record Scheme
Siwash Rock		49.31	-123.16	1967	2		BC Nest Record Scheme
Siwash Rock		49.31	-123.16	1974	6		Campbell 1976
Siwash Rock		49.31	-123.16	1976	3		BC Nest Record Scheme
Siwash Rock		49.31	-123.16	1977	4		BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Siwash Rock		49.31	-123.16	1986	8		Vermeer and Devito 1989
Siwash Rock		49.31	-123.16	2010	0	LK Blight, H Mix	LK Blight unpubl. data
Snake Island		49.22	-123.89	1958	350	JG Sarles	Drent and Guiguet 1961
Snake Island		49.22	-123.89	1959	500	Wm Merilees	Drent and Guiguet 1961
Snake Island		49.22	-123.89	1960	350	R Drent	Drent and Guiguet 1961
Snake Island		49.22	-123.89	1964	300		BC Nest Record Scheme
Snake Island		49.22	-123.89	1968	330	R & P Drent	BC Nest Record Scheme
Snake Island		49.22	-123.89	1974	558		Campbell 1976
Snake Island		49.22	-123.89	1975	610	M Lemon	M Lemon unpubl. data
Snake Island		49.22	-123.89	1977	400		BC Nest Record Scheme

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Snake Island		49.22	-123.89	1978	615	M Lemon	M Lemon unpubl. data
Snake Island		49.22	-123.89	1980	426	M Lemon	M Lemon unpubl. data
Snake Island		49.22	-123.89	1981	719	M Lemon	M Lemon unpubl. data
Snake Island		49.22	-123.89	1986	673		Vermeer and Devito 1989
Snake Island		49.22	-123.89	1999	204	M Lemon and others	Sullivan et al. 2002
Snake Island		49.22	-123.89	2010	20	LK Blight, T Osler, M Crombie	LK Blight unpubl. data
Sooke Bay		48.37	-123.77	1960	2	JA Brooks	Drent and Guiguet 1961
Sooke Bay		48.37	-123.77	1974	2		Campbell 1976
South Bedford Island		48.31	-123.60	1974	2		Campbell 1876

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
South Bedford Island		48.31	-123.60	1975	2	P Nott, G Seedhouse	BC Nest Record Scheme
South Bedford Island		48.31	-123.60	1977	21		BC Nest Record Scheme
Tent Island		48.93	-123.63	1972	1	MS Rodway, RW Campbell	BC Nest Record Scheme
Tent Island		48.93	-123.63	1974	3	MS Rodway, RW Campbell	Campbell 1976
Tent Island		48.93	-123.63	1976	5	MS Rodway, RW Campbell	BC Nest Record Scheme
Tent Island		48.93	-123.63	1977	16	MS Rodway, RW Campbell	BC Nest Record Scheme
Tent Island		48.93	-123.63	1985	11		Vermeer and Devito 1989
Tent Island	Cliffs and cliff cavities	48.93	-123.63	1986	12		Vermeer and Devito 1989

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Trial Island		48.40	-123.31	1953	50	CJ Guiguet, "MS"	Drent and Guiguet 1961
Trial Island		48.40	-123.31	1959	50	DH Franklin (lightkeeper)	Drent and Guiguet 1961
Trial Island		48.40	-123.31	1960	46	Miss June Franklin	Drent and Guiguet 1961
Trial Island		48.40	-123.31	1961	39		BC Nest Record Scheme
Trial Island		48.40	-123.31	1973	2		BC Nest Record Scheme
Trial Island		48.40	-123.31	1974	3		Campbell 1976
Trial Island		48.40	-123.31	2010	100	M Dickman (lightkeeper)	LK Blight unpubl. data
Trial Island		48.40	-123.31	2011	105	LK Blight, I Duncan	LK Blight unpubl. data
Tsawwassen	Jetty	49.02	-123.11	1974	9		Campbell 1976

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Tsawwassen	Jetty	49.02	-123.11	2010	4	R Butler, LK Blight	R Butler unpubl. data, LK Blight unpubl. data
Tsawwassen	Breakwater	49.00	-123.10	1974	115		Campbell 1976
Tsawwassen	Breakwater	49.00	-123.10	1977	160		BC Nest Record Scheme
Tsawwassen	Breakwater	49.00	-123.10	1986	238		Vermeer and Devito 1989
Tsawwassen	Breakwater	49.00	-123.10	2010	250[31]	LK Blight	LK Blight unpubl. data
Valdes Island cliffs		49.06	-123.63	1977	1	MS Rodway, RW Campbell	BC Nest Record Scheme
Valdes Island cliffs		49.06	-123.63	1978	1	GP Sirk	BC Nest Record Scheme

[31] 2010 count is an estimate, not included in analysis

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Vancouver Buildings		49.27	-123.10	1974	4		Campbell 1976
Vancouver Buildings		49.27	-123.10	1986	500		Vermeer et al 1988, Vermeer 1992
Vancouver, Burrard Bridge		49.27	-123.14	1986	9		Vermeer and Devito 1989
Vancouver, Burrard Bridge		49.27	-123.14	2010	1	LK Blight	LK Blight unpubl. data
Vancouver, Burrard Inlet		49.31	-123.10	1986	8		Vermeer and Devito 1989
Vancouver Harbour		49.29	-123.10	1986	112		Vermeer et al. 1988, Rodway 1991
Vancouver, Lions Gate Bridge		49.31	-123.14	1974	1		Campbell 1976

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Vancouver, Lions Gate Bridge		49.31	-123.14	1986	1		Vermeer and Devito 1989
Vancouver, Lions Gate Bridge		49.31	-123.14	2010	2	LK Blight	LK Blight, unpubl. data
Vancouver, Prospect Point		49.31	-123.14	1959	2	W Hughes	Drent and Guiguet 1961
Vancouver, Prospect Point		49.31	-123.14	1974	5		Campbell 1976
Vancouver, Prospect Point		49.31	-123.14	1986	4		Vermeer and Devito 1989
Vancouver, Prospect Point		49.31	-123.14	2010	0	LK Blight	LK Blight unpubl. data

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Vancouver, Second Narrows Bridge		49.29	-123.03	1984	40	D Wilson, O Dunbar, K Hobson	BC Nest Record Scheme
Vancouver, Second Narrows Bridge		49.29	-123.03	1986	40		Vermeer and Devito 1989
Victoria				1974	314		Breeding Bird Survey
Victoria				1975	230		Breeding Bird Survey
Victoria				1976	209		Breeding Bird Survey
Victoria				1977	341		Breeding Bird Survey
Victoria				1978	173		Breeding Bird Survey
Victoria				1979	220		Breeding Bird Survey
Victoria				1980	340		Breeding Bird Survey
Victoria				1981	310		Breeding Bird Survey

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Victoria				1982	233		Breeding Bird Survey
Victoria				1988	215		Breeding Bird Survey
Victoria				1989	269		Breeding Bird Survey
Victoria				1990	312		Breeding Bird Survey
Victoria				1991	116		Breeding Bird Survey
Victoria				1992	110		Breeding Bird Survey
Victoria				1993	208		Breeding Bird Survey
Victoria				1994	226		Breeding Bird Survey
Victoria				1995	55		Breeding Bird Survey
Victoria				1996	50		Breeding Bird Survey
Victoria				1998	85		Breeding Bird Survey
Victoria				1999	66		Breeding Bird Survey

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Victoria				2000	55		Breeding Bird Survey
Victoria				2001	61		Breeding Bird Survey
Victoria				2002	52		Breeding Bird Survey
Vivian Island		49.84	-124.70	1966	59		Campbell et al 1990
Vivian Island		49.84	-124.70	1970	75		BC Nest Record Scheme
Vivian Island		49.84	-124.70	1972	240		Merilees et al. 1973, BC Nest Record Scheme
Vivian Island		49.84	-124.70	1974	218		Campbell 1976
Vivian Island		49.84	-124.70	1975	245		Campbell et al 1990
Vivian Island		49.84	-124.70	1978	240		BC Nest Record Scheme
Vivian Island		49.84	-124.70	1986	208		Vermeer and Devito 1989

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
Vivian Island		49.84	-124.70	2006	0	R Butler	Rob Butler unpubl. data
Wallace Island		48.94	-123.56	1974	3	MS Rodway, RW Campbell	BC Nest Record Scheme
Wallace Island		48.94	-123.56	1977	12	MS Rodway, RW Campbell	BC Nest Record Scheme
Wallace Island		48.94	-123.56	1985	3		Vermeer and Devito 1989
Wallace Island		48.94	-123.56	1986	3		Vermeer and Devito 1989
White Islets[32]		49.42	-123.71	1968	340		BC Nest Record Scheme
White Islets		49.42	-123.71	1974	279		Campbell 1976

[32] White Islet and adjacent rock

Location	Location Description	Lat	Long	Year	No. Nests/ Pairs[1]	Collector (if known)	Source
White Islets		49.42	-123.71	1986	490		Vermeer and Devito 1989
White Islets		49.42	-123.71	2010	253	LK Blight and T Osler	LK Blight unpubl. data
Whyte Islet		49.37	-123.28	1978	6	RW Campbell	BC Nest Record Scheme
Whyte Islet		49.37	-123.28	1981	22	M Lemon	M Lemon unpubl. data
Whyte Islet		49.37	-123.28	1986	10		Vermeer and Devito 1989
Whyte Islet		49.37	-123.28	1999	0	M Lemon	M Lemon unpubl. data
Whyte Islet		49.37	-123.28	2010	0	LK Blight and T Osler	LK Blight unpubl. data