UC Santa Cruz

UC Santa Cruz Electronic Theses and Dissertations

Title

Subsidized predators and imperiled prey: the impact of avian predators on salmonids

Permalink

https://escholarship.org/uc/item/0w70j720

Author

Osterback, Ann-Marie Kristina

Publication Date

2014

Peer reviewed|Thesis/dissertation

eScholarship.org Powered by the California Digital Library
University of California

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

Subsidized predators and imperiled prey: the impact of avian predators on salmonids

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Ann-Marie K. Osterback

June 2014

The Dissertation of
Ann-Marie K. Osterback is approved:

_____
Professor Mark H. Carr, Chair

_____
Professor Jonathan W. Moore

_____
Professor Peter. T. Raimondi

_____
Professor Sean A. Hayes

_____
Tyrus Miller
Vice Provost and Dean of Graduate Studies

Copyright © by

Ann-Marie K. Osterback

2014

Table of Contents

List of Tables vi

List of Figures vii

Abstract xi

Acknowledgements xiv

Introduction 1

1. Chapter 1 - High predation on small populations: avian predation on imperiled salmonids 6
   1.1. Abstract 6
   1.2. Introduction 7
   1.3. Methods 11
      1.3.1. Study System 11
      1.3.2. Data Collection and Modeling 14
   1.4. Results 22
      1.4.1. Steelhead Recapture Study 23
      1.4.2. Transportation ("Hotdog") Experiment 23
      1.4.3. Estimating Transportation and Predation 25
   1.5. Discussion 27
   1.6. Tables 33
   1.7. Figures 35

2. Chapter 2 - Linking individual size and rearing history to survival and predation risk of threatened steelhead (*Oncorhynchus mykiss*) 43
   2.1. Abstract 43
   2.2. Introduction 43
   2.3. Methods 45
      2.3.1. Study System 46
      2.3.2. Individual characteristics of juvenile steelhead 47
      2.3.3. Effects of size and origin on predation risk 49
      2.3.4. Effects of size and origin on survival 52

2.4. Results 53
2.4.1. Effects of size and origin on predation risk 54
2.4.2. Effects of size and origin on survival 55
2.4.3. Comparing effects of size and origin between predation risk and survival 56
2.5. Discussion 56
2.6. Tables 65
2.7. Figures 67

3. Chapter 3 - Anthropogenic subsidies and the shifting resource base of a generalist predator: implications for native prey 73
3.1. Abstract 73
3.2. Introduction 74
3.3. Methods 78
3.3.1. Study System 78
3.3.2. Sample Collection 79
3.3.3. Sample Processing 81
3.3.4. Comparing shifts in resource baselines between two consumers 82
3.3.5. Quantifying relative resource use in a generalist consumer over time 83
3.3.6. Investigating individual variation and relation to foraging locations in a generalist consumer. 86
3.3.7. Linking gull population size with steelhead predation risk 87
3.4. Results 90
3.4.1. Comparing shifts in resource baselines between two consumers 90
3.4.2. Quantifying relative resource use in a generalist consumer over time 91
3.4.3. Investigating individual variation and relation to foraging locations in a generalist consumer. 92
3.4.4. Linking gull population size with steelhead predation risk 93
3.5. Discussion 94
3.6. Tables 103
3.7. Figures 104

4. Appendix A – Assumptions of the Model (Chapter 1) 109

4.1. Detection Probability 109
4.2. Transportation Probability 110
4.3. Recapture Probability: Steelhead Tagging 112

5. Appendix B – Evaluating the sensitivity of MixSIAR to input parameters (Chapter 3) 115
5.1. Fractionation Factors 115
5.2. Addressing shifts in prey isotope signatures in the marine environment 118
5.3. Figures 119

Discussion 123
Bibliography 126

List of Tables

Table 1-1. Sample sizes for the steelhead tagging experiment during each outmigration year from 2005 through 2011 at each of the six study watersheds. 33

Table 1-2. Sample sizes for the 2010 transportation experiment for each feed type (hotdogs and capelin). All data are from spring morning (AM) feedings unless otherwise indicated (i.e., PM, summer).....34

Table 2-1. Sample sizes for the predation risk and the survival analysis for Scott Creek steelhead in outmigration years 2005 through 2010. The total number of tagged steelhead (*), the number of tagged individuals subsequently recaptured on ANI after presumably being eaten by a Western Gull (†), and the number of tagged individuals that survived to return as an adult (‡), are indicated.....65

Table 2-2. Best approximating models for the predation risk and survival analysis. All models within < 2 $\Delta AICc_i$ of the best-approximating model are shown below and were incorporated into an averaged model for each analysis, which is recommended when no single candidate model contains more than 0.95 of the model weights ($\boldsymbol{w_i}$), as discussed in Grueber et al. (2011). 66

Table 3-1. Literature values for stable isotope signatures and fractionation factors for $\delta^{13}C$ and $\delta^{15}N$ of five potential prey sources of Western Gulls that were incorporated into MixSIAR. ... 103

List of Figures

Figure 1-1. The three-step process for how PIT tags from tagged juvenile salmonids are recaptured on avian predator colonies, where each step has its own probability of occurrence. For a PIT tag to be recaptured at an avian predator colony, a PIT-tagged salmonid first has to be consumed by an avian predator (with probability θ), transported to the predator colony (with probability ϕ), and then detected on the colony (with probability ψ). Therefore, the probability of recapturing a PIT tag from a tagged salmonid is the probability, or product, of all three steps occurring (with probability $\theta\phi\psi$). 36

Figure 1-2. Location of the six central California (USA) watersheds (Gazos Creek, Waddell Creek, Scott Creek, San Lorenzo River, Soquel Creek, and Aptos Creek) and the seabird breeding colony (Año Nuevo Island) that compose the study area. 37

Figure 1-3. A photo taken at the mouth of Scott Creek, just before the creek enters the ocean. Hundreds of Western Gulls congregate at shallow creek mouths to bathe, drink, and opportunistically feed on items that are transported downstream by stream flow, including outmigrating juvenile salmonids. 38

Figure 1-4. The observed proportion of PIT tags detected at Año Nuevo Island (ANI) during the steelhead tagging study (A) and the transportation experiment (B) for each watershed. The proportion recaptured (A) is based on the proportion of PIT tags recaptured at Año Nuevo Island (ANI) relative to the number of tagged wild juvenile steelhead at each site, where multiple years of recapture data are available for Waddell (N=4 years) and Scott Creeks (N=7 years). The proportion of tags transported and detected (B) is based on the proportion of PIT tags from PIT-tagged hotdogs and capelin detected at ANI relative to the number fed to adult Western Gulls at each site during the transportation experiment.....39

Figure 1-5. Mean number of birds present at each watershed during the transportation experiment, separated by species and by age class (for Western Gull species only). Data were restricted to counts conducted during the spring and morning surveys only to be comparable among sites.....40

Figure 1-6. Site-specific parameter estimates for A) posterior estimates of the probability of transportation (ϕ) of a consumed PIT tag to ANI (median +/- 90% CI), before incorporating the capelin correction factor of 2.3 and B) posterior estimates of probability of predation (θ) of a PIT-tagged steelhead, including sites with a single year of data (white) and the across-year mean predation rate from the hierarchical model for sites with > 3 years of data, which includes Waddell Creek (grey) and Scott Creek (black). Beanplots show the full posterior distribution for each quantity after incorporating the capelin correction factor of 2.3. Horizontal lines indicate median estimates. 41

Figure 1-7. Posterior estimates for the probability of predation (θ) of wild juvenile steelhead by adult Western Gulls for individual years at two sites: Waddell Creek (grey) and Scott Creek (black). Points show median estimates, thick vertical lines show interquartile range, and thin lines show 90% CI. 42

Figure 2-1. Map of the study location, including the Scott Creek watershed (California, USA) and Año Nuevo Island. 68

Figure 2-2. Model averaged parameter estimates for both the predation risk (A) and the survival (B) analysis. Effect sizes were standardized by subtracting the mean and dividing by two times its standard deviation as recommended by Gelman (2008). Effect sizes of each parameter were then compared to a reference state (dashed line with coefficient = 0) to determine how changes in a given parameter would affect the response variable. The reference state for both the predation risk and survival analysis was a wild steelhead with a mean fork length, in outmigration year 2010. All points are coefficient estimates of the averaged model, with 95% confidence intervals. 69

Figure 2-3. The probability of A) predation risk (i.e., tag recapture on ANI), and B) survival for a wild steelhead across the range of fork lengths. Estimates are based on juveniles from outmigration year 2010, which was a year with typical predation risk and survival. Estimates are calculated from the model averaged logistic regression model for both analyses. Shading indicates 95% confidence intervals. 70

Figure 2-4. The increase in odds of survival or predation risk with fork length for wild (A) and hatchery (B) steelhead. Odds ratios were calculated by dividing the survival or predation risk at a given fork length by the survival or predation risk of a fish at the smallest size (65mm). 71

Figure 2-5. Model averaged parameter estimates for both the predation risk (A) and the survival (B) analysis upon outmigration by using the adjusted fork length for wild lagoon-reared individuals. Effect sizes were standardized by subtracting the mean and dividing by two times its standard deviation as recommended by Gelman (2008). Effect sizes of each parameter were then compared to a reference state (dashed line with coefficient = 0) to determine how changes in a given parameter would affect the response variable. The reference state for both the predation risk and survival analysis was a wild steelhead with a mean fork length, in outmigration year 2010. All points are coefficient estimates of the averaged model, with 95% confidence intervals. 72

Figure 3-1. Isotope signatures of δ13C and of δ15N of breast feathers from historical and modern adult Western Gulls (A), historical and modern adult Brandt's Cormorants (B), and isotope signatures of δ13C and of δ15N of breast feathers from historical and modern Western Gulls (mean ± 95% CI) with isotope signatures of potential prey sources, after accounting for fractionation (mean ± SD; Table 3-1) (C). Note the ellipses in 1A and 1C contain identical data, but axes are at different scales. Individual feather samples are indicated by open symbols, means

are indicated by filled symbols, and 95% CI are represented by ellipses. $\delta^{13}C$ isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). 104

Figure 3-2. Proportion of diet sources that contribute to historical (A) and modern (B) Western Gulls. Data are represented as posterior densities from the mixing model output from MixSIAR, using potential prey sources from Table 3-1. $\delta^{13}C$ isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). Note that posterior densities less than 0.0 result from a smoother function to create this graphic. 105

Figure 3-3. Variation in isotopic signatures among individuals from historical (A) and modern (B) Western Gulls. Data are represented as posterior densities from the mixing model output from MixSIAR. $\delta^{13}C$ isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). Note that posterior densities less than 0.0 result from a smoother function to create this graphic. 106

Figure 3-4. The proportion of human food that contributes to individual gull diet for historical and modern Western Gulls. Data are represented as mean posteriors (points) and 90% credible intervals (lines) for prey source of human food from the mixing model output from MixSIAR. Of the 41 modern gulls with isotopic data, 27 of them were radio-tracked and their presence in different foraging locations are indicated in the legend. $\delta^{13}C$ isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007).. 107

Figure 3-5. The relative per capita predation risk (R) of modern verses historical juvenile steelhead (SH) based on the ratio of modern to historical proportion of steelhead to gull diet across a suite of relative increases in gull population size. Relative predation risk was also evaluated across a suite of proportional population decline in steelhead, where different lines denote where modern steelhead abundance is equal (black circle), 30% (dark grey circle), 20% (light grey circle), or 10% (white circle) of historical abundance. The grey shaded region represents the 90% confidence intervals of the proportion of steelhead to gull diet assuming modern steelhead abundance is 30% of the historical abundance. The red square denotes our hypotheses of relative gull and salmonid abundance. Note data are presented on a log scale, such that where x=0 denotes zero change in gull population size, and where y=0 denotes zero change in relative per capita predation risk of salmonids. 108

Figure 5-1. Comparing the proportion of diet sources that contribute to historical and modern Western Gull diet given three different fractionation scenarios: moderate (panels A,B), complex (panels C,D), and simplified (panels E,F). Data are represented as posterior densities from the mixing model output from MixSIAR and δ13C isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). Note that posterior densities less than 0.0 result from a smoother function to create this graphic and that

panels A and B are identical to Figure 3-2 in the main manuscript and are re-introduced here for comparison. See text for details of the three different fractionation scenarios. 119

Figure 5-2. Comparing the proportion of diet sources that contribute to historical Western Gull diet given two different scenarios. Panel A uses the stable isotope signature for current Brandt's Cormorants to represent the stable isotope signature of historical marine fishes and therefore assumes the historical isotope signature of marine fishes is the same across time. Panel A is identical to Figure 3-2A in the main manuscript. Panel B uses the stable isotope signature for historical Brandt's Cormorants to represent marine diet in the early 1900's, whereas all other prey data are identical to Panel A and Table 3-1 in the main manuscript. Data are represented as posterior densities from the mixing model output from MixSIAR. δ13C isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). Note that posterior densities less than 0.0 result from a smoother function to create this graphic. 121

Abstract

Subsidized predators and imperiled prey: the impact of avian predators on salmonids

by

Ann-Marie K. Osterback

Generalist predators can alter or limit the survival of individuals and the dynamics of populations, especially for imperiled prey. The effects of predation can be further exacerbated if anthropogenic subsidies provide novel food sources to predators that decouple predator-prey dynamics and contribute to extinction risk of native prey. However, quantifying predation rates on rare prey is challenging; as is identifying shifts in predator diet and resource use over time. For my research, I developed new approaches and integrated existing methods to quantify predation and evaluate the impact of predation risk of a generalist avian predator (Western Gull, *Larus occidentalis*) on threatened populations of steelhead (*Oncorhynchus mykiss*) in central California (USA), and document temporal shifts in anthropogenic resource use by gulls and the effect on predation risk for steelhead.

This dissertation focuses on three key components to disentangle the relationship between generalist gull predators, threatened steelhead prey, and the role of anthropogenic subsidies in impacting predator-prey dynamics. In Chapter 1, I quantified predation by Western Gulls on imperiled steelhead populations through a novel Bayesian integration of fish tag recoveries, an experiment to quantify tag transportation rates, and monitoring to quantify tag loss. Together, these analyses provide the most robust estimates of avian predation on these imperiled fishes to date, and I found that predation

rates are extremely high (median probability of per capita predation ≥ 0.306 per year). In Chapter 2, I compared individual traits of juvenile steelhead that influence survival to maturity and predation risk by generalist gulls through analyses of over nine years of PIT (passive integrated transponder) tag recapture data. I discovered that large and wild-origin juvenile steelhead were more than 20 times more likely to survive the marine ecosystem than small hatchery individuals, and gull predators preferably consumed wild-origin steelhead, regardless of size class. Based on these data, I estimated that gull predation provides an additive source of mortality and reduces the total population of returning adults by approximately 24%. In Chapter 3, I used stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ to conduct a 100-year retrospective analysis to identify changes in resource use by Western Gulls and implications for threatened steelhead populations. Results from this study suggest gulls have become increasingly reliant on anthropogenic food sources which likely contribute to wider gull niche width and increased predation risk to native steelhead.

Together, these dissertation chapters demonstrate that even opportunistic predation from a generalist predator (i.e., Western Gulls) can provide a significant source of additive mortality to imperiled prey (i.e., juvenile steelhead). Furthermore, my research highlights the role of humans in contributing to the degradation of coastal ecosystems. By providing new food sources from landfills, humans indirectly enhance abundance of opportunistic generalist predators such as gulls and contribute to steelhead population decline.

Dedicated to my hard-working, patient, and endlessly supportive grandparents,

Boris J. Osterback and *Anni G. Osterback*

Acknowledgements

I have been very fortunate to have such a knowledgeable and talented committee to guide me throughout my graduate career. Jon Moore's broad ecological perspective, creative problem-solving, and ability to distill the complexity of ecological puzzles inspired me to take new and unique approaches to my research. Jon also has been a patient and supportive mentor and has served as a great example of how to balance career, family, and recreation. When Jon transitioned to Simon Fraser University, Mark Carr enthusiastically welcomed me into his lab. Mark is an absolute joy to work with, with an infectiously positive attitude and passion for ecology. Despite not being a freshwater ecologist by training, Mark provided unique ecological insight that greatly influenced the direction of my research. I also want to sincerely thank Pete Raimondi for his creativity and incredible intuition for overcoming dataset limitations. With Pete's guidance, I was able to distill complicated results in clear and intuitive ways, while remaining statistically sound. Pete's mentorship and endless patience provided critical encouragement when it was needed most. Last, but very far from being least, I want to thank Sean Hayes. Sean was my biggest supporter when I was considering pursuing a PhD. His encouragement and confidence in my success is what allowed me to start and complete my dissertation. Furthermore, his passion for salmon and keen awareness for information gaps in salmonid conservation and management ensured my research would be useful in addressing important questions that could be applied to salmonid recovery.

Other members of the gull predation group—Scott Shaffer, Danielle Frechette, and Morgan Bond—all contributed greatly to my dissertation. Although Scott was not officially on my committee, he provided critical funding sources and much-needed

guidance on topics such as avian ecology and stable isotope analysis. Danielle Frechette's collaboration, incredibly strong work ethic, and keen observations provided insight and data that contributed immensely to my research. The impressive amount of work and thought that Morgan Bond put into this project before I arrived as a graduate student set the stage for a successful research project, and his continued collaboration has improved my research. As a result, the first Chapter of this dissertation was published in Ecosphere (Osterback et al. 2013), and was a result of the collaborative effort with these talented individuals.

None of my research would have been possible without financial and logistical support. I received financial assistance from the California Department of Fish and Game Fisheries Restoration Grant Program, California SeaGrant College R/FISH-205, the Marilyn C. and Raymond E. Davis Memorial Professional Development Award, the Dr. Earl and Ethel M. Myers Oceanographic and Marine Biology Trust, the International Order of Runeburg and the Services for Transfer and Re-entry Students at UC Santa Cruz. Access to my study sites would not have been possible without Big Creek Lumber, Steve Auten and Brian Dietterick from Swanton Ranch, and Dave Streig and Carla Moss at the Monterey Bay Salmon and Trout Project. Access to Año Nuevo Island would not have been possible without skilled zodiac operation, provided by Pat Morris, Guy Oliver, Rick Condit, Michelle Hester, and Ryan Carle. Furthermore, feather sample collection from the Museum of Vertebrate Zoology and by volunteers at the BeachCOMBERS Program was critical for my research.

It turns out that research and life can present a lot of challenges over six years, so I am especially grateful for the support and friendship of other graduates. Starting at Day

1, Cohort '08 is likely the greatest group of women (+ 1 man) that I have met—of 17 people, I respect and enjoy the company of every single one of them. I am excited to continue to cross paths with them as we progress in our careers. Corey Phillis, Mike Beakes, and Mark Novak—the original Moore Labbies—thank you for the hugs, support, and nudges when I needed a jump start. When the Moore Lab migrated north, the RC lab didn't skip a beat in welcoming me into the lab, even though I didn't SCUBA or poke around in the intertidal; thank you for your kindness and great senses of humor.

Despite my shift in lab affiliation, my association with the Southwest Fisheries Science Center (NMFS) remained strong throughout my graduate career, and I am thankful for their friendship and support. In particular, Cyril Michel has been my NMFS-labmate for the last 6 years, and with his humor and sincerity has been a great friend and colleague. Cyril also introduced me to Dinner Clubbers- Alice, Rodrigo, Alicia, Jimmy, and Sally- who have brought a ton of laughter and the appreciation of preparing great food into my life. I also want to thank Nic Retford, Jeff Perez, Joe Kiernan, and the many volunteers and undergraduate interns that have kept Scott Creek operational, especially during lapses in funding. If it wasn't for your hard work-ethic and love of salmon, I would have never made it this far.

Many individuals have guided me through tough datasets, error messages in R, and theoretical questions about ecology and data analysis. In particular, Ole Shelton patiently introduced me to Bayesian statistics; he is a great teacher and friend. Through Ole, I became part of the Ole Hour contingent which included many wonderful and bright researchers at NMFS and UCSC- Aaron, Heather, Cameron, Will, Arliss, Autumn-

Lynn, Melinda, and Melissa—all who have been incredibly supportive with data analysis, graphics, and easing graduate frustrations.

Of course, I would have never even gone to grad school if it weren't for the friends and family that encouraged and supported me along the way. I thank my previous employers, Stillwater Sciences—and all the wonderful friends and colleagues there—that gave me the skills to feel confident in pursuing a graduate degree and the friendship that supported me once I began. I thank my closest friends— Kristin, Nikki, Sabrina, Paul, David, and Shannon—for reassurance during times of doubt. I also cannot thank my parents, Ralph and Carita, and my brother Kaj enough. When struggling with whether to continue for a PhD, they overwhelmingly supported and encouraged me to continue my research. Conversations with them are what led to my decision to pursue a doctorate.

It's impossible to thank Bill enough for being my partner throughout this process. His relentless support and positive attitude are inspiring and I am forever grateful.

Introduction

Predator-prey relationships are important components of ecosystems that can drive co-evolution (Brodie et al. 2002), structure communities (Paine 1966), and regulate populations (Holling 1959). While population regulation can occur between a single predator and single prey species (Elton and Nicholson 1942), predation can also create complex interactions and indirect effects within an ecosystem. For example, asymmetric apparent competition occurs when the presence or increased abundance of one prey species increases the population of a shared generalist predator and results in the subsequent decline of another prey population (Holt 1977). Human subsidies can contribute to asymmetrical apparent competition by providing renewable food sources that sustain populations of generalist predators and result in continued predation pressure on native prey (DeCesare et al. 2010, Oro et al. 2013). Thus, subsidies can decouple predator -prey relationships and can result in the loss of one or many species (Huxel and McCann 1998).

Coastal ecosystems are particularly susceptible to the effects of anthropogenic alterations due to concentrated human populations and high rates of resource extraction from coastal environments. Many populations of opportunistic gull species (*Larus* spp.) thrive in these altered coastal landscapes where anthropogenic food sources from fisheries discards or human food at landfills have subsidized their diet and contributed to population increases (Blokpoel and Spaans 1991, Yorio and Giaccardi 2002, Duhem et al. 2008). In some cases, subsidized gull populations subsequently contribute to the decline of native prey (Voorbergen et al. 2012). On the central California coast (USA), Western Gulls (*Larus occidentalis*) have been observed feeding on a wide variety of

resources, including anthropogenic sources (e.g., landfills) and threatened and endangered populations of juvenile salmonids (*Oncorhynchus spp.*). Furthermore, the breeding population of Western Gulls has increased and is currently 2-4 times larger than in the 1980's (Hester et al. 2013). For my dissertation, I was motivated to disentangle the relationship between generalist gull predators, their imperiled salmonid prey, and the role of human subsidies in shaping predator-prey dynamics. Specifically, I aimed to quantify predation rates by Western Gulls on juvenile steelhead (*O. mykiss*) to understand whether gull predation may limit the recovery of imperiled salmonids, and explore whether anthropogenic resources indirectly contribute to salmonid decline by subsidizing gull diet.

Until recently, the impact of avian predation on salmonids was largely unknown, especially in central California (Bond et al. 2008, Evans et al. 2011, Frechette et al. 2012). Furthermore, quantifying predation on small populations is inherently difficult, so methods that provide robust estimates for rare predation events were lacking. Therefore, for Chapter 1 of my dissertation, I aimed to provide the first estimate of Western Gull predation on juvenile steelhead and developed a novel technique to estimate predation indirectly. Within a Bayesian modeling framework, I was able to indirectly estimate the probability a juvenile steelhead would be consumed by a Western Gull by incorporating estimates of salmon tag recoveries on a gull breeding colony, an experiment to quantify tag transportation rates, and monitoring to quantify tag loss. Out of the six study creeks, juvenile steelhead in the three creeks closest to the gull breeding colony experienced the highest predation rates, consuming approximately 30% or more of the tagged juvenile steelhead population per year. The results of this chapter provide a novel approach to

indirectly estimate rare predation events and also demonstrate that opportunistic generalists can have a significant impact even through opportunistic and incidental predation.

The impact of predation on prey populations largely depends on whether predation is *additive* such that it contributes to the overall prey mortality rate, or *compensatory* such that prey would otherwise die from other causes (Burnham and Anderson 1984). For example, predators that target prey with high chances of survival have a larger impact on the prey population than if they targeted individuals susceptible to mortality from other sources such as from other predators or climactic stress (Griffin et al. 2011). Therefore, Chapter 2 of my dissertation evaluated whether Western Gulls remove individual steelhead from the population that have characteristics that lend them to high survival and are likely to contribute to the productivity of these imperiled prey populations. To do this, I compared individual characteristics of juvenile steelhead such as origin (hatchery verses wild) and body size that were consumed by gulls to the characteristics of juveniles that survived to maturity. The results of this study show overlap in the characteristics that end in these two fates, such that wild-origin steelhead were both more likely to survive and to be eaten by gulls. Interestingly, gulls consumed individuals across the entire range of steelhead body sizes, while large individuals experienced greater survival to maturity. The results of this study suggest that while gulls are not selecting steelhead based on body size, they are removing a higher proportion of wild steelhead from the population, including the large individuals that are important for population recovery. As a result, I estimate gull predation may reduce the spawning adult

population by approximately 24%, and likely provide at least a partially additive source of mortality for threatened and endangered salmonids.

The previous two dissertation chapters document the impact of Western Gull predation on juvenile steelhead population dynamics and recovery; in Chapter 3 of my dissertation I evaluate the underlying sources that contribute to high rates of gull predation. For this chapter, I used a 100-year retrospective stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ to identify how long-term changes in gull diet, gull population size, and steelhead population size contribute to predation risk of juvenile steelhead. Through the use of Bayesian stable isotope mixing models (*MixSIAR;* Stock and Semmens 2013), I determined that gull reliance on anthropogenic resources has increased substantially over the last 100 years, while the contribution of steelhead to gull diet has declined. Even though modern gulls consume relatively less steelhead per individual, the large increase in gull populations and precipitous decline in steelhead populations over the last 100 years results in approximately 2.4 times the per capita predation risk for modern individual juvenile steelhead. These data support the possibility that anthropogenic sources may be contributing to increased gull predation on steelhead, although many other factors may also be contributing to gull population increases. This link between anthropogenic sources and gull population increase has been suggested in many other systems (Blokpoel and Spaans 1991, Yorio and Giaccardi 2002, Duhem et al. 2008). Regardless of the source of gull population increase, this study documents gulls have increased reliance on anthropogenic sources over the last century, and along with rising gull populations and plummeting salmonid populations, individual steelhead experience higher predation risk.

Human alteration to the landscape can significantly alter predator-prey interactions, and can even result in decline of native prey (DeCesare et al. 2010, Oro et al. 2013). This dissertation contributes novel research that provides robust quantitative estimates of predation rates by gulls on juvenile steelhead, reveals predation provides an additive source of mortality thus impacting steelhead population sizes, and incorporates the role of human subsidies in contributing to predation risk of salmonids. Together, these chapters emphasize that even incidental predation or opportunistic generalist predators have a significant impact on the native prey species, and humans are likely contributing to increased predation rates by providing gulls with human food at landfills and other urban areas. These data suggest that management might consider reducing subsidies to generalist predators to reduce predation on imperiled steelhead. More generally, our data suggest that management of imperiled salmon should consider the food webs that they inhabit, including their predators. By further understanding the impact of Western Gull predation on juvenile steelhead and the sources that contribute to predation risk, we can better inform management actions directed at recovery of imperiled salmonids.

1. Chapter 1 - High predation on small populations: avian predation on imperiled salmonids

1.1. Abstract

Generalist predators can contribute to extinction risk of imperiled prey populations even through incidental predation. Quantifying predation on small populations is important to manage their recovery, however predation is often challenging to observe directly. Recovery of prey tags at predator colonies can indirectly provide minimum estimates of predation, however overall predation rates often remain unquantifiable because an unknown proportion of tags are deposited off-colony. Here, we estimated overall predation rates on threatened wild juvenile steelhead (*Oncorhynchus mykiss*) by generalist adult Western Gulls (*Larus occidentalis)* in six central California (USA) watersheds. We estimated predation rates by gulls from the recapture of PIT (passive integrated transponder) tags that were originally inserted into steelhead and were subsequently deposited at a Western Gull breeding colony, Año Nuevo Island (ANI). We combined three independent datasets to isolate different processes: (1) the probability a tagged steelhead was consumed during predation, (2) the probability a consumed tag was transported to ANI, and (3) the probability a transported tag was detected at ANI. Together, these datasets parameterized a hierarchical Bayesian model to quantify overall predation rates while accounting for tag loss between when prey were tagged and subsequent tag detection at ANI. Results from the model suggest that low recovery rates of PIT tags from steelhead at ANI were mostly driven by low probabilities of transportation (≤0.167) of consumed tags to ANI. Low transportation probabilities

equate to high per-capita probabilities of predation (≥0.306 per yr) at the three watersheds in closest proximity to ANI, whereas predation rates were uncertain at watersheds farther from ANI due to very low transportation rates. This study provides the first overall estimate of Western Gull predation rates on threatened wild juvenile steelhead and suggests gull predation on salmonids is a larger source of mortality than was previously estimated from minimum predation rates. This study thus represents an important example of high rates of incidental predation by a generalist consumer on an imperiled prey and provides a quantitative framework to inform robust estimates of predation rates on small populations that can be applied to other systems where direct observation of predation is not feasible.

1.2. Introduction

Predation on imperiled populations may contribute to extinction risk or limit their recovery. In some cases, small prey populations may be relatively buffered from predation when refuges are available or if predators switch to target more abundant prey (Holling 1959, Ackerman 2002, Twardochleb et al. 2012). Furthermore, if predators are specialists, their populations may decline following the decline of their prey, thereby reducing predation rates (Elton and Nicholson 1942, Hanski et al. 2001). Alternatively, if generalist predators continue to prey on small populations, these prey populations may suffer local extinction (Spiller and Schoener 1998) or may experience further population decline even when predation is incidental (Vickery et al. 1992). In these scenarios, there may be few prey individuals relative to the number of predators, and even incidental predation can result in high predation rates (Wittmer et al. 2005). Therefore, the role of

predation by generalist predators can be an important factor in the dynamics of small prey populations.

Quantifying predation rates on imperiled populations is often difficult as predation is a rare event with few prey relative to predators. For this reason, researchers have applied a variety of approaches to estimate predation rates indirectly. Estes et al. (1998) estimated predation rates on sea otters (*Enhydra lutris*) by comparing long-term population trends in locations with and without predatory killer whales (*Orcinus orca*). Visual observations and bioenergetics models were combined to quantify the impact of killer whale predation on sea otter populations (Estes et al. 1998, Williams et al. 2004). Alternatively, Fernández-Olalla et al. (2012) combined long-term monitoring of population decline of a vulnerable grouse species (*Tetrao urogallus*) with the removal of mesopredators to quantify the impact of predation on the grouse population growth rate which guided management strategies for population recovery. In both studies, long-term datasets and natural or intentional experiments facilitated quantification of the impact of predators on the decline of native prey. However, long-term population data are rare, especially in conjunction with manipulations of predator populations. Therefore, estimating predation in the absence of long-term data may be necessary to identify significant sources of mortality for populations at risk of extirpation.

In systems with central-place foragers, the return of predators with prey items to their roosting or nesting sites can be used to estimate rates of predation. Specifically, where prey can be uniquely marked with identification tags, recovery of regurgitated or defecated prey tags at predator roosting or breeding sites can be used to quantify minimum predation rates. This method has been applied in freshwater and marine

systems where fish tags were recovered within colonies of piscivorous avian predators (e.g., Evans et al. 2011, Frechette et al. 2012). For example, passive integrated transponder (PIT) tags are often used to individually mark juvenile salmonids (*Oncorhynchus* spp). These tags can be subsequently detected at piscivorous avian predator colonies once predators have regurgitated or defecated the consumed tag. For example, by using the recovery of PIT tags, Evans et al. (2012) estimated that predation by Caspian Terns (*Hydroprogne caspia*) and Double-crested Cormorants (*Phalacrocorax auritus)* constitute between 2.5% and 16% of juvenile salmonid mortality in the Columbia River. Because PIT tags are passive and therefore cannot be detected remotely, estimates of predation rates using recoveries of prey tags require that tags are (1) consumed during predation, (2) transported to the predator colony, and then (3) successfully detected at the colony with a mobile PIT tag antenna (Figure 1-1). Successful recoveries of tags, therefore, only represent consumed tags that undergo all three steps and therefore do not include tags that were lost between steps. Thus, as acknowledged by previous studies, predation estimates from tag recoveries only represent minimum predation rates (Evans et al. 2012, Frechette et al. 2012). To this point, no peer-reviewed study has incorporated estimates of these three processes and their uncertainty to estimates of predation.

Pacific salmon and steelhead (*Oncorhynchus mykiss*) populations along the west coast of North America have declined over the last century due to destruction of habitat, climate change, artificial propagation from hatcheries, construction of dams, over-harvest, and other anthropogenic and natural factors (Ruckelshaus et al. 2002, Gustafson et al. 2007). Consequently, approximately half of the unique Pacific salmon populations

in the United States (managed as Evolutionary Significant Units for salmon or Distinct Population Segments for steelhead) have been listed as threatened or endangered under the Endangered Species Act (Good et al. 2005). Whereas anthropogenic factors have substantially reduced many salmon populations (Sheer and Steel 2006, Selbie et al. 2007), the added impacts of predation may drive further population decline or impede recovery. Concerns regarding the impact of avian predation on salmonid populations has resulted in extensive research in large river systems such as the Columbia River Basin (Collis et al. 2001, Antolos et al. 2005, Good et al. 2007, Evans et al. 2012) and the Sacramento-San Joaquin River Basin (Evans et al. 2011, Adrean et al. 2012), whereas relatively little is known about the impact of avian predators on salmonids in the many small coastal watersheds along the coast of California (but see Frechette et al. 2012). California salmon populations are at the southern extent of the species' ranges and are of particular concern as many populations are declining (Moore et al. 2011). For example, coastal populations of endangered coho salmon in small central California watersheds are nearing extinction (Miller 2010). Due to a lack of data on natural sources of mortality, the recently released central coast coho salmon recovery plan recommended an assessment of avian predation on coho salmon to determine the impact predation has on salmon mortality (National Marine Fisheries Service 2012). Therefore, quantifying predation on imperiled populations of salmon may identify a critical factor that influences their recovery or extirpation.

Here we estimate predation rates on imperiled populations of threatened wild juvenile steelhead by adult Western Gulls (*Larus occidentalis)* in central California watersheds. Western Gulls are abundant generalist predators that feed on trash, carrion,

and are known to prey on outmigrating juvenile salmonids (Frechette et al. 2012). In this study, we ask: what are overall predation rates by Western Gulls on wild juvenile steelhead and how do predation rates by these central-place foragers vary among watersheds and years? We use a large dataset of tagged juvenile steelhead and associated recaptured tags at Año Nuevo Island (ANI) where a large Western Gull colony is located to provide estimates of predation. We develop a Bayesian model that integrates three datasets to provide estimates of gull predation that account for tag loss between the initial PIT tagging of juvenile steelhead and the subsequent detection of PIT tags at ANI. These methods provide the first overall estimate of adult Western Gull predation rates on threatened populations of central California coast steelhead. From a methodology perspective, this research highlights the importance of estimating multiple processes of unobserved tag loss and using a robust quantitative framework to accurately estimate predation rates.

1.3. Methods

1.3.1. Study System

We studied six coastal watersheds within San Mateo and Santa Cruz counties (California, USA) and Año Nuevo Island (ANI), a small island (10 ha) located 1.6 km off Point Año Nuevo (Figure 1-2). ANI provides habitat to many species of seabirds and marine mammals, and is one of the three largest Western Gull colonies in central California (Carter et al. 1992, Capitolo et al. 2009). All six study watersheds (Gazos Creek, Waddell Creek, Scott Creek, San Lorenzo River, Soquel Creek, and Aptos Creek)

drain directly into the Pacific Ocean and support wild populations of threatened central California coast steelhead. The populations of steelhead in the study watersheds are small; for instance, the abundance of adult steelhead in Scott Creek from 2004 through 2012 ranged from only 109 to 440 individuals (Hayes et al. 2013). We focused on wild juvenile steelhead for this study because they are the only salmonid species present at all six study watersheds. It is worth noting that Scott Creek also supports hatchery-raised steelhead and a small run of wild and hatchery-raised endangered coho salmon (*Oncorhynchus kisutch*). The Scott Creek population of coho salmon is generally recognized as the southernmost population of coho (Federal Register 2005) and although they are also likely exposed to gull predation, their numbers are too small to quantify predation.

The study region is dominated by a Mediterranean climate with warm dry summers and mild wet winters. Stream flow in the study creeks varies with episodic rainfall in the winter, whereas in the late summer and fall the combination of low stream flow and oceanic wave action at creek mouths result in a bar-built estuary that creates a freshwater lagoon. Typically, sand bar formation creates a barrier between creek surface flow and the ocean, thereby restricting the timing of juvenile salmonid outmigration to the winter and spring seasons when the creeks are connected to the ocean (Hayes et al. 2008, 2011, Bond et al. 2008).

During the juvenile salmonid outmigration period (typically December through June), Western Gulls use shallow creek mouths to drink, bathe, and opportunistically prey on outmigrating juvenile salmonids as they migrate to the ocean (Figure 1-3). Therefore, Western Gulls prey primarily on juvenile steelhead after steelhead survived the mortality bottlenecks within their first year of life and completed the freshwater

rearing phase of their lifecycle. The number of adult Western Gulls breeding at ANI increased by almost an order of magnitude from 1976 to 2003 (Thayer and Sydeman 2004). This increase is possibly due to accessibility of anthropogenic food sources, including local waste management facilities (i.e., landfills), which may subsidize the gull population and could contribute to incidental predation and local extinction of steelhead populations (Chapter 3).

There is both direct and indirect evidence that Western Gulls are predators of juvenile salmonids in the study region. First, we directly observed both juvenile and adult Western Gulls feeding on outmigrating juvenile salmonids at the shallow mouth of Scott Creek (Frechette 2010). These predation events were infrequent or sporadic enough that quantifying predation rates through direct observation alone was not feasible. Second, we previously documented that between 0.1 and 4.6% of all PIT tags from juvenile salmonids from each of the six study watersheds were detected at ANI (Frechette et al. 2012). Although other species of piscivorous birds and mammals use ANI for breeding and roosting habitat, we identified adult Western Gulls as the primary predator species and age class responsible for deposited PIT tags at ANI (Hayes et al. 2012, Frechette et al. 2012). The predation rate estimates reported by Frechette et al. (2012) represent minimum estimates because PIT tags were recaptured after being consumed during predation by a gull, transported to ANI, and subsequently detected at ANI (Figure 1-1). As a result, overall predation rates are potentially much higher than the reported minimum predation rate estimates.

1.3.2. Data Collection and Modeling

We combined three independent datasets to parameterize the variables required to estimate overall predation rates of juvenile wild steelhead by adult Western Gulls at each of the six study watersheds. We describe the first two datasets in turn. The third dataset is from a previous study (Frechette et al. 2012) and is incorporated in the model parameters. We then detail a model for estimating predation rates from these data. Therefore this study evaluates all three steps of tag recapture at ANI, and quantifies the probability tagged steelhead were preyed on, transported to, and detected at ANI (Figure 1-1).

Steelhead Tag Recapture Study —We and the National Marine Fisheries Service (NMFS) PIT-tagged wild juvenile steelhead in the six study watersheds and subsequently scanned ANI annually to detect any deposited PIT tags that were regurgitated or defecated by Western Gulls. This component of the study represents the recapture probability, which is the net probability of predation, transportation, and detection probabilities (Figure 1-1). PIT tagging of juvenile steelhead in the study watersheds was conducted by the NMFS between 2003 and 2011. Fish were captured through a combination of downstream migrant trapping, beach seining, and backpack electrofishing. At Gazos Creek, San Lorenzo River, and Aptos Creek, juvenile steelhead were captured exclusively in the lagoon by beach seining. Although fish were also captured with beach seining in the lagoons of the other three watersheds (Waddell, Scott, and Soquel Creeks), steelhead were also captured in downstream migrant traps in the creek mainstem (Waddell and Scott Creeks only) and during electrofishing surveys in the upper watershed (Scott and Soquel Creeks only). Individuals tagged in the lagoon are

predominately age 0+ and age 1+ steelhead, whereas individuals tagged in the creek mainstem and upper watershed include the entire range of age classes, some of which may never attempt to out-migrate (Hayes et al. 2008). Therefore, our estimates reflect Western Gull predation on the entire tagged wild juvenile steelhead population in each watershed as they migrate out to the ocean. All juvenile steelhead were handled according to Hayes et al. (2004), where date, time, watershed, and morphometric features (fork length and weight) were recorded for each fish. We quantified watershed distance as the linear distance of the creek mouth to Año Nuevo Island (ANI). Beginning in 2006, we scanned ANI annually to recapture deposited PIT tags. We conducted scans by traversing the entire island with a mobile PIT antenna (for equipment specifications, see Bond et al. 2007) and GPS to mark location and identification of deposited tags (for more details, see Frechette et al. 2012). Because annual scans at ANI did not begin until 2006, we excluded from our analysis all steelhead PIT-tagged prior to 2005. This was done to avoid the complication of potential loss of tags to wave action or burial in years prior to annual scanning that could skew recapture rates for those years.

To account for the variation in outmigration timing of juvenile steelhead, we assigned each steelhead an outmigration year based on the date each fish was last handled and the date of lagoon closure at Scott Creek. For example, tagged juvenile steelhead last handled prior to lagoon closure (January until lagoon closure) were assumed to out-migrate that same calendar year before low stream flow resulted in lagoon closure. Tagged juveniles last handled after lagoon closure were categorized as outmigrants in the following year because outmigration cannot resume until the following winter when adequate rainfall opens the lagoon and reconnects the creek with

the ocean. The date of lagoon closure at Scott Creek was applied to the other five watersheds because consistent data are lacking on the timing of lagoon closure at other sites.

Transportation ("Hotdog") Experiment —In 2010, we fed between 43 and 586 PIT tags to adult Western Gulls at each creek mouth and then subsequently scanned ANI to quantify the proportion of experimental tags that were successfully transported and detected on the island. Therefore this experiment evaluated the last two steps of tag recapture at ANI: transportation and detection (Figure 1-1). From 18 March 2010 through 7 July 2010, we fed gulls at two watersheds on each sampling day using stratified sampling to randomly select watershed and order (first or second site of the day). Stratified sampling was conducted to minimize effects of season and time of day on transportation rates by ensuring that all sites were visited at least once before any one site was revisited, and all sites were visited with a similar representation of first or second feedings of the day. PIT tags were fed to gulls at creek mouths using two different vehicles of delivery. For the first method, PIT tags were inserted into miniature hotdogs (Hillshire Farm Beef Lit'l Smokies®) and tossed out with a folding slingshot to maximize the number of different individual gulls that ingested tags. Hotdogs were used as an economical way to deliver PIT tags to gulls. We also inserted PIT tags into pre-thawed Icelandic capelin (*Mallotus villosus*) in a paired experiment to evaluate whether hotdogs were appropriate substitutes for PIT-tagged fish. The Icelandic capelin is a pelagic fish similar in size and shape to juvenile steelhead. The two delivery methods (hotdogs and capelin) were used as proxies for juvenile steelhead since feeding tagged juvenile steelhead to avian predators was not permitted due to the threatened status of these fish.

A primary observer directly observed tag consumption by gulls with the unaided eye and a second observer confirmed each consumption event using 8 x 42 binoculars. Species and age class were recorded for each bird that consumed an experimental tag, and the total count of each species and age class of all birds at the creek mouth were recorded at each site after all tags were fed.

To evaluate whether feed type, time of day, or season influenced transportation rates of PIT tags to ANI, we conducted paired analyses at the three most northern watersheds: Gazos Creek, Waddell Creek, and Scott Creek. We evaluated these comparisons at the northern watersheds only because we postulated watersheds closer to ANI would have the highest transportation rates and therefore yield a larger sample size to adequately address these comparisons. We evaluated the influence of feed type on transportation rates by feeding both hotdogs and Icelandic capelin at all three of these watersheds. To evaluate whether time of day influences transportation rates, we also conducted paired evening (between 18:00 and 19:00) and subsequent morning (between 07:00 and 11:00) feedings at Gazos Creek. We also compared transportation rates between seasons at Waddell Creek in order to capture variation in transportation rates due to different periods of juvenile salmonid outmigration activity, such as (1) the peak outmigration period (March-May), and (2) after the completion of outmigration (June-July). To reflect these different outmigration periods, seasonal feedings were categorized into Spring (2 April 2010 through 7 May 2010) and Summer (16 June 2010 through 6 July 2010) at Waddell Creek. After completion of the feeding experiments, we scanned Año Nuevo Island for PIT tags from hotdogs and Icelandic capelin. The entire colony

was scanned twice, once during 2010 and once during early 2011, to increase our probability of detecting deposited experimental tags.

We restricted our analysis of predation and transportation rates to experimental PIT tags eaten by adult Western Gulls only, because they overwhelmingly represent the dominant species and age class of gulls that use ANI for breeding and roosting habitat and were identified as the dominant species and age class responsible for tag deposition at ANI (Frechette et al. 2012). If an adult Western Gull was uniquely identifiable (e.g., natural external markings or location during feeding) and ate more than one tag during a single feeding event, we only included one tag in the analysis to preserve sample independence. Additionally, we restricted the analysis to fed PIT tags where the observers were confident of bird species identification, age classification, and confirmation that the tag was consumed. Therefore, we excluded tags from our analysis that were either out of the observers' sight before being consumed by a gull or when gull species and age class were uncertain. We used a Fisher's Exact test to evaluate whether adult Western Gulls exhibited significantly different transportation and detection rates depending on differences in feed type, time of day, or season of each feeding.

Estimating Transportation and Predation —In this section, we present a hierarchical Bayesian method to combine all three datasets to estimate the annual predation rate of adult Western Gulls on wild juvenile steelhead at each watershed, and when possible, each year. We assigned θ_{iy} as the probability that a wild PIT-tagged juvenile steelhead is consumed by an adult Western Gull in outmigration year y at watershed i. Let ϕ_i be the probability that a tagged steelhead is transported to ANI

given it was consumed at watershed i, and ψ be the probability that a PIT tag is detected at ANI given it was transported to the island. The parameters θ_{iy}, ϕ_i, and ψ are bounded between 0 and 1. Assuming independence among the three steps of predation (θ_{iy}), transportation (ϕ_i), and detection (ψ), the probability of recapturing a PIT tag from a steelhead tagged at a given site and year is the product of these three probabilities: $\theta_{iy}\phi_i\psi$. Similarly, the probability of observing a PIT tag from a tagged hotdog or capelin at ANI that was fed to an adult Western Gull is $\phi_i\psi$ because all PIT tags included in the analysis were consumed by a gull in this experiment and therefore $\theta_{iy} = 1$. For the probability of detecting a PIT tag that had been deposited at ANI (ψ), we used the estimated probability of tag capture (0.644 ± 0.083 SE) reported by Frechette et al (2012). Briefly, this detection probability was generated using the POPAN variant of the Jolly-Seber model within Program MARK, for combined PIT tag recapture data from all six study watersheds during scans of ANI conducted between 2006 and spring 2009 (see Frechette et al. 2012 for detailed methods). From surveys of ANI, we observed k_{iy} PIT tags from tagged steelhead out of n_{iy} deployed during steelhead tagging (see Table 1-1 for sample sizes) and observed l_i PIT tags from tagged hotdogs or capelin out of m_i that were fed to adult Western Gulls during the transportation experiment (see Table 1-2 for sample sizes).

We assume the probability of transportation is a smooth function of the distance of each site from ANI in kilometers d_i, and can be modeled as a logistic function.

$$\phi_i = \frac{1}{1+exp(-(\alpha+\beta d_i))} \quad (1)$$

We estimated the predation rate hierarchically at the two sites for which we have at least four years of salmonid PIT tags detected at ANI (Waddell Creek and Scott Creek) and only estimated a single θ_i at the remaining four sites. For hierarchical sites, we modeled the predation rate in each year as a draw from a site-specific beta distribution, $\theta_{iy} \sim Beta(\gamma_i \delta_i)$. This formulation allows for inference about among-year variation in predation at each site.

We were interested in estimating the joint posterior distribution of all of the parameters given the observed data. Throughout, bold symbols indicate vectors. For notational simplicity let $\boldsymbol{\Omega}$ indicate the set of non-hierarchical parameters, $\boldsymbol{\Omega} = \{\alpha, \beta, \psi\}$ and $\boldsymbol{x}$ indicate the observed data, $\boldsymbol{x} = \{k, n, l, m, d\}$. Then $p(\boldsymbol{\Omega}, \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\delta} | \boldsymbol{x})$ is the joint posterior distribution of the parameters given the data, $p(\boldsymbol{x} | \boldsymbol{\Omega}, \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\delta})$ is the joint likelihood, and $p(\boldsymbol{\Omega}, \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\delta})$ is the joint prior distribution for the parameters. By Bayes' theorem,

$$\begin{aligned} p(\boldsymbol{\Omega}, \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\delta} | \boldsymbol{x}) &\propto p(\boldsymbol{x} | \boldsymbol{\Omega}, \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\delta})\, p(\boldsymbol{\Omega}, \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\delta}) \\ &\propto p(\boldsymbol{x} | \boldsymbol{\Omega}, \boldsymbol{\theta})\, p(\boldsymbol{\theta} | \boldsymbol{\gamma}, \boldsymbol{\delta})\, p(\boldsymbol{\Omega}, \boldsymbol{\theta}, \boldsymbol{\gamma}, \boldsymbol{\delta}) \end{aligned} \quad (2)$$

with the second line in Eq. 2 showing how the likelihood can be factored into two components. The second term, $p(\boldsymbol{\theta} | \boldsymbol{\gamma}, \boldsymbol{\delta})$, is the beta likelihood for the hierarchical parameters. For a single site i ,

$$p\left(\theta_i \middle| \gamma_i, \delta_i\right) \propto \prod_{y=1}^{Y} \frac{\Gamma\left(\gamma_i + \delta_i\right)}{\Gamma\left(\gamma_i\right) + \Gamma\left(\delta_i\right)} \left(\theta_{iy}\right)^{\gamma_i - 1} \left(1 - \theta_{iy}\right)^{\delta_i - 1} \quad (3)$$

Where $\Gamma(\ )$ indicates the gamma function and Y is the number of years observed. For the sites where we do not estimate hierarchical parameters and assume $p\left(\boldsymbol{\theta} \middle| \boldsymbol{\gamma}, \boldsymbol{\delta}\right)$ is proportional to 1.

The first component of the likelihood, $p\left(\boldsymbol{x} \middle| \boldsymbol{\Omega}, \boldsymbol{\theta}\right)$ is the product of two binomial likelihoods corresponding to the steelhead tag recaptures and transportation experiments, respectively, where I indicates the total number of sites,

$$p\left(\boldsymbol{x} \middle| \boldsymbol{\Omega}, \boldsymbol{\theta}\right) \propto \prod_{i=1}^{I} \prod_{y=1}^{Y} \left[\left(\theta_{iy} \phi_i \psi\right)^{k_{iy}} \left(1 - \theta_{iy} \phi_i \psi\right)^{n_{iy} - k_{iy}} \right] \times \prod_{i=1}^{I} \left[\left(\phi_i \psi\right)^{l_i} \left(1 - \phi_i \psi\right)^{m_i - l_i} \right] \quad (4)$$

Finally, we specified independent prior distributions for parameters. Because previous research estimated detection probabilities for PIT tags at ANI (Frechette et al. 2012), we used a strongly informative independent beta prior distribution for ψ, $p\left(\psi\right) \sim Beta\left(21.05, 11.65\right)$; this is the methods-of-moments estimator for ψ derived from the detection probabilities reported in Frechette et al. (2012). For all other parameters we used diffuse priors. The deposition parameters of α and β exist on the real line, so we used normal distributions with very large variances: $p\left(\alpha\right) \sim N\left(0, 10000^2\right)$, $p\left(\beta\right) \sim N\left(0, 10000^2\right)$. These priors are effectively uniformly distributed. The hierarchical parameters γ and δ must be positive, so we used uniform priors for both

sites: $p(\gamma) \sim Unif(0,25), p(\delta) \sim Unif(0,25)$. Alternate priors had negligible effects on the estimated posterior.

We estimated all parameters for the model using standard Markov chain Monte Carlo (MCMC) approaches in R (v. 2.15.0; R Development Core Team 2012). MCMC sampling was conducted with 1,020,000 draws; the first 20,000 iterations were removed as burn-in. We retained every 200th posterior sample to provide 5,000 independent draws from the posterior distribution. We ran three replicate chains and confirmed model convergence using Gelman-Rubin diagnostics (Gelman and Rubin 1992).

Model Assumptions —Estimated predation rates are based on assumptions made during our individual parameter estimates and our comparisons of tagged fish between watersheds. We mention the major assumptions of the model here and refer readers to the appendix for a thorough justification of the model. The above model assumes (1) the probability of detecting tags is constant across all years; (2) transportation probabilities are constant among years; (3) experimental transportation rates are comparable to transportation rates of consumed steelhead, 4) PIT tags recovered at ANI were transported by adult Western Gulls, and 5) PIT-tagged steelhead are representative of the outmigrating steelhead population. In most cases, our assumptions are necessary and will tend to slightly under-estimate gull predation rates (see discussion and Appendix A).

1.4. Results

1.4.1. Steelhead Recapture Study

We recaptured PIT tags at ANI that were originally inserted into wild juvenile steelhead. In total, we PIT-tagged 16,701 wild juvenile steelhead in the six study watersheds combined and 218 of these were recaptured at ANI (Table 1-1). We observed a higher proportion of recaptured PIT tags from fish from watersheds with increasing proximity to ANI (Figure 1-4). For Waddell Creek, the watershed in closest proximity to ANI, the observed proportion of recaptured tags for all years combined was 3.98%, whereas zero tags were recovered from the furthest watershed from ANI, Aptos Creek (Figure 1-4). The proportion of recaptured PIT tags at ANI represent the proportion of all PIT tags from juvenile steelhead that were recaptured at ANI from predation, after accounting for tag loss from transportation, and detection (Figure 1-1).

1.4.2. Transportation ("Hotdog") Experiment

From visual counts, we observed variation in gull species composition and Western Gull age class composition between sites. Of all gulls counted at creek mouths (N=5,403), Western Gulls were the most abundant species (85.4%), with fewer (14.3%) California Gulls (*Larus californicus*) and a very small percentage of other gull species (0. 3%) including Heermann's Gulls (*Larus heermanni*) and Glaucous-winged Gulls (*Larus glaucescens*). Adult Western Gulls were the most abundant species and age class at the three watersheds closest to ANI, whereas they accounted for less than one-third to one-tenth of the species composition at the three watersheds furthest from ANI (Figure 1-5).

The transportation (hotdog) experiment revealed low but spatially variable probabilities of transportation. The vast majority of PIT tags deposited at ANI from the

transportation experiment were originally fed to adult Western Gulls (95%), further supporting the hypothesis that adult Western Gulls are the primary species and age class responsible for PIT tag deposition at ANI (see Appendix A for more details). Of 1,470 PIT-tagged capelin and hotdogs fed to adult Western Gulls during the transportation experiment, 56 tags were subsequently detected at ANI (Table 1-2). All of the detected tags were from one of the three watersheds closest to ANI, whereas no PIT tags were recovered at ANI from gulls that were fed at the San Lorenzo River, Soquel Creek, or Aptos Creek (Figure 1-4). Thus, watersheds in closer proximity to ANI had higher transportation probabilities.

Feed type, season, and time of day had variable influence on the transportation rates of PIT tags fed to gulls during the transportation experiment. Although feed type did not result in statistically significant differences in transportation rates (Waddell Creek, $p=0.208$; Scott Creek, $p= 0.070$), capelin were almost always transported at higher rates than hotdogs to ANI (Table 1-2, Figure 1-4). When compared to hotdogs, capelin transportation rates were 1.5 times higher at Waddell Creek and 4.1 times higher at Scott Creek, which results in a weighted average where capelin were transported 2.3 times the rate of hotdogs. Therefore, in order to compare transportation rates among all study watersheds, we removed capelin and only used hotdog data for subsequent analyses because they were the only feed type used at all six study watersheds. After removing capelin from the analysis, we detected no significant differences in hotdog transportation rates for season at Waddell Creek ($p=0.589$). Gazos Creek had too few tag recoveries to conduct statistical analyses on whether time of day influenced hotdog transportation rates, however given similar sample sizes, transportation rates were similar for morning

(1/209 = 0.005) and evening feedings (1/159= 0.006). Therefore we combined the data for both seasons and time of feeding for all hotdog tags fed at each watershed (N=1,137; Table 1-2) to inform the transportation portion of the following model.

1.4.3. Estimating Transportation and Predation

We estimated the posterior probability distributions for transportation rates as a component of the Bayesian model. Due to the differences in transportation rates between hotdogs and capelin, we restricted the model to include hotdog data only to provide among site comparisons. Estimated transportation rates based on hotdog data were low and declined as a function of distance from ANI. At the three watersheds closest to ANI, the median probability that a tagged hotdog consumed by an adult Western Gull was transported to ANI each year was 0.073 (0.051-0.103, this and the following represent 90% CI), 0.063 (0.045-0.088), and 0.032 (0.023-0.046) at Waddell Creek, Gazos Creek, and Scott Creek, respectively (Figure 1-6A). Median estimates of transportation probability declined sharply at the three watersheds furthest from ANI, where less than 0.003 of all consumed tagged hotdogs were predicted to be transported to the island. To convert hotdog transportation rates into corrected transportation rates more representative of consumed steelhead, we incorporated a correction factor of 2.3 into the model, which multiplied hotdog transportation estimates by the average relative difference from capelin transportation rates. This is equivalent to replacing ϕ_i in the first line of eqn 4 with $c\phi_i$ and letting c = 2.3. As a result, the corrected transportation rates remain low, but increased to 0.167, 0.146, 0.074 at Waddell Creek, Gazos Creek, and

Scott Creek, respectively, whereas transportation rates were less than 0.005 at all other watersheds. We conducted analyses using both the corrected and uncorrected transportation rates but present only the predation results using the corrected transportation rates below.

Low transportation rates translate into high predation rates because tags detected at ANI represented a relatively small proportion of the total number of consumed tags. Overall, the probability that a wild juvenile steelhead was consumed as it passed the gauntlet of Western Gulls at the watershed mouth was highest in watersheds closest to ANI (median hierarchical estimates for Waddell = 0.464 (0.260-0.726 90% CI) and Scott 0.306 (0.183-0.480); non-hierarchical median for Gazos = 0.387 (0.234-0.616); Figure 1-6B). Predation rates at the southernmost watersheds farther from ANI were highly uncertain (Figure 1-6B) due to the relatively few recaptures of steelhead tags at ANI from these watersheds (Table 1-1) and the lack of transported PIT tags from the transportation experiment (Table 1-2).

For sites with multiple years of wild steelhead recaptures at ANI, gull predation rates were highly variable among years. Median predation rates at Scott Creek ranged from 0.075 to 0.673, over the seven years estimated (Figure 1-7). At Waddell Creek, median predation rates ranged from 0.113 to 0.823 across the four years estimated. Patterns of interannual variation were similar between the two watersheds for the four years that both watersheds were sampled (Figure 1-7). Specifically, in both Waddell and Scott Creeks, the median probability of predation was relatively high in 2006 and 2010, average in 2009, and relatively low at both creeks in 2008 (Figure 1-7). Comparisons of

predation rates between watersheds were not possible for 2005, 2007, and 2011 because no steelhead were tagged in Waddell Creek during those years.

1.5. Discussion

We developed a robust quantitative framework to better understand the impact of predation by an abundant generalist predator, adult Western Gulls, on populations of threatened wild juvenile steelhead in central California watersheds. Our results suggest predation rates at the three watersheds closest to ANI are high (median probability of predation ≥0.306) and variable, ranging from 0.075 to 0.823 depending on the watershed and year. Predation rate estimates increase with proximity to the breeding colony for the three sites closest to ANI and grow increasingly uncertain at watersheds furthest from ANI (≥ 33 km), driven in part by spatial patterns of transportation rates. Annual patterns of predation varied similarly among years at the two sites where time-series data were available. With the approach and model developed in this study we are able to generate overall Western Gull predation rates on juvenile steelhead and further understand the spatial and temporal influence of a central-place forager on threatened prey populations.

The predation rates estimated in this study provide the first estimate of overall predation rates of adult Western Gulls on juvenile wild steelhead. Predation rate estimates are almost an order of magnitude higher than minimum predation rates from tag recoveries (Figure 1-4A), mark-recapture methods at ANI (Frechette et al. 2012), and avian predation estimates on salmonids in other California watersheds (Evans et al. 2011, Adrean et al. 2012). Therefore, our study reveals minimum estimates from tag recovery may considerably underestimate predation rates and suggests predation by avian

predators is a more significant source of mortality for juvenile salmonids than previously recognized. In addition, PIT tags from critically endangered coho salmon from Scott Creek have also been observed on ANI (Frechette et al. 2012) and while populations were too small to quantify gull predation rates during this study, we expect gull predation is a significant source of mortality for coho populations as well. Furthermore, because we estimate predation for a single colony of the most common species and age class of avian predator (adult Western Gulls), we have not quantified overall predation by avian predators, including those species and age classes that do not breed or roost at ANI. Thus the total avian predation is likely higher than the already substantial rates reported here.

We observed that transportation rates are low and declined with increased distance from the Western Gull breeding colony (Figure 1-4B), controlling the spatial scale of inference. Specifically, our model estimated the median transportation probability was highest at Waddell Creek, the watershed in closest proximity to ANI, and transportation probabilities declined rapidly for the three locations furthest from ANI (Figure 1-6A). Because tags from distant sites are rarely transported to ANI, our estimates of predation grow increasingly uncertain as distance from ANI increases, and we could not make strong inference about predation rates at those sites (Figure 1-6B). One possible explanation for the decline in transportation rates with distance from ANI is the increased time between predation and return to ANI may result in higher rates of tag loss. Alternatively, gulls that forage at watersheds further from ANI may be more likely to be non-breeders (Figure 1-5) or may use breeding and roosting locations other than ANI, which would reduce transportation rates from these more distant watersheds.

Low transportation rates by Western Gulls may also be influenced by species-specific behavior while on the colony, including how adults provision their chicks, where Western Gulls feed chicks through regurgitation whereas other avian predators (e.g., terns) may feed whole fish to their chicks. Thus, different predator foraging behaviors such as generalists (i.e., gulls) verses piscivorous specialists (e.g., terns) may likely control the spatial scale of inference for this type of tag-recapture study. Our results thus provide the first example that low transportation probabilities may dramatically alter estimates of predation rates.

Estimated predation rates varied similarly across years at Scott and Waddell Creeks (Figure 1-7). In other systems, variation in predation rates over time by visual predators has been attributed to changes in regional environmental variables such as stream flow (Antolos et al. 2005, Hostetter et al. 2012), ontogenetic requirements that trigger diet switching (Annett and Pierotti 1989), or change in the abundance of prey (Type II or III functional response [Holling 1959], Keefer et al. 2012). These factors may have contributed to temporally coherent predation rates at Scott and Waddell creeks. Furthermore, annual variation in tagging effort at different locations of the watershed (i.e, upper watershed vs. lagoon) could be contributing to variation in estimates of predation rates. The effect of tagging effort on predation rates is supported by an observed negative correlation between annual predation rates and the number of steelhead tagged in the upper watershed in Waddell Creek (Pearson's correlation, $p=0.028$) and Scott Creek (Pearson's correlation, $p=0.150$). Therefore, we hypothesize years with higher estimated predation rates were driven, in part, by the fact that a larger proportion of steelhead were PIT-tagged in the lagoon. Lagoon-reared steelhead are

more susceptible to gull predation because they are more likely to attain the size threshold needed to survive the ocean phase of life and as a result are more likely to out-migrate (Bond et al. 2008, Hayes et al. 2011). High predation rates of wild steelhead that utilize lagoon habitat are of particular concern because lagoon-rearing individuals constitute over 87% of the returning adult steelhead population (Bond et al. 2008) and are therefore a critical component of the population for recovery of local steelhead.

High predation rates such as those observed in this study have significant implications for small populations because the loss of a few individuals can dramatically affect the probability of extirpation (Brook et al. 2008). At small population sizes, rare and random events contribute to driving population variability (Lande 1998). The effect of stochastic predation on small prey populations has been shown to decimate specific cohorts; for instance predation events by mountain lions (*Felis concolor*) resulted in significant mortality of desert tortoises in 2003 and 2007 (Medica et al. 2012). In more severe cases, stochastic predation may lead to the extirpation of populations. For example, there is a greater than 50% chance that unpredictable mountain lion predation events may result in the extirpation of isolated bighorn sheep populations (*Ovis canadensis*) (Festa-Bianchet et al. 2006) and a greater than 23% chance that striped bass (*Morone saxatilis*) predation will result in the quasi-extinction of winter-run Chinook salmon populations (*Oncorhynchus tshawytscha*) (Lindley and Mohr 2003). Similar to these examples, we documented high but variable predation rates by gulls on juvenile salmonids. Although salmonid predation is likely rare from the perspective of the gulls, incidental and stochastic predation can account for a large proportion of mortality for

small salmonid populations and may contribute to salmon decline or potential extirpation.

The impact of predation is likely exacerbated in this system by anthropogenic subsidies to a generalist predator (Harrington et al. 1999, Kristan and Boarman 2007, Esque et al. 2010). Previous research on Western Gulls has shown that landfills provide one of the most important foraging habitats for most age classes of Western Gulls (Spear 1988), and in other systems anthropogenic subsidies have been identified as the source of increased gull populations (Duhem et al. 2008), gull reproductive success (Weiser and Powell 2010), and juvenile and adult gull survival (Mudge 1978, Mudge and Ferns 1982). On-going research is investigating the linkages between anthropogenic subsidies and Western Gulls to better understand the role of subsidies in limiting the recovery of imperiled salmonid populations (Chapter 3).

Small populations are particularly challenging to manage and are also the most at risk of extirpation. Effective management of small populations requires quantification of mortality sources, such as predation, that may contribute to further population decline. Although directly quantifying predation on small populations is difficult, here we have demonstrated how managers can estimate multiple sources of tag loss to result in indirect, yet realistic, estimates of predation rates. Our approach of combining a Bayesian model with experimental and monitoring data can be broadly applied to other systems to estimate predation rates by central-place foragers. Predation rates, such as those presented in this study, are critical to inform an ecosystem management approach for fisheries, which depend on accurate estimates of the role of predation and other trophic

interactions in fisheries population dynamics (Mangel and Levin 2005, Ward et al. 2012, Naiman et al. 2012).

1.6. Tables

Table 1-1. Sample sizes for the steelhead tagging experiment during each outmigration year from 2005 through 2011 at each of the six study watersheds.

Watershed	**Outmigration year**							**Total**
	2005	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	
Waddell								
Tagged†	…	153	…	556	631	192	…	**1532**
Detected‡	…	10	…	5	22	24	…	**61**
Gazos								
Tagged†	474	68	…	…	…	…	…	**542**
Detected‡	16	3	…	…	…	…	…	**19**
Scott								
Tagged†	947	1199	1204	1856	1501	1981	940	**9628**
Detected‡	5	26	9	5	21	31	37	**134**
San Lorenzo								
Tagged†	252	9	…	…	…	…	…	**261**
Detected‡	1	0	…	…	…	…	…	**1**
Soquel								
Tagged†	823	1068	850	680	185	274	524	**4404**
Detected‡	1	1	1	0	0	0	0	**3**
Aptos								
Tagged†	222	112	…	…	…	…	…	**334**
Detected‡	0	0	…	…	…	…	…	**0**
Totals								
Tagged†	**2718**	**2609**	**2054**	**3092**	**2317**	**2447**	**1464**	**16701**
Detected‡	**23**	**40**	**10**	**10**	**43**	**55**	**37**	**218**

† The total number of wild juvenile steelhead PIT-tagged at each watershed and outmigration year, which corresponds with values of n in the model.

‡ The number of PIT tags from wild juvenile steelhead that were subsequently detected at Año Nuevo Island (ANI), which correspond with values of k in the model.

Table 1-2. Sample sizes for the 2010 transportation experiment for each feed type (hotdogs and capelin). All data are from spring morning (AM) feedings unless otherwise indicated (i.e., PM, summer).

Watershed (km†) and Feed	Tags Fed‡	Tags Detected§
Waddell (5.5)		
Hotdog	253	14
Hotdog (summer)	78	6
Capelin	131	9
Capelin (summer)	124	14
Gazos (6.6)		
Hotdog	209	1
Hotdog (PM)	159	1
Capelin	35	0
Capelin (PM)	22	0
Scott (12)		
Hotdog	228	8
Capelin	21	3
San Lorenzo (33)		
Hotdog	71	0
Soquel (38)		
Hotdog	96	0
Aptos (41)		
Hotdog	43	0
Totals	**1470**	**56**

† The linear distance (km) between the mouth of a given watershed and Año Nuevo Island (ANI).

‡ The total number of PIT tags fed to adult Western Gulls for a given feed type, season, and time of day. For a given watershed, sample sizes for season and time of day were combined (hotdog data only) and correspond with values of m in the model. Capelin were excluded from the model (see text for more details).

§ The number of PIT tags fed to adult Western Gulls that were subsequently detected on Año Nuevo Island (ANI). For a given watershed, sample sizes for season and time of day were combined (hotdog data only) and correspond with values of l in the model. Capelin were excluded from the model (see text for more details).

1.7. Figures

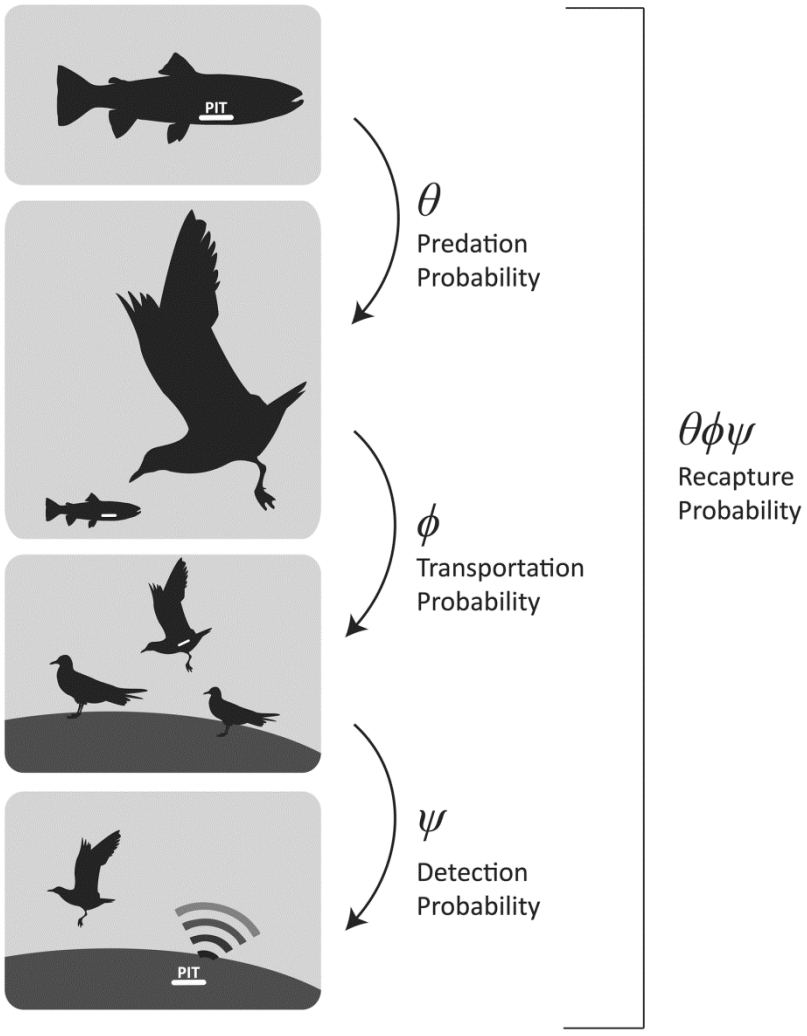


Figure 1-1. The three-step process for how PIT tags from tagged juvenile salmonids are recaptured on avian predator colonies, where each step has its own probability of occurrence. For a PIT tag to be recaptured at an avian predator colony, a PIT-tagged salmonid first has to be consumed by an avian predator (with probability θ), transported to the predator colony (with probability ϕ), and then detected on the colony (with probability ψ). Therefore, the probability of recapturing a PIT tag from a tagged salmonid is the probability, or product, of all three steps occurring (with probability $\theta\phi\psi$).

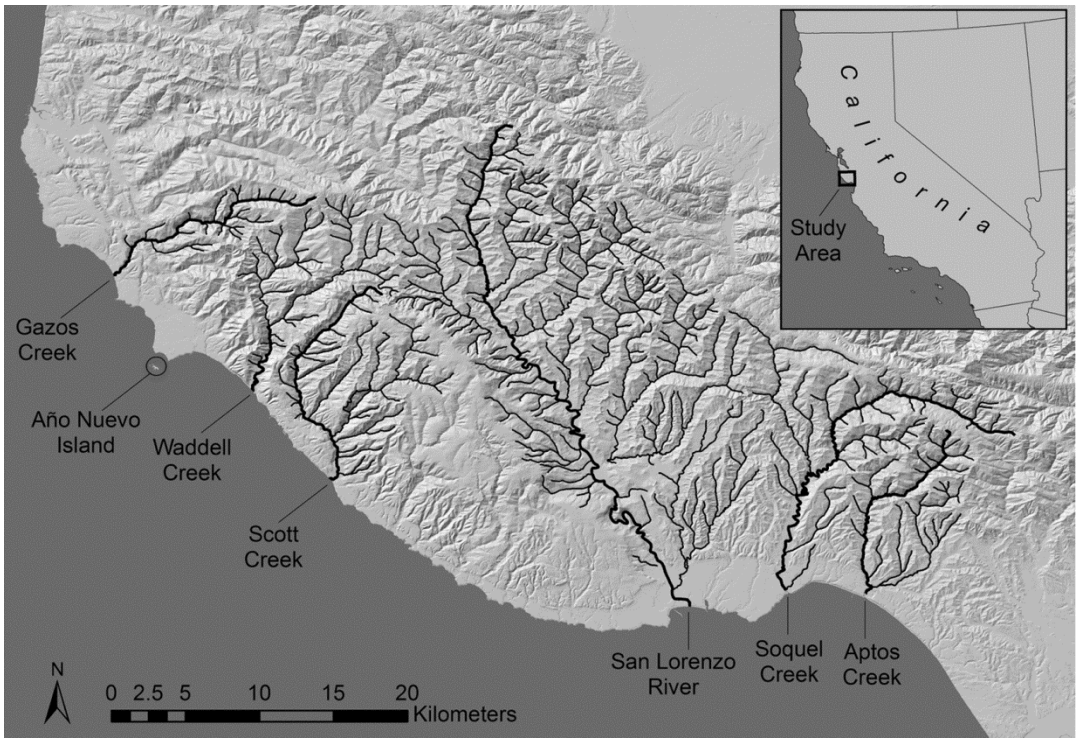


Figure 1-2. Location of the six central California (USA) watersheds (Gazos Creek, Waddell Creek, Scott Creek, San Lorenzo River, Soquel Creek, and Aptos Creek) and the seabird breeding colony (Año Nuevo Island) that compose the study area.



Figure 1-3. A photo taken at the mouth of Scott Creek, just before the creek enters the ocean. Hundreds of Western Gulls congregate at shallow creek mouths to bathe, drink, and opportunistically feed on items that are transported downstream by stream flow, including outmigrating juvenile salmonids.

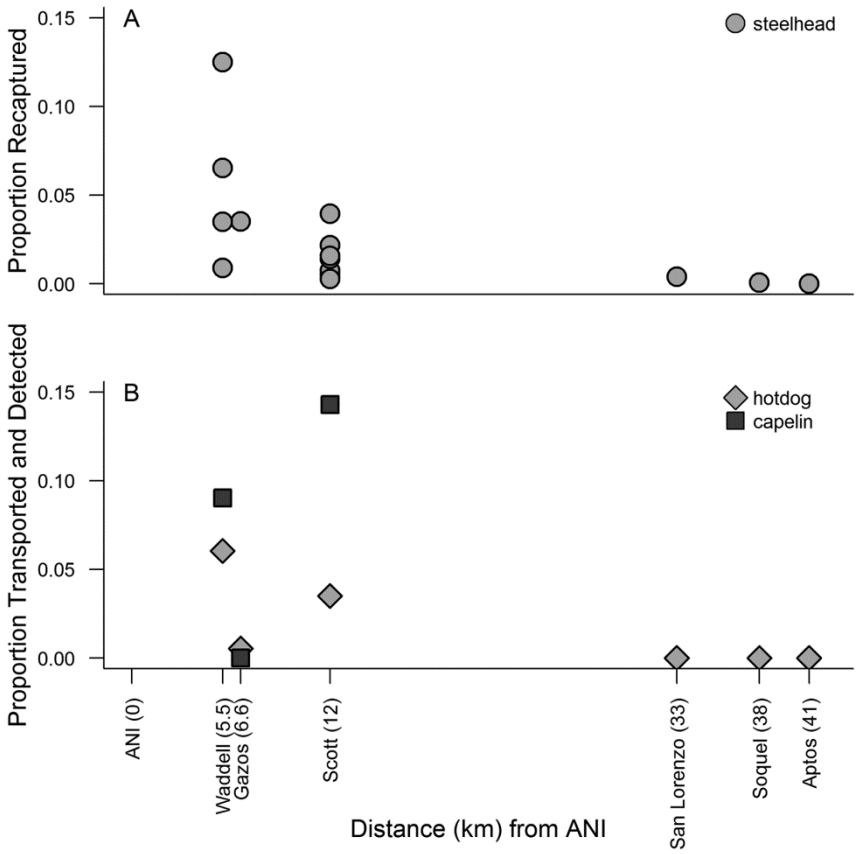


Figure 1-4. The observed proportion of PIT tags detected at Año Nuevo Island (ANI) during the steelhead tagging study (A) and the transportation experiment (B) for each watershed. The proportion recaptured (A) is based on the proportion of PIT tags recaptured at Año Nuevo Island (ANI) relative to the number of tagged wild juvenile steelhead at each site, where multiple years of recapture data are available for Waddell (N=4 years) and Scott Creeks (N=7 years). The proportion of tags transported and detected (B) is based on the proportion of PIT tags from PIT-tagged hotdogs and capelin detected at ANI relative to the number fed to adult Western Gulls at each site during the transportation experiment.

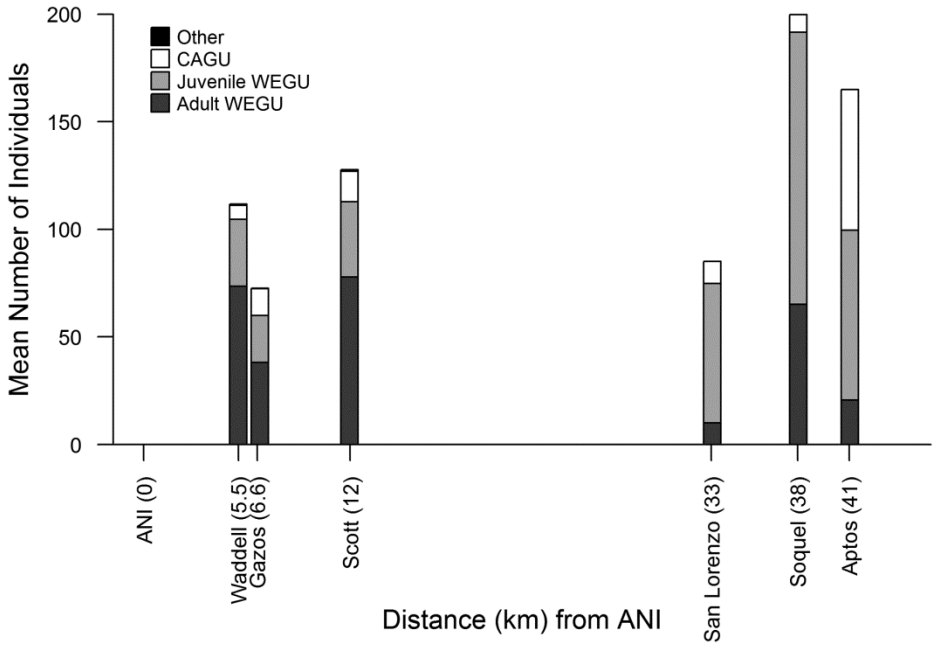


Figure 1-5. Mean number of birds present at each watershed during the transportation experiment, separated by species and by age class (for Western Gull species only). Data were restricted to counts conducted during the spring and morning surveys only to be comparable among sites.

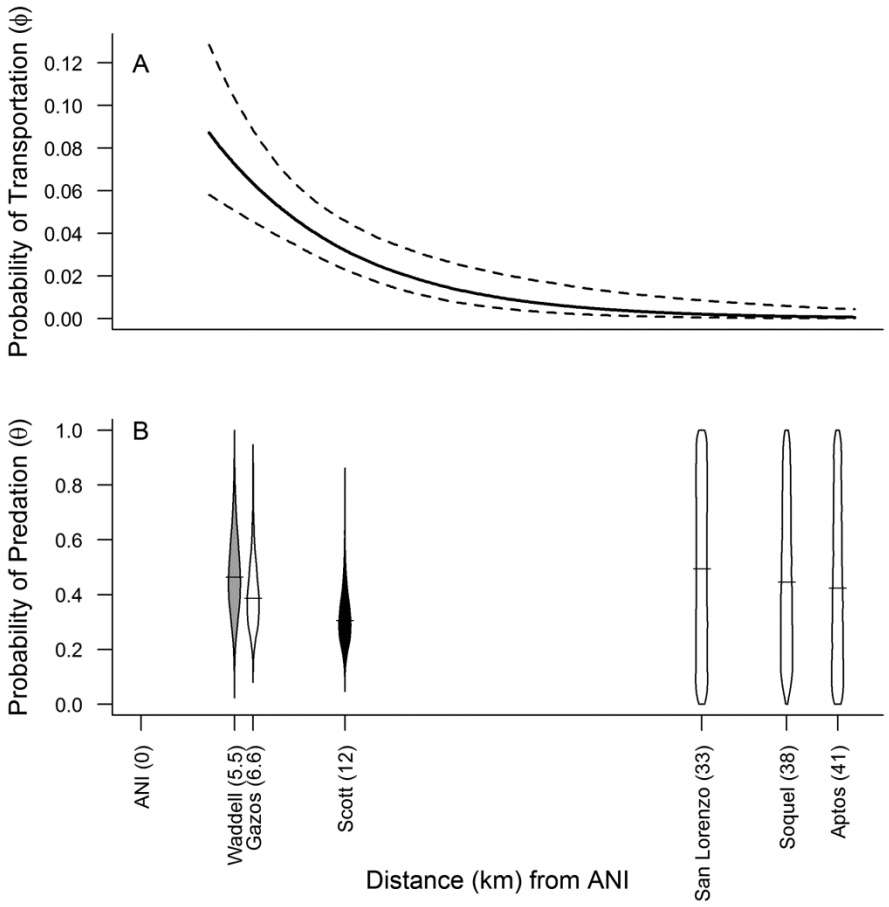


Figure 1-6. Site-specific parameter estimates for A) posterior estimates of the probability of transportation (ϕ) of a consumed PIT tag to ANI (median +/- 90% CI), before incorporating the capelin correction factor of 2.3 and B) posterior estimates of probability of predation (θ) of a PIT-tagged steelhead, including sites with a single year of data (white) and the across-year mean predation rate from the hierarchical model for sites with > 3 years of data, which includes Waddell Creek (grey) and Scott Creek (black). Beanplots show the full posterior distribution for each quantity after incorporating the capelin correction factor of 2.3. Horizontal lines indicate median estimates.

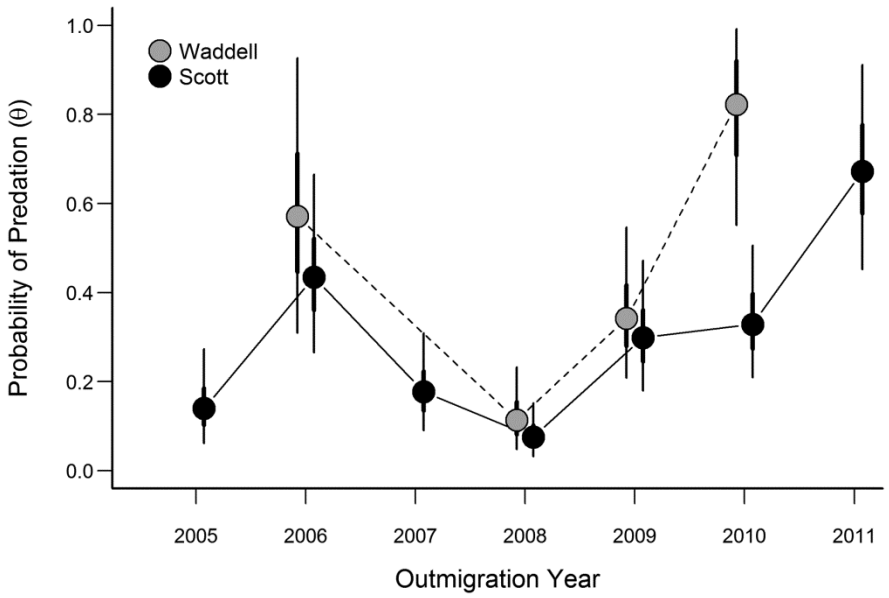


Figure 1-7. Posterior estimates for the probability of predation (θ) of wild juvenile steelhead by adult Western Gulls for individual years at two sites: Waddell Creek (grey) and Scott Creek (black). Points show median estimates, thick vertical lines show interquartile range, and thin lines show 90% CI.

2. Chapter 2 - Linking individual size and rearing history to survival and predation risk of threatened steelhead (*Oncorhynchus mykiss*)

2.1. Abstract

In this study, we found that individual characteristics of steelhead strongly influence their predation risk and marine survival. We identified characteristics associated with both increased predation risk of individual threatened juvenile steelhead (*Oncorhynchus mykiss*) by a generalist avian predator (Western Gull; *Larus occidentalis*) and those associated with survival to reproduction by tracking the fate of juvenile steelhead tagged with passive integrated transponder (PIT) tags. Across six cohorts (2005-2010), the largest steelhead experienced marine survival rates 20 to 40 times higher than the smallest individuals, whereas, predation risk did not vary significantly with steelhead size, suggesting predation by Western Gulls is not size-selective. Wild steelhead experienced both higher predation risk and higher survival rates than hatchery fish of the same size. Although gulls may not be size-selective, they are removing large wild steelhead from the population that otherwise experience the highest adult return rates, potentially reducing escapement by 24%. Instead of focusing on population size alone, conservation measures could also be guided towards the recovery of individuals with specific characteristics whose survival is paramount for population recovery.

2.2. Introduction

Individual traits influence ecological parameters such as population dynamics and survival (Palkovacs and Hendry 2010, Bolnick et al. 2011), which necessitates the incorporation of phenotypic variability into fisheries management (Fraser 2013). For most species of fishes, the greatest mortality rates occur during early life stages and only a few individuals survive to reproduction (Type III survivorship curve; Deevey 1947). In declining populations of Pacific salmon (*Oncorhynchus spp.*) where <0.1% of eggs survive to maturity (Shapovalov and Taft 1954), the few survivors may bear traits influential in shaping ecology and population dynamics. This likely explains the tremendous individual variation in traits across Pacific salmon including morphology (Roni and Quinn 1995), physiology (Hinch and Rand 1998), and life history strategies (Thorpe 2007).

Early ocean mortality may be the most critical life stage in determining salmon population dynamics (Kareiva et al. 2000). Individual traits such as size (Ward et al. 1989, Sogard 1997), estuarine residence time (Magnusson and Hilborn 2003, Bond et al. 2008) and origin (wild or hatchery; Jonsson et al. 2003, Beamish et al. 2012) are commonly associated with marine survival, but the relationship between these traits may differ across systems or species. For example, size at outmigration is not always associated with increased marine survival (Ward 2000). Therefore, identifying individual characteristics which influence marine survival continues to be an important research direction and critical for managing imperiled populations.

Predation is a significant source of mortality for many species (Sih et al. 1985),therefore traits that influence vulnerability to predation can impact prey population dynamics (Pettorelli et al. 2011). The influence of predation will be substantially higher if predators target prey with characteristics associated with high rates of survival compared

to prey with characteristics already susceptible to other sources of mortality (Griffin et al. 2011). For juvenile salmon in the Columbia River, some avian predators select for larger and hatchery-raised individuals (Collis et al. 2001, Ryan et al. 2003), which may affect salmonid population dynamics in this system by providing an additive source of mortality (Roby et al. 2003). The impact of avian predation on prey population dynamics in other systems remains less understood. Previously, we estimated that Western Gulls (*Larus occidentalis*) may consume approximately 30% of outmigrating juvenile steelhead *(Oncorhynchus mykiss)* in a small California watershed (Osterback et al. 2013). However it is unknown whether these predators select individuals that might otherwise survive.

Here we compare the individual characteristics of threatened juvenile steelhead that were consumed by a generalist predator (Western Gull) or survived to return as a spawning adult. We ask: (1) Are juvenile characteristics (i.e., size and origin) associated with predation risk by Western Gulls? (2) Are these characteristics associated with survival to maturity? (3) Do these characteristics overlap? By comparing the characteristics of juveniles that are consumed to those that survive to maturity, we can better understand whether predators are removing individuals from the population that otherwise tend to have high marine survival and are likely to contribute to the productivity of these imperiled populations.

2.3. Methods

2.3.1. Study System

The study area includes Scott Creek, a small (~70 km^2) central California coastal watershed and Año Nuevo Island (ANI), a small coastal island (10 ha) which hosts the third largest Western Gull breeding colony in central California (Capitolo et al. 2009) and is located ~12 km north from the mouth of Scott Creek (Figure 2-1). Scott Creek supports wild populations of threatened central California coast steelhead (Federal Register 2006) and represents the putative southern range of endangered coho salmon, *O. kisutch* (Federal Register 2005). A conservation hatchery on Scott Creek releases a few thousand age-1+ hatchery steelhead and coho salmon into Scott Creek each winter or spring, where individuals are progeny of wild adults captured in Scott Creek and are at least one generation removed from the hatchery (Hayes et al. 2004).

Scott Creek is a dynamic system; the creek mouth is closed during part of the year, which influences patterns of juvenile steelhead outmigration and predation by Western Gulls. In the late summer and fall, the combination of low stream flow and sand deposition from oceanic wave action results in a sand bar that separates the creek from the ocean and creates a freshwater lagoon (Hayes et al. 2008, Bond et al. 2008). Thus, the seasonal formation of the sand bar limits timing of juvenile salmonid outmigration to the winter and spring when connectivity between the creek and ocean exists (typically December through June). Concurrent with salmonid outmigration, Western Gulls gather at the shallow mouth of Scott Creek to drink, bathe, and opportunistically prey on items floating downstream, including outmigrating juvenile salmonids (Frechette et al. 2012). Recovery of prey tags from the Western Gull breeding areas on ANI revealed that gull predation may account for greater than 30% of the

tagged wild juvenile steelhead population in Scott Creek during some years (Osterback et al. 2013).

Recent research in Scott Creek highlights the prevalence of individual variation of steelhead and how phenotypic traits influence survival or predation risk. For example, size of an individual in conjunction with habitat-specific growth and mortality rates can be used to predict habitat use, movement patterns, and timing of outmigration for juvenile steelhead (Satterthwaite et al. 2012, Phillis et al. 2014). Specifically, the seasonal lagoon provides high growth opportunities but at the cost of high mortality (Satterthwaite et al. 2012), and as a result individuals who rear in lagoon habitat experienced both higher rates of marine survival (Bond et al. 2008) and higher predation pressure from avian predators (Frechette et al. 2013), including Western Gulls (Frechette et al. 2012). In contrast, hatchery steelhead are less variable in their rearing patterns and typically migrate directly out to the ocean after being released into Scott Creek as age-1+ juveniles (Hayes et al. 2004). To our knowledge, individual characteristics associated with predation risk and survival in Scott Creek, or any other system have not been explicitly compared to date.

2.3.2. Individual characteristics of juvenile steelhead

To identify individual characteristics of juvenile steelhead in Scott Creek, we and the National Marine Fisheries Service Southwest Fisheries Science Center captured juvenile steelhead between 2005 and 2010 through a combination of downstream migrant trapping, seining, and backpack electrofishing, as well as tagging at the Monterey Bay Salmon and Trout Project (MBSTP) conservation hatchery on Scott Creek. All

steelhead were handled according to the methods described by Hayes et al (2004) and had complete information for the following individual characteristics: origin (wild or hatchery-raised), fork length (mm), and outmigration year. Each individual was assigned an outmigration year to account for variation in outmigration timing. Outmigration year was the same as calendar year for hatchery juveniles because they were released in the late winter or spring as age 1+ juveniles and typically migrate out to the ocean soon after release (Hayes et al. 2004). For wild individuals captured in the lagoon, we assigned the outmigration year for the following year (calendar year + 1) because outmigration can only occur the following winter after the lagoon opens and the creek is no longer separated from the ocean (see Hayes et al. 2008 for more details on outmigration timing of juvenile salmonids in Scott Creek).

All individuals were PIT (passive integrated transponder) tagged to provide a unique identification for each tagged individual. PIT tags have high tag retention rates (>95%; Sogard et al. 2009) and contain no battery so they can last beyond the lifespan of a tagged individual. As a result, PIT tags can provide unique information on an individual many years after the initial tagging event (i.e., recaptured as an adult 1-3+ years after tagged as a juvenile) and even beyond an individual's lifespan (i.e., recaptured after deposition on ANI).

For this study, we only included wild and hatchery juvenile steelhead that were present in Western Gull foraging areas during lagoon residence or outmigration. For wild steelhead, we included individuals that were observed in lagoon habitat near the mouth of Scott Creek and therefore spatially overlapped with Western Gulls. All wild steelhead included in the analysis were observed during seining events in the Scott Creek lagoon,

which typically occurred in the late summer and fall when the lagoon was separated from the ocean. We excluded wild steelhead that were never directly observed using lagoon habitat because many of these individuals were likely a younger age class that may not have initiated downstream migration towards the lagoon or ocean (Hayes et al. 2008). For hatchery juveniles, we restricted our analyses to individuals that were tagged at MBSTP in late winter/early spring just prior to being released into Scott Creek as age 1+ juveniles and were assumed to outmigrate soon after release (Hayes et al. 2004).

2.3.3. Effects of size and origin on predation risk

We hypothesized that gulls selectively consumed steelhead with characteristics that also benefit marine survival, thus predation risk would be higher for large individuals of wild origin. To test this hypothesis, we compared the characteristics (i.e., size and origin) of PIT-tagged juvenile steelhead in Scott Creek to those steelhead whose PIT tags were deposited on Año Nuevo Island by Western Gull predators (Osterback et al. 2013). To control for unmeasured inter-annual variation in other biotic and abiotic factors, comparisons were only made between fish of the same outmigration year.

We identified which juvenile steelhead were consumed by gulls by scanning Año Nuevo Island annually from 2006 through 2013 to recapture PIT tags from steelhead that had been consumed and deposited by Western Gulls. Scans of ANI include traversing the island with a portable PIT antenna and GPS to document the location and unique identification code of each deposited tag (for more details, see Frechette et al. 2012). Mobile PIT antenna specifications are described in Bond et al. (2007). It is important to note that the recapture of PIT tags addresses relative predation risk and

does not quantify overall predation rates. Overall predation rates are much higher than the recapture rates reported in this study because the majority of consumed tags are deposited off-colony (Osterback et al. 2013).

We quantified factors associated with predation risk of juvenile steelhead in Scott Creek with a Generalized Linear Model (GLM) with a logit transformation, where the binary response variable was "recaptured on ANI" (1) or "not recaptured on ANI" (0). "Recaptured on ANI" individuals were juveniles whose PIT tags were detected on ANI after presumably being consumed and defecated by Western Gull predators. For "not recaptured on ANI" individuals, we have no evidence they were consumed by gulls. Four factors were included as possible predictors in the candidate models: the main effects of fork length (mm), origin (hatchery vs. wild), and outmigration year, and an interaction between origin and fork length. We included the interaction term to determine whether the influence of size on predation risk varied depending on the origin. Outmigration year was included as a random factor to account for interannual variation to assess whether the effect of fork length and origin on predation risk was consistent among years. Due to the limited years of data (N=6) we were unable to assess specific factors that drive year to year variation.

We used a multimodel inference approach to identify parameters that best support the data (Burnham and Anderson 2002, Grueber et al. 2011). With the MuMIn package in Program R (R Development Core Team 2013), we used the dredge function to evaluate the set of all possible candidate models and used Akiake's Information Criteria for small sample sizes (AICc) to compare model fit between candidate models. We conducted model-averaging which is recommended when the weight of the top

model is less than 0.9 and multiple candidate models are within two ΔAICc units of the best approximating model (Grueber et al. 2011). We used the natural average method of estimating parameter weights because all parameters are of interest and some may have relatively weak effects when compared with other factors (Grueber et al. 2011).

To estimate the relative effects of each parameter within the averaged models, we standardized the input data of the continuous variable (i.e., fork length) by subtracting the mean and dividing by two times its standard deviation to allow comparisons of all parameters on a similar scale (Gelman 2008). Data standardization was conducted using the arm package in Program R (R Development Core Team 2013), where fork length was modeled as a continuous parameter and the other parameters of origin and outmigration year were modeled as categorical factors. Effect sizes of each parameter were then compared to a reference state to determine how changes in a given parameter would affect the response variable. The reference state for all analyses was a wild steelhead with a mean fork length in outmigration year 2010.

The above modeling approach assumed that fork length at last capture was indicative of an individual's size when exposed to gull predators, however it is possible that the majority of gull predation does not occur in the greater lagoon area but instead occurs upon outmigration in the winter or spring during the last several meters of the lagoon just before it enters the ocean (Frechette 2010). For hatchery steelhead, the vast majority of individuals are known to outmigrate to the ocean soon upon release into Scott Creek (Hayes et al. 2004), so individual measurements taken at the hatchery before their release are likely relatively equivalent to their size during exposure to gull predation. However, the size of wild lagoon-reared steelhead may have been recorded from one day

to several months before outmigration and therefore if gull predation happens upon outmigration, their recorded size may be substantially smaller than their size upon outmigration. In order to address this potential bias, we used the same modeling approach as described above, except we replaced the observed fork length with an adjusted fork length for wild lagoon-reared individuals. The adjusted fork length is the estimated size of a wild lagoon-reared individual upon outmigration, and is based on the estuarine specific growth rate equation in Hayes et al. (2008) and the number of days between when an individual was last captured in the lagoon and the first date the lagoon opened for that given outmigration year. Comparisons between this model and the previous model will reveal whether the effect of fork length on predation risk changes depending on when predation occurs.

2.3.4. Effects of size and origin on survival

We hypothesized that survival will be highest for large, wild steelhead when compared to smaller individuals or individuals of hatchery origin. To identify characteristics (i.e., size and origin) associated with survival, we compared the characteristics of PIT-tagged juveniles to those individuals that survived the marine ecosystem and returned to Scott Creek 1-3+ years after ocean entry as mature adults. Size and origin of the juveniles that survived to spawn were then compared to the size and origin of all juveniles that were assigned the same outmigration year.

To identify PIT-tagged juveniles that survived to become spawning adults, we captured adults returning to Scott Creek during the spawning season (typically December through June) between 2005 and 2013 through a combination of snorkel surveys and

daily operation of a floating resistance panel weir (Bond et al. 2008). All returning adults were scanned for PIT tags and cross-referenced with juvenile PIT tag data to identify the juvenile characteristics of each returning adult from juvenile outmigration years 2005 through 2010.

To identify characteristics associated with survival, we used the same analysis as the predation risk analysis, including a Generalized Linear Model (GLM) with a logit transformation, a multimodel inference approach, and data standardization for effect sizes to identify factors that inform the response variables. For the survival analysis, the binary response variables included "survived to spawner" (1) and "did not survive to spawner" (0). "Survived to spawner" included juveniles that were subsequently captured in Scott Creek as an adult and therefore survival was confirmed. Individuals defined as "did not survive to spawner" included the remaining juvenile tagged steelhead that did not return as adults, for which we have no evidence they survived to spawn. The same four factors assessed in the predation risk analysis were included as possible predictors for the survival analysis: the main effects of fork length (mm), origin (hatchery vs. wild), and outmigration year, and an interaction between origin and fork length. Similar to the predation risk analysis, we re-ran the model using the adjusted fork length to assess whether the effect of size on survival for wild individuals is sensitive to the timing of predation (i.e., in the lagoon verses upon outmigration).

2.4. Results

Between outmigration years 2005 and 2010, we PIT-tagged 7,523 juvenile steelhead in Scott Creek (Table 2-1). Of the tagged juveniles, 93 were subsequently

recaptured on ANI after presumably being consumed by a Western Gull, 61 individuals returned to Scott Creek as spawning adults, and 7,369 individuals had an unknown fate (Table 2-1). Thus, average annual recapture rates of PIT tags on ANI were 3.2% for wild lagoon-reared steelhead and 0.7% for hatchery juveniles. Average annual survival rates were 2.9% for wild lagoon-reared steelhead and 0.3% for hatchery juveniles. Because recapture probabilities are high both for detecting PIT tags on ANI (~64%, Frechette et al. 2012) and for capturing returning adults in Scott Creek (~73%, Hayes et al. 2013), there is a low probability that individuals of unknown fate either were deposited on ANI or returned as an adult and went undetected. Instead, individuals of unknown fate likely died while in the freshwater or marine environment, which is supported by typically very low smolt to adult survival for Scott Creek steelhead (~1.6%; Hayes et al. 2013)

2.4.1. Effects of size and origin on predation risk

Predation risk was influenced by the individual characteristics of steelhead in Scott Creek. Origin and outmigration year were the strongest predictors of predation risk, as demonstrated by their inclusion in all of the best-approximating models (Table 2-2). Wild steelhead were consistently more susceptible to predation than were hatchery-raised individuals (Figure 2-2A), where predation risk was over three times higher for wild individuals when compared to individuals that were reared at the hatchery (Figure 2-3A). Predation risk was almost twice as high for juvenile steelhead that outmigrated in 2006 (Figure 2-2A), when compared to individuals that outmigrated during the reference year (2010), which had similar predation risk as the other four years of the study (Figure 2-2A). In contrast to our predictions, fork length was a weak predictor of predation risk

(Figure 2-2A), where predation risk was similar across all size classes (Figure 2-4). Although the interaction between fork length and origin were also included in the averaged model (Table 2-2), the interaction was a relatively weak predictor of predation risk (Figure 2-2A).

The adjusted fork length for wild lagoon-reared individuals had little effect on the model, suggesting that regardless of predation timing, size remained a weak predictor of predation risk. The model using adjusted fork length (Figure 2-5A) had similar results to the original model (Figure 2-2A), where predation risk was highest for wild steelhead (Figure 2-5A). The year effects were also similar between the original model and the model using adjusted fork length, where predation risk was highest in 2006. These results suggest the influence of size on predation risk is similar whether using observed length at capture or predicted length at outmigration.

2.4.2. Effects of size and origin on survival

Individual characteristics of juvenile steelhead strongly influenced the probability an individual survived to return as a spawning adult. Consistent with our predictions, survival was best predicted by origin, fork length, and outmigration year, whereas an origin by fork length interaction had a relatively weak effect (Table 2-2; Figure 2-2B). Origin had a significant effect on survival rates; wild individuals experienced over ten times the survival rate of hatchery fish (Figure 2-3B). The most influential factor was fork length; the largest wild individuals (250 mm) were over 20 times more likely to survive than the smallest wild individuals (65 mm), and the largest hatchery-raised individuals were over 40 times more likely to survive than the smallest hatchery

individuals (Figure 2-4). Individuals that outmigrated in 2009 experienced less than one fifth the survival rate as individuals that outmigrated during the reference year (2010), which was similar to the other years of the study (Figure 2-2B). The results from the survival analysis support our hypothesis that large wild steelhead experience the highest survival rates.

The influence of size, origin, and year on survival did not change significantly when using the model with predicted fork length at outmigration (Figure 2-5B) when compared to the original model that included the observed fork length at last capture (Figure 2-2B). In the adjusted model (Figure 2-5B), survival remained highest for large, wild individuals, and those migrating in 2009 experienced the lowest survival.

2.4.3. Comparing effects of size and origin between predation risk and survival

Similar factors influenced predation risk and survival. Wild juvenile steelhead experienced both higher predation risk by Western Gulls and also experienced higher survival when compared to juveniles raised at the hatchery. While predation risk was similar across all fork lengths, the odds of survival increased dramatically with each incremental increase in fork length, such that the largest individuals are more than 20 to 40 times more likely to survive when compared to the survival rate of the smallest individuals (Figure 2-4). Therefore, origin may similarly affect an individuals' susceptibility to predation and survival, whereas fork length may increase an individual's probability of survival significantly more than its probability of predation.

2.5. Discussion

Here we examined individual characteristics that influenced survival and predation. We found that wild individuals experience more than three times the predation risk and over ten times the survival rates than those reared at the hatchery. Large individuals experience a minimal increase in predation risk, and over 20 to 40 times the survival rates than smaller individuals. Thus, if large, wild juveniles can survive the gauntlet of gull predation during their outmigration to the ocean, they will likely experience high survival once in the ocean and contribute to the overall productivity of the population. Although previous work in Scott Creek identified or predicted characteristics associated with survival of juvenile salmonids (Bond et al. 2008, Satterthwaite et al. 2012, Sogard et al. 2012) and documented high rates of Western Gull predation on these same populations (>30%, Osterback et al. 2013), it was unknown whether gulls consumed individuals that would otherwise experience high survival rates. The results from this study provide the first empirical evidence that though gulls may not target large individuals, they are consuming wild steelhead across all size classes, including the large wild individuals that are critical to the persistence of the population.

We observed strong evidence that origin influenced predation risk of juvenile steelhead, where wild individuals experienced over three times the predation risk than individuals raised at the hatchery (Figure 2-2A, Figure 2-3A). This is contrary to many systems where hatchery-raised individuals experience similar or increased predation rates (Collis et al. 2001, Ryan et al. 2003). There are several mechanisms that may predispose hatchery fish to predation in other systems but do not apply to Scott Creek. For example, hatchery-reared salmonids may also be more susceptible to predation risk than wild fish because they feed closer to the surface and are therefore more conspicuous to

visual predators (Collis et al. 2001). However, in Scott Creek depth preference is not a factor as the shallow creek mouth forces all steelhead to travel near the surface, making both hatchery and wild fish susceptible to avian predation. Hatchery fish typically experience increased predation rates from genetic domestication (Berejikian 1995). However, in Scott Creek, hatchery steelhead may share more characteristics with their wild counterparts when compared to other systems because they are raised in a small conservation hatchery where stock are progeny of wild-reared adults (Hayes et al. 2004). However, other studies have shown hatchery fish even just one generation removed from the wild can result with maladaptive antipredator responses (Jackson and Brown 2011). One important factor that may lead to higher predation risk on wild fish verses hatchery steelhead is predator satiation, where increased abundance of outmigrating juveniles may reduce the risk of any one fish to predation (Ryan et al. 2003, Hostetter et al. 2012). In Scott Creek, hatchery steelhead are released into the creek as age-1+ juveniles and most individuals outmigrate to the ocean within one month (Hayes et al. 2004). In contrast, wild steelhead outmigrate from Scott Creek in smaller numbers and over a period of several months which may increase the time exposed to predators and the individual risk of predation. Regardless of the mechanism, the individual risk of being eaten by an avian predator is greater for wild fish compared to hatchery fish.

Interestingly, size of an individual had a weak and non-significant relationship with predation risk. Our results are contrary to much of the existing literature, where size of an individual is often directly related to predation risk. For example, small individuals can be more susceptible to predation because they have reduced swimming ability (Taylor and McPhail 1985) or are less likely to survive the physiological challenges

associated with transition from fresh to salt water (Beakes et al. 2010). In contrast, avian predators are one of the few predators of teleost fishes that prefer larger individuals as prey (Sogard 1997), as is supported by a study in the Columbia River where Caspian terns preferred larger juvenile steelhead to smaller juvenile Chinook salmon (Collis et al. 2001). Interestingly, we found a non-significant relationship with size and predation risk in Scott Creek which suggests Western Gulls are not size-selective, but instead are eating across the size ranges of steelhead available. In general, gulls are generalists and have a flexible diet (Pierotti and Annett 1990), however Western Gulls have demonstrated individual specialization for specific prey (Annett and Pierotti 1999) including size-selective predation of urchins in the rocky intertidal (Snellen et al. 2007), and selection of larger prey by larger males when compared to smaller females (Pierotti 1981). Therefore, although Western Gulls may be size-selective of certain prey species, we did not observe strong size-selection of juvenile salmonids by gull predators in this study.

Survival rates were generally low across all years of the study, but survival increased dramatically for large individuals (Figure 2-3B). We found that a large individual has 20-40 times the survival rate than a small individual (Figure 2-4), which suggests the characteristics of individuals may be just as, if not more important, than the number of individuals for population recovery. Our results support our predictions and are similar to other studies that have shown relative body length is an important predictor of survival within juvenile salmonid populations (Henderson and Cass 1991, Zabel and Achord 2004). Additionally, increased growth rates can be attained by rearing in estuarine habitat (Hayes et al. 2008), which may contribute to higher survival (Levy and Northcote 1982). Previous research in Scott Creek has shown the importance of

lagoon habitat, which provides elevated growth opportunities that allow individuals to attain large body sizes and experience higher survival. As a result, lagoon-reared individuals contribute more than 87% of the returning adult steelhead population (Bond et al. 2008). Therefore, our finding that large individuals experience higher survival rates is consistent with other studies and previous research conducted in Scott Creek.

Consistent with our predictions, we found wild steelhead had significantly higher survival rates than hatchery-raised individuals (Figure 2-3B). In a recent review article (Araki et al. 2008), results suggest the reproductive success (e.g. fitness) of salmonids is typically lower for hatchery fish, even if they are progeny of local wild-reared individuals. Decreased fitness of hatchery salmonids is often attributed to relaxed or maladaptive selection for the natural environment (Lynch and O'Hely 2001) because individuals avoid selection events at the hatchery that they would have been exposed to in the wild. Interestingly, hatchery and wild steelhead have demonstrated similar relative reproductive success once they return to Scott Creek (Charrier et al. *In Prep*). Therefore, management approaches that focus on increasing juvenile survival by addressing avian predation and restoring lost lagoon rearing habitat may result in disproportionately more individuals reaching adulthood than other restoration or management activities.

We found strong overlap among some characteristics associated with predation risk and those associated with increased survival. Consequently, our results suggest that gulls consume large wild steelhead juveniles, and were it not for gull predation many of these individuals may otherwise experience a relatively high probability of survival. Specifically, we estimate that in the absence of gull predation, we might expect approximately an additional 50 wild and 3 hatchery adults to return to Scott Creek,

which would increase the average annual adult escapement by approximately 24% (average Scott Creek steelhead escapement is 219 adults; Hayes et al. 2013). These estimates were calculated by multiplying 1) the average number of wild steelhead that recruit to the Scott Creek lagoon or are released from the hatchery each year (1,876 and 5,581 individuals, respectively; Hayes et al. 2013), 2) the average proportion of the juvenile wild lagoon-reared population (0.671) and hatchery population (0.147) that are expected to be consumed by gulls each year, and 3) the average survival rates of wild (0.029) and hatchery (0.003) individuals from this study, corrected for the capture efficiency of adults that return to Scott Creek (73%; Hayes et al. 2013). The proportion of wild (0.671) and hatchery (0.147) juveniles expected to be consumed by gulls were estimated from the average recapture rates of tags on ANI for wild (0.032) and hatchery (0.007) juveniles from this study, divided by the probability that a consumed tag at Scott Creek is transported to ANI (0.074; Osterback et al. 2013) and the probability a transported tag is detected on ANI (0.644; Frechette et al. 2012). This indicates gull predation is an additive source of mortality, similar to modeling work from the Columbia River Basin, which predicted an increase in salmonid population growth with a reduction in Caspian tern predation (Roby et al. 2003). However, gulls are not the only predators that may contribute additive sources of mortality. The relatively stronger relationship between size and survival when compared to size and predation risk (Figure 2-2, Figure 2-3) suggests other sources of mortality besides gull predation, such as that by predatory fishes (e.g., Willette 2001) likely drive size-based survival patterns. Our results suggest, therefore, that gulls are removing wild individuals from the population, including the large ones that are important for juvenile steelhead population recovery and may increase

total escapement by 24%. However other factors are also contributing to size-dependent survival rates.

Both predation risk and survival rates varied among years; however the mechanism for interannual variability remains unclear. Predation risk was relatively high in 2006, whereas survival was relatively low for those individuals that outmigrated in 2009 (Figure 2-2). Predation risk and survival of salmonids can be affected by many environmental and biological factors including stream flow (Connor and Tiffan 2012, Hostetter et al. 2012), upwelling (Scheuerell and Williams 2005), and the abundance of prey (Type II or III functional response; Holling 1959). Demographic stochasticity can also contribute to variability in mortality rates and contribute to extinction risk, particularly for small populations (Lande 1998).The mechanisms contributing to the interannual variability observed in this study could not be identified with such few years of data (N=6). Environmental, biological, and demographic factors may contribute to annual fluctuations in survival and predation risk, and can contribute to extinction risk or inhibit recovery of salmonid populations.

Size-based patterns of survival and predation risk were robust to relaxing assumptions about fork length. For the original model (Figure 2-2), we assumed the fork length measurements taken at the hatchery (for hatchery individuals) or at the lagoon (for wild individuals) were representative of their size when exposed to gull predation or marine entry. However, since the timing of predation is unknown, especially for wild lagoon steelhead, we re-ran both the survival and predation risk analysis using the adjusted fork length (an estimated fork length at the end of lagoon rearing) and found similar results to those presented in the original model, where fork length was still a weak

predictor of predation risk and a strong predictor of survival (Figure 2-5). Therefore, we demonstrated potential biases in size assignment for wild lagoon steelhead are not substantial enough to eliminate the relationship between size and predation risk or survival. Furthermore, the strong relationship between size and survival has been documented in other studies with wild steelhead in Scott Creek (Bond et al. 2008) and was observed with hatchery individuals in this study (Figure 2-4), where size assignment was more robust.

Identifying successful management and conservation measures is a priority for imperiled populations of Pacific salmon. Although conservation efforts often focus on increasing population size by improving habitat or altering hatchery practices (Sharma et al. 2005), the results of this study emphasize that recovery actions should consider individuals whose characteristics contribute disproportionately to population productivity. In Scott Creek, large (>200 mm fork length) wild individuals are less than 1% of the outmigrating steelhead population yet experienced 10-20 times the survival rate than small wild individuals. Therefore, restoration activities that increase growth and size of steelhead could have dramatic impacts on population size. For instance, future management actions could include efforts to restore the Scott Creek lagoon to its original larger size which would expand rearing habitat and high growth opportunities that support larger, wild individuals. Although Western Gulls were not size-selective, they still removed large, wild individuals from the population. Therefore, reducing gull predation is a potential management option, especially since Western Gull populations have increased (Hester et al. 2013) perhaps from increased anthropogenic subsidies

(Chapter 3). The results from this study can inform conservation approaches towards the recovery of individuals whose survival is paramount for population recovery.

2.6. Tables

Table 2-1. Sample sizes for the predation risk and the survival analysis for Scott Creek steelhead in outmigration years 2005 through 2010. The total number of tagged steelhead (*), the number of tagged individuals subsequently recaptured on ANI after presumably being eaten by a Western Gull (†), and the number of tagged individuals that survived to return as an adult (‡), are indicated.

Origin/ Location	# Individuals	Outmigration Year						Totals
		2005	2006	2007	2008	2009	2010	
Wild/ Lagoon	Tagged†	170	261	57	192	393	465	**1538**
	Recaptured on ANI‡	1	8	5	3	16	16	**49**
	Returned as Adult§	6	17	1	4	1	15	**44**
Hatchery	Tagged†	499	534	474	961	2955	562	**5985**
	Recaptured on ANI‡	6	19	2	6	7	4	**44**
	Returned as Adult§	4	0	0	8	3	2	**17**

Table 2-2. Best approximating models for the predation risk and survival analysis. All models within < 2 $\Delta AICc_i$ of the best-approximating model are shown below and were incorporated into an averaged model for each analysis, which is recommended when no single candidate model contains more than 0.95 of the model weights (w_i), as discussed in Grueber et al. (2011).

Response Variable	Independent Variables	$AICc_i$	$\Delta AICc_i$	w_i
EATEN (Recaptured on ANI)	Origin + Outmigration Year + Fork Length + Fork Length:Origin	946.8	0.00	0.381
	Origin + Outmigration Year	946.9	0.06	0.370
	Origin + Outmigration Year + Fork Length	947.7	0.91	0.242
SURVIVED (Returned as adult)	Origin + Outmigration Year + Fork Length	597.5	0.00	0.648
	Origin + Outmigration Year + Fork Length + Fork Length:Origin	598.7	1.22	0.352

2.7. Figures

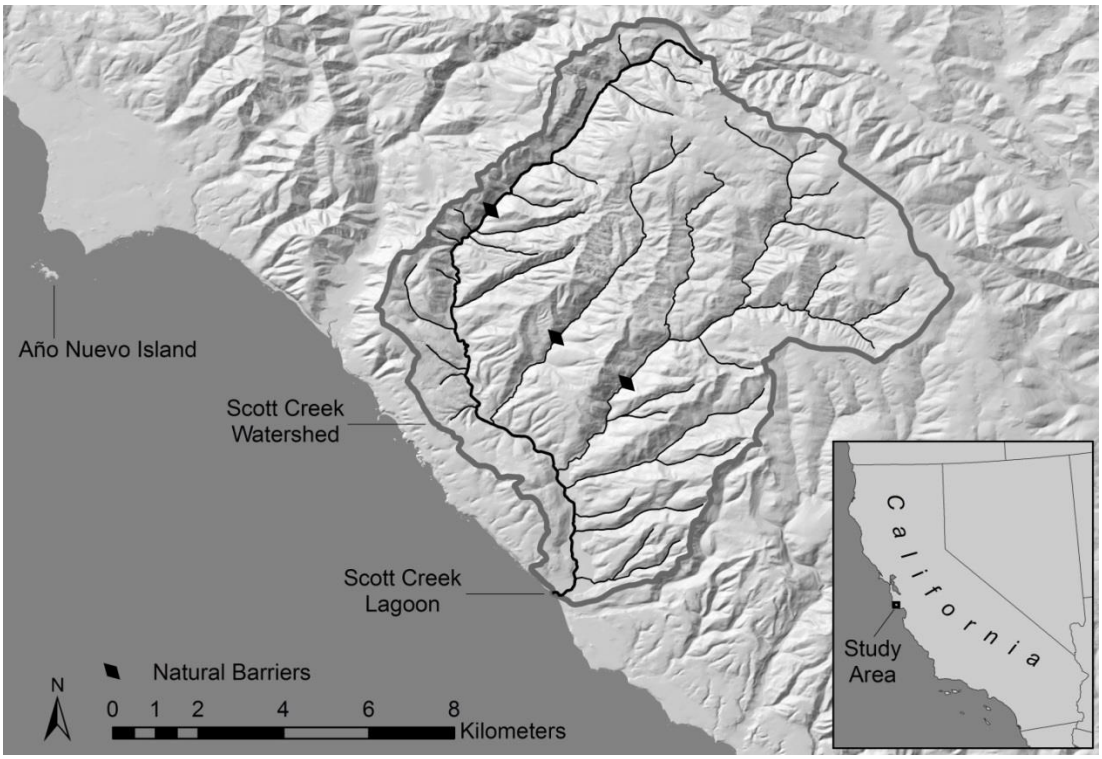


Figure 2-1. Map of the study location, including the Scott Creek watershed (California, USA) and Año Nuevo Island.

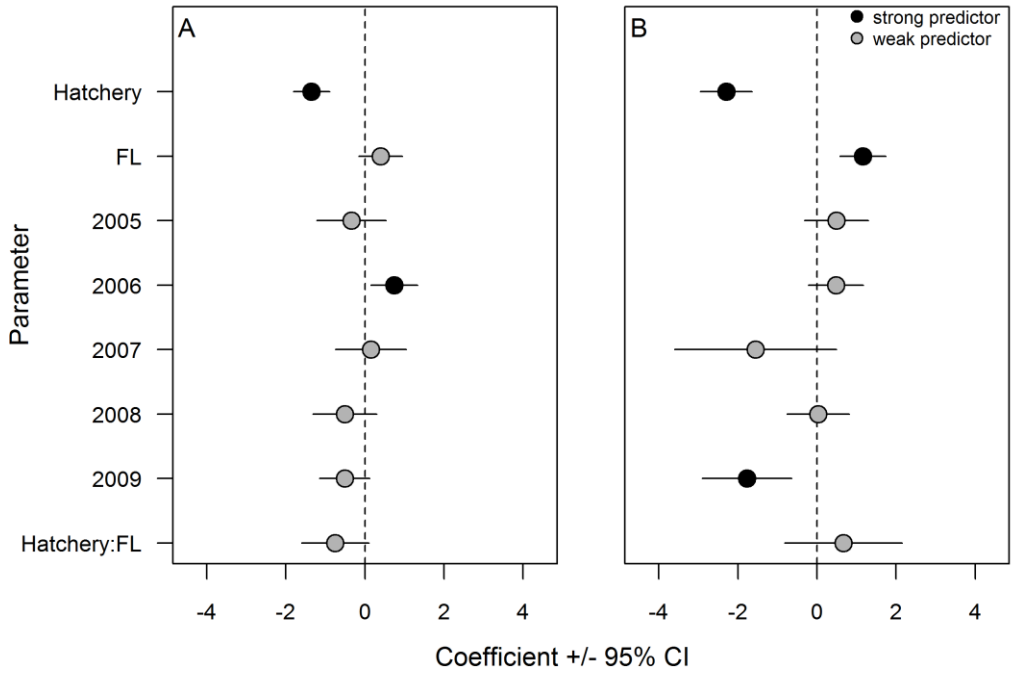


Figure 2-2. Model averaged parameter estimates for both the predation risk (A) and the survival (B) analysis. Effect sizes were standardized by subtracting the mean and dividing by two times its standard deviation as recommended by Gelman (2008). Effect sizes of each parameter were then compared to a reference state (dashed line with coefficient = 0) to determine how changes in a given parameter would affect the response variable. The reference state for both the predation risk and survival analysis was a wild steelhead with a mean fork length, in outmigration year 2010. All points are coefficient estimates of the averaged model, with 95% confidence intervals.

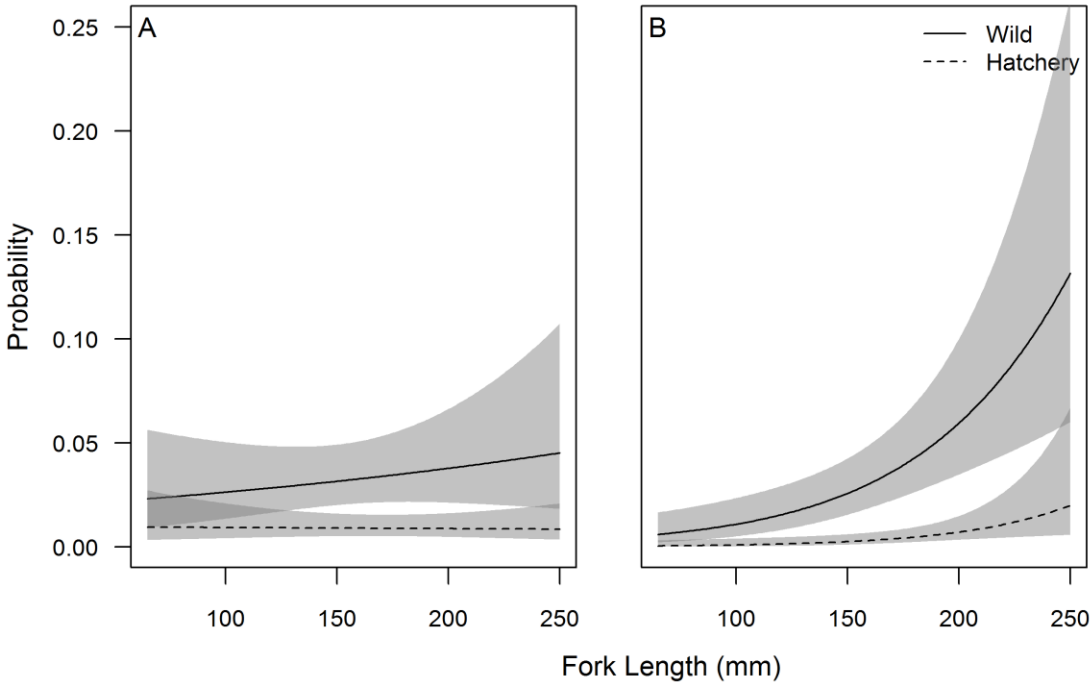


Figure 2-3. The probability of A) predation risk (i.e., tag recapture on ANI), and B) survival for a wild steelhead across the range of fork lengths. Estimates are based on juveniles from outmigration year 2010, which was a year with typical predation risk and survival. Estimates are calculated from the model averaged logistic regression model for both analyses. Shading indicates 95% confidence intervals.

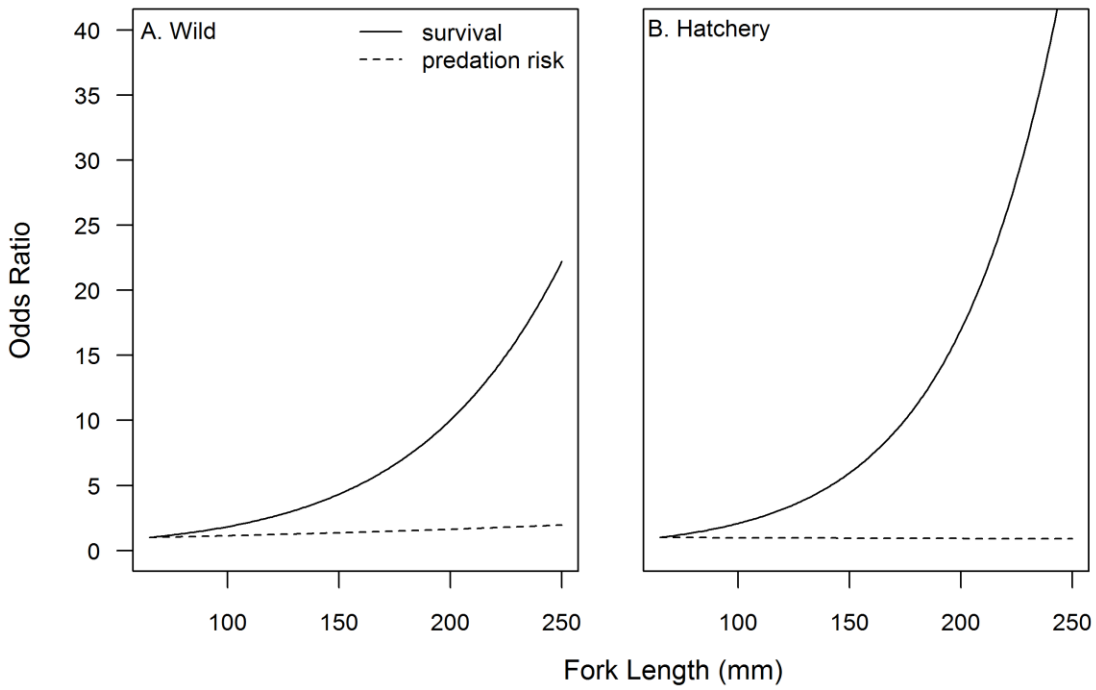


Figure 2-4. The increase in odds of survival or predation risk with fork length for wild (A) and hatchery (B) steelhead. Odds ratios were calculated by dividing the survival or predation risk at a given fork length by the survival or predation risk of a fish at the smallest size (65mm).

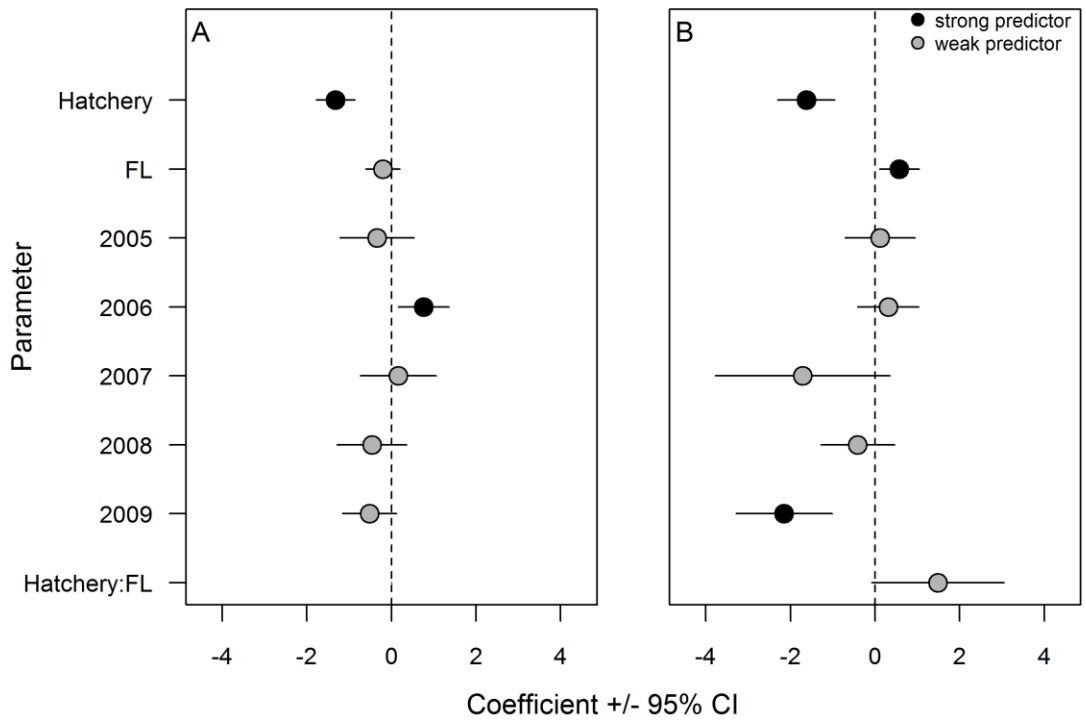


Figure 2-5. Model averaged parameter estimates for both the predation risk (A) and the survival (B) analysis upon outmigration by using the adjusted fork length for wild lagoon-reared individuals. Effect sizes were standardized by subtracting the mean and dividing by two times its standard deviation as recommended by Gelman (2008). Effect sizes of each parameter were then compared to a reference state (dashed line with coefficient = 0) to determine how changes in a given parameter would affect the response variable. The reference state for both the predation risk and survival analysis was a wild steelhead with a mean fork length, in outmigration year 2010. All points are coefficient estimates of the averaged model, with 95% confidence intervals.

3. Chapter 3 - Anthropogenic subsidies and the shifting resource base of a generalist predator: implications for native prey

3.1. Abstract

Over the last century, human activities have altered coastal ecosystems by fishing down the marine food web and increasing anthropogenic resources (e.g. landfills), which together can have cascading effects on native predator-prey interactions. In this study, we used stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ to conduct a 100-year retrospective analysis of changes in resource use of a generalist (Western Gull, *Larus occidentalis*) and piscivorous seabird (Brandt's Cormorant, *Phalacrocorax penicillatus*) in Monterey Bay (California, USA). We applied a Bayesian mixing model (MixSIAR) to historical (early 1900's) and modern (early 2000's) populations of Western Gulls to investigate temporal shifts in relative resource use, individual variation and niche width, and the implications of gulls` shifting resource use on one of their native prey—threatened steelhead populations (*Oncorhynchus mykiss*). Our results document a significant decline in the $\delta^{15}N$ value for both seabird species, suggesting prey in the marine environment has shifted to a lower trophic level in the last 100 years. Interestingly, the shift in $\delta^{15}N$ was significantly larger for Western Gulls, suggesting a shift in gull resource use to prey not in the marine environment. Mixing models suggest anthropogenic resources (e.g., landfills) comprise the majority of modern gull diet, whereas it contributed relatively little to gull diet in the early 1900's. In addition, we estimated relative predation risk of steelhead by Western Gulls between historical and modern populations and found although steelhead

contribute relatively less to overall modern gull diet, increasing gull populations and simultaneous steelhead population decline likely results in higher per capita predation risk to modern steelhead populations. This study highlights the impact of human activities on coastal predators and the potential consequences for native imperiled prey.

3.2. Introduction

Human exploitation and alterations to food webs have caused disturbances to coastal and marine ecosystems worldwide (Jackson et al. 2001, Oro et al. 2013). However, anthropogenic effects on ecosystems typically occur incrementally and these shifting baselines may go unnoticed or under-estimated (Pauly 1995). Over time, shifting baselines in fisheries exploitations have resulted in a decline in the mean trophic level of ocean fishes (Pauly et al. 1998), phase shifts in species abundance and diversity (Hughes 1994), and species extinctions (Dulvy et al. 2003, Jackson 2008). Anthropogenic effects not only include the removal of species, but also the addition of new resources that induce ecosystem change. For example, human subsidies such as unintended byproducts of agriculture, commercial fishing, waste discharge, and access to human refuse (e.g., landfills) can provide novel resources which can alter population dynamics and the state of ecosystems (Oro et al. 2013).

Temporal shifts in resource use or population size of generalist predators can have important consequences throughout the food web and can contribute to declines of native prey. The introduction of novel food sources can subsidize generalist predator populations beyond what native prey can support, thereby increasing per capita predation risk for native prey (Polis et al. 1997), sometimes described by terms including

hyper-predation, apparent competition, or subsidized predation. Furthermore, human subsidies provide predictable and renewable food sources that sustain populations of generalist predators and can result in extinction of native prey (DeCesare et al. 2010). For example, an increase in anthropogenic resources in the Mojave Desert subsidized multiple predatory species that subsequently increased mortality rates of their prey, the threatened desert tortoise (*Gopherus agassizii*; Kristan et al. 2004, Esque et al. 2010). Therefore, identifying shifting resource availability for generalist consumers and the impact of subsidized populations may provide insight into the management of imperiled species.

Seabirds reside at the nexus of two major human-induced changes, where overfishing has reduced the mean trophic level of their marine prey resource (Becker and Beissinger 2006, Wiley et al. 2013), and increased accessibility to fishery discards and human refuse can subsidize seabird diets and populations (Yorio and Giaccardi 2002, Weiser and Powell 2010). The consequences of shifting ocean and anthropogenic resources are particularly noticeable with gull populations (*Larus spp.*), where human trash via expanding landfills, increasing urban development, or fishery discards are thought to have contributed to the expansion and increase in gull populations worldwide (Conover 1983, Blokpoel and Spaans 1991, Vidal et al. 1998, Duhem et al. 2008). Consequently, these subsidized populations can contribute to increased predation rates on native prey species. For example, increased availability to human food has contributed to a rising population of kelp gulls (*L. dominicanus*) in South Africa, and subsequently increased predation pressure on a near-threatened Cape Cormorant (*Phalacrocorax capensis*) population (Voorbergen et al. 2012). Within subsidized seabird

populations, the impact of an individual seabird on prey species can vary substantially due to the large variation in the composition of prey species that contribute to individual seabird diet (Votier et al. 2010). In central California (USA), Western Gulls (*L. occidentalis*), are native generalist seabirds and are an important predator of imperiled salmon populations (Frechette et al. 2012, Osterback et al. 2013), potentially reducing adult steelhead returns in some watersheds by approximately 24% (Chapter 2; Osterback et al. *In Review*). Furthermore, Western Gull populations in central California (USA) have increased over the last 30 years (Hester et al. 2013). Although the exact mechanism for gull population increase remains unknown, it is possible that local landfills and urban waste have increasingly subsidized gulls. Understanding the relationship between anthropogenic subsidies, the gull population increase, and subsequent increase in predation risk to salmonids is of critical importance for the recovery of imperiled salmonids, yet has not been investigated to date.

Identifying human-induced changes to food webs can be especially challenging in systems without historical monitoring, however the use of stable isotope analyses can provide a tool to retrospectively document changes in food web dynamics over long periods of time (Schmidt et al. 2009). This method is particularly useful in avian ecology, where the stable isotope signature of feathers can be sampled non-lethally from the current population of birds and can be compared to feathers of historical museum skins to determine changes in diet over time (Becker and Beissinger 2006, Hilton et al. 2006, Rayner et al. 2011, Farmer and Leonard 2011, Pedro et al. 2013, Bond and Lavers 2014). Diet can be inferred from the stable isotope signature of feathers because the relative abundances of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes vary predictably by environment and

trophic level, and therefore create a "signature" for a given organism (Hobson and Clark 1992). Thus, relative abundances of $\delta^{13}C$ and $\delta^{15}N$ in tissues of an organism compared between modern and historical populations can give insight to changes in the diet of an organism over time.

Here we used retrospective stable isotope analysis to ask the question: how has the resource base of coastal avian predators changed over time and what are the potential implications of these shifts on native threatened steelhead prey? Specifically, we compared stable isotope signatures between a generalist consumer (Western Gull) and a marine piscivore (Brandt's Cormorant, *Phalacrocorax penicillatus*) to evaluate the shifting baseline of marine and anthropogenic resources for seabirds in central California (USA) over the last 100 years and explore the potential consequences for threatened steelhead. The four objectives of this study are to 1) compare shifts in the resource base over the last 100 years between a generalist consumer and a marine piscivore to determine potential shifts in the marine prey resource base verses other prey resources, 2) quantify temporal change in the relative resource use of the generalist consumer through application of stable isotope mixing models, 3) investigate changes in individual variation and niche width as a result of shifts in resource use over time, and 4) examine how changes in gull and steelhead abundances over the last 100 years translate to predation risk of steelhead. This study investigates the role of human activities in supporting predators that may contribute to the decline of endangered prey populations, such as imperiled salmon, and may also inform actions towards recovery of salmonid populations.

3.3. Methods

3.3.1. Study System

We conducted our study on Western Gulls and Brandt's Cormorants in the Monterey Bay area (California, USA), including Año Nuevo Island, Monterey Bay, and coastal creek mouths in Santa Cruz County (California, USA). Año Nuevo Island (ANI) is a rookery just north of Monterey Bay that hosts a suite of seabirds and marine mammals including breeding populations of Brandt's Cormorants and the third largest Western Gull breeding territory in California (Capitolo et al. 2009). Over the last couple decades, the number of breeding Brandt's Cormorants on ANI has fluctuated, likely due to variation in ocean productivity (Hester et al. 2013). In contrast, the Western Gull breeding population on ANI has increased and the current breeding population is 2-4 times larger than in the 1980's (Hester et al. 2013). Western Gulls are known to consume human refuse at landfills (Spear 1988, Annett and Pierotti 1989), thus one potential reason for the recent increase in Western Gull populations on ANI is because of an increase in anthropogenic resources (e.g., landfills, urban beaches) that subsidize gulls or buffer gulls from years with poor ocean productivity. Although human refuse and marine fishes contribute to the majority of modern gull diet (Annett and Pierotti 1989), gulls are opportunistic generalists that feed on a wide variety of organisms from marine mammals, intertidal organisms, and estuarine fishes, including federally threatened steelhead populations.

We included Brandt's Cormorants, a marine piscivore, in this study to represent the marine baseline resource over time for both Western Gulls and Brandt's

Cormorants. Brandt's cormorants are an appropriate seabird to provide a baseline for available marine prey in Monterey Bay for both species over time because they consume similar prey to Western Gulls when gulls forage in the marine environment. The diet of Brandt's Cormorants primarily includes fishes such as northern anchovy (*Engraulis mordax*), juvenile rockfish (*Sebastes* spp.), and sanddabs (*Citharichthys* spp.) as well as some cephalopods such as market squid (*Loligo opalescens*; Baltz and Morejohn 1977, Ainley et al. 1981, Webb 2013). These diet items are similar to those consumed by Western Gulls when gulls forage in the marine environment: Western Gull marine prey includes a variety of marine forage fishes such as northern anchovy, midshipman (*Porichthys notatus*), and juvenile rockfish as well as some marine invertebrates such as euphausiids and squid (Pierotti 1981, Annett and Pierotti 1989, Sydeman et al. 1991). In addition, these two species likely experience spatial overlap while foraging in Monterey Bay because both species breed on ANI (Hester et al. 2013) and are unique in that they both reside year-round in Monterey Bay, whereas other seabird species occur seasonally (Baltz and Morejohn 1977).

3.3.2. Sample Collection

We collected breast feathers for stable isotope analysis from the historical (1910-1941) and current (2008-2013) populations of adult Western Gulls and Brandt's Cormorants near Monterey Bay (California, USA). We used breast feathers from adults only to standardize sampling technique and to reduce variability in tissue turnover rates among tissue types. Feathers integrate stable isotope signatures from diet items over the time period during which they were grown (Kelly 2000). However, molt sequences in

Western Gulls are a relatively continual process and occur over a long time frame (>6 months; Howell and Corben 2000), making it difficult to identify which season is represented by the isotopic signature for a single breast feather. Similarly, feather molt is a continuous process in Brandt's Cormorants (Bridge 2006), allowing for weak inference on seasonal time of feather growth. Therefore, we assume that because we collected feathers from multiple seasons and years, that combined they are representative of average seabird diet throughout the historical and modern time periods.

In May 2008, and February and May 2009, we captured live Western Gulls at the mouths of two coastal creeks (Scott and Waddell Creeks, Santa Cruz County, California) and sampled breast feathers for stable isotope analysis. To capture gulls, we positioned and concealed two cannon nets on the beach near the creek mouth where gulls typically congregate. Bait such as human food (e.g., bread) lured gulls within range of the canon nets, and black powder and compressed air catapulted projectiles and the net over the feeding gulls. All gulls were disentangled from the net and transported back to the National Marine Fisheries Service Southwest Fisheries Center lab in Santa Cruz, California (USA). Sample collection for this project was conducted in collaboration with another project that entailed more intensive sampling and thus required transportation of live gulls to the lab (for more details on gull capture and handling, see Frechette et al. *In Review*). At the lab, breast feathers were sampled from each adult Western Gull, and feathers were stored in a dry location until samples were prepared for stable isotope analysis. All gulls were subsequently released at their beach of capture.

In collaboration with the Coastal Ocean Mammal and Bird Education and Research Surveys (BeachCOMBERS), we collected breast feathers from the current

population of adult Brandt's Cormorants from carcasses on beaches surrounding Monterey Bay. BeachCOMBERS volunteers survey Monterey Bay beaches on a monthly basis to provide an estimate of seabird and marine mammal mortality (Nevins et al. 2011). In October 2012 and May 2013, we added the additional objective of collecting breast feathers from adult Brandt's Cormorant carcasses when encountered. Volunteers sampled breast feathers from each encountered carcass and stored them in a dry location until samples were prepared for stable isotope analysis.

Historical adult Western Gull and Brandt's Cormorant feathers were sampled from study skins at the University of California Berkeley's Museum of Vertebrate Zoology. Individuals chosen for analysis included adults collected near Monterey Bay from 1910 through 1941. Breast feathers were sampled from each individual and were stored in a dry location until samples were prepared for stable isotope analysis. To correct for the change in carbon isotope ratios in atmospheric CO_2 over time (called the 'Suess Effect'), we applied the correction factor described in Equation 4 by Verburg (2007) to $\delta^{13}C$ values to historical feathers only. We used 2000 as the reference year to compare with modern samples.

3.3.3. Sample Processing

All feathers were cleaned, dried, and analyzed on a mass spectrometer for stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$. To remove surface lipids and contaminants, individual feathers were placed in 15ml vials, completely submerged in a 2:1 methanol-chloroform solution, and placed in a sonic water bath for 2 minutes. The process was repeated twice, using only methanol as a solvent. Feathers were dried at 60°C for 48 hours and

subsequently stored in airtight vials. We cut feather barbs into small pieces and weighed approximately 0.70 mg of sample into 5x9 mm tin capsules (Costech Analytical Technologies). We ran each sample for $\delta^{13}C$ and $\delta^{15}N$ on a Carlo Erba 1108 elemental analyzer coupled to a ThermoFinnigan Delta Plus XP isotope ratio mass spectrometer (University of California, Santa Cruz Stable Isotope Laboratory). All samples were corrected with standards (i.e., Pugel and Acetanilide), and we ran duplicates for 12% of the samples to ensure consistency of sample preparation ($R^2 > 0.96$ for both $\delta^{13}C$ and $\delta^{15}N$ signatures).

3.3.4. Comparing shifts in resource baselines between two consumers

To identify shifts in the resource baseline over the last 100 years, we compared the mean $\delta^{13}C$ and $\delta^{15}N$ signatures of modern and historical breast feathers between a generalist consumer (Western Gulls) and a marine piscivore (Brandt's Cormorants). By tracking the stable isotope signature of Brandt's Cormorants over a long time period (~100 years), we can identify changes to the marine resource baseline. As a result, we can compare the shift in resource baselines of Western Gulls to those of Brandt's Cormorants to determine if shifts in gull diet can be mostly attributed to shifts in the marine resource baseline or is likely due to changes in other resources. For example, if the stable isotope signatures are similar between historical and modern gulls when compared to historical and modern Brandt's Cormorants, then we may conclude that a change in gull isotopes is the reflection of the shift in in the marine environment. Alternatively, if the change in Western Gull stable isotope signatures differs from that observed with Brandt's Cormorants, then we can infer that their shift in isotopes comes

from a different prey resource (e.g., anthropogenic, intertidal, etc.). Mean stable isotope signatures were compared between species and time periods using a Welch Two Sample t-test (R Development Core Team 2013).

3.3.5. Quantifying relative resource use in a generalist consumer over time

To determine relative contributions of different resources to the current and historical diet of adult Western Gulls, we used MixSIAR, a stable isotope mixing model that uses a Bayesian approach and a mixed effects framework to estimate relative contributions of potential prey items to the consumer population in addition to estimates for individual consumers (Stock and Semmens 2013). Thus, the model structure of MixSIAR allows for estimates of variation in diet among individuals by including individuals as a random effect. Within MixSIAR, we conducted Markov chain Monte Carlo (MCMC) sampling by running three replicate chains each with 1,020,000 draws. We removed the first 20,000 iterations as burn-in and kept every 200th posterior sample, resulting in 5,000 independent draws from the posterior distribution. We confirmed model convergence using Gelman-Rubin diagnostics (Gelman and Rubin 1992).We did not use any informative priors (i.e., flat priors) for gull diet because quantitative diet composition for modern Western Gulls is lacking. We selected five potential prey sources that represent the prey items available within a range of different habitats in which gulls forage: estuarine fishes (e.g., steelhead), human food (e.g., in landfills), intertidal invertebrates, marine fishes, and marine mammals (Table 3-1).

Stable isotope signatures of potential prey were compiled from published literature and from data collected during this study (Table 3-1). The $\delta^{13}C$ and $\delta^{15}N$ stable

isotope signature of estuarine fishes are represented by lagoon-reared steelhead from Scott Creek (Collins 2008) because steelhead represent the dominant biomass for estuarine fishes in most Santa Cruz County lagoons (Beck et al. 2006). For marine mammals, we used the stable isotope signature of muscle tissue from Stellar sea lions (*Eumetopias jubatus*) from Año Nuevo Island (Sydeman et al. 1997); Western Gulls are known to feed on sea lion placenta and carcasses (Schreiber 1970). Although Stellar sea lions are currently less common on Año Nuevo Island, they have similar diets to California sea lions (*Zalophus californianus*), which are the most common pinniped near central and southern California (Antonelis and Fiscus 1980) and is the most abundant marine mammal species on Año Nuevo Island. For intertidal invertebrates, we used the $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures reported by Newsome et al. (2009) for three common intertidal invertebrate species in Monterey Bay (snails- *Tegula* spp.; mussels- *Mytilus californianus*; and seastars- *Pisaster* spp.), which are all documented prey of Western Gulls (Hunt and Hunt 1976, Snellen et al. 2007, Rogers and Elliott 2013). We then calculated a weighted mean stable isotope signature among these three species by incorporating their relative percent cover at seven biodiversity sites near Año Nuevo Island. Percent cover of intertidal invertebrates was estimated by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) between 2006 and 2008. To represent an integrated isotopic signature of modern human food, we used the stable isotope signature of human fingernails from a local population in Menlo Park, California (USGS 2006), which has a similar stable isotope signature to other human populations in the United States (Nardoto et al. 2006). For marine fishes, we chose modern Brandt's Cormorant diet to represent an integrated signature of marine forage fishes available in

the greater Monterey Bay area, thus we applied feather stable isotope values from the current population of Brandt's Cormorants reported in this study to represent Brandt's cormorant diet (i.e., marine fishes).

The isotopic signatures of consumers are typically enriched by +3-5‰ $\delta^{15}N$ and 0-2‰ $\delta^{13}C$ when compared to their diet because bonds of lighter isotopes break easier during biochemical processes and are thus preferentially excreted (Fry and Sherr 1984, Peterson and Fry 1987) . However fractionation values are specific to many factors including species, diet type, and diet quality (Caut et al. 2009), therefore identifying appropriate fractionation values is important to correctly interpret the data from food web studies (Bond and Jones 2009). Due to a lack of data, we used the mean and standard deviation of published fractionation factors for related species, following the methods of previous studies (Weiser and Powell 2011, Steenweg et al. 2011, Lavoie et al. 2012). To correct for trophic enrichment of Western Gulls and Brandt's Cormorants, we used the mean fractionation factor for diet to feathers of different seabird populations summarized by Becker et al. (2007) and calculated a standard deviation from these values (N=11). Therefore, the diet-feather fractionation factor we used for this study is 1.4± 0.9 $\Delta^{13}C_{prey\text{-}feather}$ and 3.6± 0.6$\Delta^{15}N_{prey\text{-}feather.}$ Because trophic fractionation is different between seabirds and humans, we took two steps in order to compare the stable isotope signature of finger nails to seabird feathers. First, we corrected for trophic enrichment between human diet and fingernails by combining the fractionation factor between diet- human hair calculated from humans in the USA (Schoeller et al. 1986; +1.4‰ $\Delta^{13}C_{food\text{-}hair}$ and +4.4‰ $\Delta^{15}N_{food\text{-}hair}$) and the fractionation factor between human hair and human fingernails (O'Connell et al. 2001; +0.2‰ $\Delta^{13}C_{hair\text{-}nail}$ and -0.65‰ $\Delta^{15}N_{hair\text{-}nail}$). Second, we

calculated the difference between the seabird diet-feather fractionation and the human diet-nail fractionation in order to get a fingernail-feather correction factor. Because fractionation values vary among individuals, we applied the standard deviation in isotopic signatures in human hair reported among individuals by Schoeller et al. (1986 ; ± 0.5‰ $\delta^{13}C$ and ± 0.6‰ $\delta^{15}N$) to the variation among fractionation factors between diet and human hair, which is consistent with individual variation in fractionation factors within other human populations (Hedges et al. 2009). To examine the sensitivity of our results to alternative fractionation values, we also ran the mixing model using alternative published fractionation factors that are species-specific in order to account for possible variation between gull and cormorant diet-feather fractionation. The results of this alternative mixing model were similar (Appendix B, Figure 5-1). Therefore, we focus on results based on the fractionation factors in Table 3-1.

3.3.6. Investigating individual variation and relation to foraging locations in a generalist consumer

We investigated how individual variation in resource use and niche width varied with time period and foraging locations. First, we compared variation among individual inferred diets (i.e., posterior distributions of standard deviation across individuals estimated by MixSIAR) between historical and modern Western Gulls as an index of intra-population dietary differences. To identify if these distributions of individual variation among groups are significantly different, we calculated the difference between the modern and historical posterior distributions. If the resulting distribution does not significantly overlap with zero, then the individual variation among historical individuals

is significantly different than modern individuals. Second, we used a subset of the modern individual gulls to compare their diet (relative proportions of prey) with their occurrence in different foraging locations around Monterey Bay. Paired stable isotope data with occurrence in foraging locations was possible because feather collection from modern Western Gulls during this study was conducted in collaboration with a radio-tracking study for Western Gulls (Frechette et al. *In Review*). Therefore, we sampled feathers for isotope analyses and then a subset of these gulls was subsequently outfitted with VHF radio-transmitters. For the few months following feather sampling and initial radio-tagging, researchers identified the location of radio-tagged individuals through a combination of active tracking, passive listening stations, and aerial surveys (for more details, see Frechette et al. *In Review*). Tracking locations included Año Nuevo Island, coastal creek mouths, the Santa Cruz landfill, and the Santa Cruz wharf. Even though stable isotope diet data from feathers (diet previous to sampling) and radio-tracking data (foraging after sampling) do not temporally overlap, these paired datasets may still reveal whether known presence at distinct foraging locations can be predicted by stable isotope data.

3.3.7. Linking gull population size with steelhead predation risk

We used results from the mixing models and previous research to explore how predation rates on steelhead may have changed over the last century. Specifically, we compare modern to historical per capita predation risk of steelhead by incorporating historical and modern estimates of Western Gull and steelhead population sizes, and the proportion of gull diet comprised of steelhead. Because robust estimates of Western

Gull and steelhead abundances in the early 1900's are lacking, we created a suite of realistic scenarios that included hypothesized historical gull and steelhead abundances and included them as inputs into the model. The relative per capita predation risk (*R*) is defined as,

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

where each factor in the equation is the ratio between modern and historical values: *d* is the ratio of the relative contribution of steelhead of modern gull diet compared to historical diet, *g* is the ratio of the modern population size of Western Gulls on ANI compared to historical abundances, and *s* is the ratio of modern steelhead population abundances compared to historical abundances. For example, when *g*=1 or 3, modern population sizes of Western Gulls on ANI are equal to or three times that of the historical population size in the early 1900's, respectively. If s=0.3, modern steelhead population size is 30% of the historical population size. Values of R are log-transformed such that R=0 suggests no change in relative risk to steelhead between modern and historical time periods, and negative and positive values of R suggest modern steelhead have decreased or increased predation risk to gulls, respectively.

We used a series of parameter estimates to explore potential changes in predation risk. The relative contribution of steelhead to the diet of modern and historical Western Gull populations (*d*), is taken directly from the mean of the MixSIAR posterior distributions from both groups. To incorporate uncertainty around our estimate of *d*, we calculated 15,000 possible ratios of *d* by dividing all draws from the modern posterior

distribution that estimates the contribution of steelhead to gull diet by all draws from the historical posterior distribution. We subsequently substituted the upper and lower 90% CIs into the predation risk model to identify upper and lower CIs of relative predation risk. We explored a potentially realistic range of the relative change in Western Gull populations (g) where the modern gull population is 0.5, 0.75, equal, 2, 3, 5 or 10 times the historical population. Among these possible values of g, we hypothesize that the modern Western Gull population is likely at least three times larger than it was historically, and potentially much larger. Although there is no reliable estimate of gull abundance in the early 1900's, we know that over the last 30 years Western Gull populations on ANI have increased (Hester et al. 2013). ANI was a functioning light station until 1948, with full-time residents that likely occupied much of today's Western Gull breeding areas. Furthermore, in the early 1900's the Western Gull population at the nearby Farallon Islands was one-third of what it was in 2008 due to human disturbance and egg harvesting (Ainley and Lewis 1974, Warzybok et al. 2012). Other species of gulls also increased during a similar time period: the breeding number of Calfornia gulls in the western United States increased by 2.7 times between 1930 and 1980 (Conover 1983). Thus, we suspect there was likely at least a three-fold difference between historical and modern Western Gull population sizes on ANI. To assess how the relative per capita predation risk of steelhead (R) is influenced by changes in steelhead population size, we calculated R where modern steelhead abundance was 10%, 20%, and 30% of the historical population. Central California coast steelhead abundances have declined by 80-90% in the last 50 years (Moyle et al. 2008), though the exact magnitude of this difference is unknown. However, in 1910, 437 adult female steelhead were captured in

Scott Creek (Moore et al. 2011), whereas only 131 adult female steelhead were captured in 2008 after extensive sampling (Hayes et al. 2013). Thus, we can conservatively estimate that modern populations are less than one-third of the historical population.

3.4. Results

3.4.1. Comparing shifts in resource baselines between two consumers

We collected breast feathers from a total of 80 adult seabirds, including modern populations of Western Gulls (N=41) and Brandt's Cormorants (N=11), and historical museum study skins of Western Gulls (N=15) and Brandt's Cormorants (N=13). Stable isotope signatures of both Western Gulls and Brandt's Cormorants shifted over time, based entirely on significantly lower mean $\delta^{15}N$ isotopic signatures of modern feathers (Figure 3-1A and Figure 3-1B). The shift suggests modern consumers may be feeding at a lower trophic level than historical consumers. In contrast, $\delta^{13}C$ signatures were similar across species and time (Figure 3-1A and Figure 3-1B). Interestingly, the difference in $\delta^{15}N$ signature for modern (14.7 ± 1.9 SD ‰ $\delta^{15}N$) and historical (17.4 ± 1.0 SD ‰ $\delta^{15}N$) Western Gulls was greater than the difference between modern (16.2 ± 0.9 SD ‰ $\delta^{15}N$) and historical (17.0 ± 0.7 SD ‰ $\delta^{15}N$) Brandt's Cormorants, suggesting different resource use between the two species. There were no significant differences between the mean $\delta^{13}C$ isotopic signature for all pairwise comparisons between the $\delta^{13}C$ isotopic signature for modern gulls (-16.1 ± 0.8 SD ‰ $\delta^{15}N$), modern cormorants (-15.4 ± 1.3 SD ‰ $\delta^{15}N$), and mean Suess-corrected $\delta^{13}C$ isotopic signature for historical gulls (-16.2 ± 0.5 SD ‰ $\delta^{15}N$) and cormorants (-16.2 ± 1.6 SD ‰ $\delta^{15}N$).

3.4.2. Quantifying relative resource use in a generalist consumer over time

The range of stable isotope signatures of potential prey sources was wide and encompassed the range of isotope signatures observed in both historical and modern Western Gull feathers (Figure 3-1C). Prey sources spanned over 5 parts per mil for $\delta^{13}C$ and over 10 parts per mil for $\delta^{15}N$ (Table 3-1), and gull isotope signatures were distributed throughout this range, suggesting the relative contribution of prey sources varied among individuals (Figure 3-1C).

The posterior distributions from MixSIAR suggest the relative contribution of prey sources to gull diet differed substantially between modern and historical Western Gulls (Figure 3-2). The largest temporal differences in gull diet was the increase in the mean relative contribution of human food to modern gull diet (0.31; 0.18-0.44 95% credible intervals (CI)) when compared to historical gull diet (0.10; 0.01-0.26 CI). Another substantial difference was the smaller contribution of steelhead to modern gull diet (0.06; 0.00-0.16 CI) when compared to historical diet (0.25; 0.08-0.41 CI). Relative changes in the proportion of other prey sources to gull diet over time were highly uncertain. There was little to no difference in the relative contribution of Western Gull diet over time for intertidal organisms (modern = 0.20; 0.05-0.38 CI; historical =0.10; 0.00-0.25 CI), marine fishes (modern = 0.16; 0.01-0.40 CI; historical = 0.16; 0.01-0.41 CI), or marine mammals (modern = 0.26; 0.13-0.37 CI; historical = 0.39; 0.27-0.52 CI).

3.4.3. Investigating individual variation and relation to foraging locations in a generalist consumer

Individual variation in the diet of modern gulls was significantly larger than historical gulls ($p<0.05$; Figure 3-3), suggesting modern gulls encompass a larger niche space. This difference is likely driven by significantly larger variance in $\delta^{15}N$ signature of modern gulls when compared to historical gulls (F test; $p=0.011$; Figure 3-1A, Figure 3-1C). Greater individual variation in the diet among modern gulls is also demonstrated by the increased range in the relative contribution of a specific diet item (e.g., human food) to modern gulls when compared to historical gulls. Specifically, the proportion of human food comprises a large and variable proportion of modern gull diet (mean posteriors were between 0.23 and 0.43; Figure 3-4), whereas human food contributes a smaller and less variable proportion to historical gull diet (mean posterior was between 0.09 and 0.11; Figure 3-4).

Paired stable isotope signatures and individual tracking data suggest presence of gulls in foraging habitat is not clearly related to relative contributions of specific sources to overall diet. Of the 41 adult modern Western Gulls sampled for stable isotope analysis, 27 of them were successfully tracked using radio-telemetry for a related study (Frechette et al. *In Review*). There were no systematic differences in relative proportion of human food to gull diet among gulls observed in different foraging habitat, suggesting observed location of gulls does not predict past relative diet sources of an individual (Figure 3-4). Whereas we determined via radio-telemetry that gulls move between different habitats (Frechette et al. *In Review*): the stable isotope data suggest gulls forage while in these different habitats.

3.4.4. Linking gull population size with steelhead predation risk

We explored the sensitivity of predation risk to the estimates of historic and modern gull consumption of steelhead. Even though the mean contribution of steelhead to gull diet has apparently decreased over time (modern gull diet is estimated to be approximately 24% of what it was historically; Figure 3-2), the relative per capita risk of steelhead to predation by gulls is still likely much higher for modern gulls than for historical gulls (Figure 3-5). This is because increasing gull populations and declining steelhead populations result in increased predation risk to modern steelhead despite contributing relatively less to gull diet. For example, even if we assume no change in the population of Western Gulls on Año Nuevo Island (x=0), only a 24% reduction in steelhead populations would result in increased predation risk to steelhead. Similarly, if we assume no change in steelhead abundance (Figure 3-5, black points), only a 4-fold increase in the gull population would result in increased predation risk to steelhead. We hypothesized that both of these trends have occurred, such that gull populations have likely tripled, and steelhead populations are likely no more than 30% of their historical values (Figure 3-5, red square). After incorporating 90% confidence intervals (CI) for d, we estimated the mean ratio in the contribution of steelhead to gull diet between modern and historical populations (d) was 0.24 with 90% CI that ranged from 0.024 to 0.766. Through this process of incorporating uncertainty, and given this scenario where gull populations have tripled and steelhead abundances are 30% of historical, we estimate the mean per capita predation risk of modern steelhead is 2.4 times the predation risk when compared to historical steelhead, but based on 90% CI, may range from 0.24 to 7.7

(Figure 3-5, red square). Of the possible values of *d* included within the 90% CIs, 77% of them result in positive estimates of predation risk (R), further suggesting per capita predation risk has increased for steelhead over the last 100 years.

3.5. Discussion

In this study we used stable isotope analysis to retrospectively document a shifting baseline of resources in the marine environment in Monterey Bay, demonstrating that both modern generalist and piscivorous seabirds now feed at a lower trophic level than they did historically. Our results also suggest anthropogenic food sources have become a larger component of modern gull diet; however the contribution of human food to modern gull diet can vary substantially between individuals, thereby increasing the niche width of modern gulls. Although it remains unknown as to whether anthropogenic sources (e.g., landfills) have directly contributed to gull population growth, our results indicate that human food is the dominant resource of most modern gulls, which may contribute to sustaining the current population size of Western Gulls and the increased predation risk of native prey, such as threatened steelhead. Therefore, our results demonstrate how the human activities have impacted a coastal food web and may indirectly limit recovery of threatened and endangered salmonids.

We observed a decline in $\delta^{15}N$ for Western Gulls and Brandt's Cormorants over the last 100 years suggesting modern birds are eating at a lower trophic level; however the magnitude of decline varied between species suggesting different resource use between modern populations (Figure 3-1). Decline in the trophic level of the marine food web due to fisheries exploitation has been documented in other systems, where

modern seabirds feed lower in the food chain when compared to historical populations (Hilton et al. 2006, Farmer and Leonard 2011, Pedro et al. 2013). Similar patterns have been observed in Monterey Bay, where Becker and Beissinger (2006) documented that over 100 years the diet of modern endangered Marbled Murrelets declined by 14% - 38% of a trophic level (0.5 - 1.4 ‰ $\delta^{15}N$), depending on the season and ocean conditions. Lower $\delta^{15}N$ values were attributed to eating lower trophic level prey and not due to a temporal shift in the isotope signature of the base of the food web because research on zooplankton in the California Current suggests $\delta^{15}N$ has not changed significantly since 1951 (Rau et al. 2003). As a result, change in $\delta^{15}N$ of seabirds likely reflects change in identity of relative consumption of prey items and not change in stable isotope composition of similar prey over time. We found a similar decline in the marine environment as Becker and Beissinger (2006) over the same temporal and spatial scale, where modern Brandt's Cormorants diet in this study declined by 22% of a trophic level (0.8 ‰ $\delta^{15}N$). Thus, our results in conjunction with previous studies provide more evidence of a region-wide decline in marine trophic level at which seabirds feed. Interestingly, we found a relatively larger decline in $\delta^{15}N$ of Western Gulls over time when compared to Brandt's Cormorants, suggesting an increase in the relative resource use of prey in a location other than in the marine environment.

Mixing models allowed reconstruction of the potential temporal shifts in resource use of different prey (Figure 3-2). The most notable difference is the larger contribution of anthropogenic resources to modern gull diet when compared to historic gull diet, which is likely driving the relatively larger decline in $\delta^{15}N$ in Western Gulls when compared to Brandt's Cormorants, a primarily marine-feeding species (Figure 3-1).

Increased reliance on anthropogenic sources is well-documented in seabirds, especially for gulls (Duhem et al. 2008, Pedro et al. 2013). In Monterey Bay, we have observed thousands of gulls foraging at local Santa Cruz County landfills, and new GPS tracking data confirms regular daily foraging trips to local landfills by Western Gulls breeding on Año Nuevo Island (Shaffer, *unpublished data*), confirming use of the landfill resource by breeding gulls. The second largest temporal change in gull diet was the decreased contribution of steelhead to modern gull diet. A reduction in steelhead to gull diet is not surprising, given that steelhead populations have declined in the area (Moyle et al. 2008, Moore et al. 2011). There was no clear difference in the proportion of intertidal organisms, marine fishes, or marine mammals between modern and historical gull diet. It is surprising the contribution of marine mammals to gull diet did not increase over time because California sea lion populations were historically exploited but have experienced extremely high growth rates in the last 30+ years (Lowry and Maravilla-Chavez 2005, NMFS 2011). This suggests that relative abundances of prey is not the only factor driving diet composition of gulls. For example, diet of Western Gulls is often not controlled by relative abundances of prey, but instead is driven by preference for specific species or prey size (Snellen et al. 2007, Rogers and Elliott 2013). In addition, gulls live on coastal islands so regardless of their foraging destination they have consistent overlap with marine prey, which may result in more consistent use of those resources. Our results suggest that gull diet has changed over time, and now includes a higher proportion of anthropogenic sources.

There was higher individual variation of inferred diets for modern gulls than historic gulls (Figure 3-3). Increased individual variation in diet increases the niche width

of the population, which can result when individuals within the population exploit different subsets of resources (Bolnick et al. 2007). One potential reason for increased niche width in modern gulls is the increased amount of anthropogenic food (e.g., landfills) available to gulls now when compared to the early 1900's. This is supported by the rising human population and production of refuse, where in only the last 50 years the population of Santa Cruz more than doubled (SCPL 2000) and the per capita amount of trash generated by each individual in the United States increased by 11% (USEPA 2008). This addition of refuse may have added another axis to the gulls' niche. Increased niche width from heterogeneous use of resources between individuals within a population can increase population stability (Layman et al. 2007), which could contribute to increased gull populations and therefore affect population dynamics and interactions with prey. The relative contribution of prey sources to overall diet was not related to presence of individuals at foraging sites (Figure 3-4). It appears that the foraging behavior of individuals is not a perfect predictor of apparent consumption patterns. This is likely because tracking data only captured a snapshot in time of individuals foraging over a large area and presence data at other prey source locations went unrecorded. Furthermore, these results suggest individual gulls forage in multiple environments and likely do not specialize or limit their prey to only one or a few species or locations. Thus, the results from this study show movement of individual gulls between prey source locations, however the relative importance of each prey source is more variable between modern individual gulls.

Our study demonstrates that anthropogenic sources have become increasingly important to modern gull diet as gull populations have increased. We acknowledge we

cannot directly identify anthropogenic subsidies as the mechanism for gull population increase; however this link has been made in other systems. For example, a long-term study in the French Mediterranean demonstrated that gull populations increased on islands with increasing availability to anthropogenic food sources (Duhem et al. 2008). Previous research has shown anthropogenic sources are particularly important to gull diet when ocean productivity is low (Spear 1988), which suggests human food may buffer gull populations from prey fluctuations in the marine environment. However, increased access to refuse is likely not the only possible reason for increased gull populations but might instead be a result of other environmental change, such as a decrease in pesticides. For example, bald eagles (*Haliaeetus leucocephalus*) made remarkable population recoveries following the 1972 ban of DDT, a widespread insecticide that caused egg shell thinning and reduced clutch success (Stokstad 2007). DDT has been found both in Brandt's Cormorants (Jarman et al 1996) and Western Gulls (Jimenez-Castro et al 1995). The relative role of DDT and anthropogenic subsidies to gull population increase remains unknown and should be the focus of future research.

Regardless of the mechanism for growth of gull populations, the results from our predation risk model show that predation risk of steelhead has likely increased over the last 100 years (Figure 3-5). Even though modern gulls apparently consume less steelhead on an individual basis than historically, the decline in steelhead abundance and increasing gull population leads to increased risk of an individual steelhead being eaten. However, it is important to consider the uncertainty associated with parameters that informed the relative predation risk model. While we are confident that gull populations have increased and steelhead populations have declined over the last 100 years, the magnitude

of these shifts remain largely unknown. And although alternative modeling scenarios support that steelhead have become a smaller proportion of gull diet over time (Appendix B, Figure 5-1), our estimates of the relative contribution of steelhead to gull diet over time were uncertain (Figure 3-5). Thus, if gulls substantially decrease predation on steelhead or switch to alternative prey altogether, relative per capita predation risk for steelhead may decline (Figure 3-5). However, if gulls continue to rely on predictable anthropogenic food subsidies, it can continue to stabilize predator populations (Oro et al. 2013) and contribute to the extinction of native prey (DeCesare et al. 2010).

Stable isotope analysis provides a powerful tool to evaluate the relative contribution of diet sources to a consumer (Moore and Semmens 2008), retrospectively document change in diet over time (Pedro et al. 2013), and evaluate niche breadth within a population (Newsome et al. 2007). Here we discuss and evaluate some assumptions associated with our mixing models. For example, temporal mismatch between prey and consumer tissue samples used for stable isotope analysis can lead to incorrect interpretation of the data (Inger and Bearhop 2008), as can inappropriate use of fractionation factors. For this study, we collected feathers across a broad range of seasons, years, and locations and therefore assume we captured general trends in regards to changes in gull diet over time and minimize seasonal variability. In addition, we also ran the model using an alternative set of fractionation factors and concluded they had minimal effect on the overall results from this study (Appendix B, Figure 5-1). As with all stable isotope mixing models, we assumed our prey sources were representative of all gull diet items. It is particularly difficult to capture all prey items for generalist predators, such as gulls, which is why most prey sources were presented as a weighted average for

multiple species within a common gull foraging habitat. Additionally, consumer data were encompassed by all prey species in isotope space (Figure 3-1C), further supporting that we captured the range of diet items consumed by gulls. Another assumption was that the stable isotope signatures of modern prey have not changed since the early 1900's and that a shift in the $\delta^{15}N$ over time (in both Brandt's Cormorants and Western Gulls) was due to a change in prey identity, not changing stable isotope signatures for the same prey over time. Changes in $\delta^{13}C$ and $\delta^{15}N$ for prey sources since 1900 were not available for most prey species in our specific study system, however previous studies suggest there has been little change in the $\delta^{15}N$ of the base of the marine food web in the California current since the 1950's (Rau et al. 2003, Ohman et al. 2012). To further address this, we re-ran the mixing model for historical gull diet using the historical stable isotope signature of Brandt's Cormorants to represent historical marine fishes and found virtually no change to the model results (Appendix B, Figure 5-2), suggesting shift in prey baselines have little effect on overall model trends. Regardless, the relatively larger decrease in $\delta^{15}N$ for Western Gulls when compared to Brandt's Cormorants (Figure 3-1) suggests the change in gull diet occurred in a location other than in the marine environment. Lastly, we assumed feather samples from gulls and cormorants were represented equally between species and sampling periods. Although sample sizes differed between groups, Bayesian modeling takes into consideration sample size and variation and incorporates this uncertainty to provide robust estimates of gull diet. While it is impossible to determine if feather samples from museums, carcasses, and live individuals were representative of the live population for a given species and time, we

were limited by the samples available. Although retrospective stable isotope analysis requires these assumptions, we believe the general conclusions are robust.

By altering coastal ecosystems with commercial fisheries (Pauly et al. 1998, Essington et al. 2006) and increasing the availability of alternative food sources, humans have modified the resource landscape for mobile generalist predators and this has cascading consequences throughout the food web. In this study, we demonstrated a shift in the marine resources over time for both generalist Western Gulls and piscivorous Brandt's Cormorants. Furthermore, generalist Western Gulls demonstrated shifts in their diet, including increased reliance on anthropogenic resources and relatively less reliance on estuarine fishes such as steelhead. Despite consuming fewer steelhead per individual gull, the combination of increasing gull populations and declining steelhead populations suggest that there is increased predation risk to steelhead. Based on current patterns of predation, we previously estimated that Western Gulls can eat approximately 30% of the juvenile steelhead population each year at some central California coast watersheds (Osterback et al. 2013). One potential management option to reduce predation rates would be to manage the anthropogenic subsidies to gulls such as reducing access to landfills. Suggested management actions to prevent gulls from accessing anthropogenic subsidies in other systems have included prohibiting fishery discards (Bicknell et al. 2013) or selective culling (Thiériot et al. 2012), however the effectiveness of these actions on native prey populations remains unknown. Selective culling may not be feasible in this system because most individual gulls exhibit a generalist diet, thus it is not only specific individuals that impact steelhead populations, but the collective sum of many. Given anthropogenic subsidies to generalist predators may have profound

consequences to their native prey, it is necessary to expand management scopes to address this issue.

3.6. Tables

Table 3-1. Literature values for stable isotope signatures and fractionation factors for $\delta^{13}C$ and $\delta^{15}N$ of five potential prey sources of Western Gulls that were incorporated into MixSIAR.

Sources	Stable Isotope Signatures					Fractionation Factors			
	Mean $\delta^{13}C$	SD $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{15}N$	n	Mean $\delta^{13}C$	SD $\delta^{13}C$	Mean $\delta^{15}N$	SD $\delta^{15}N$
steelhead[1]	-20.6	1.2	11.2	0.6	11	1.4	0.9	3.6	0.6
human food[2]	-18.8	0.8	9.2	0.6	485	0.2	0.5	-1.45	0.6
Intertidal[3]	-16.2	0.8	9.9	0.3	7	1.4	0.9	3.6	0.6
marine fishes[4]	-15.4	1.3	16.2	0.9	11	0	0.9	0	0.6
marine mammals[5]	-15.2	0.5	19.8	0.6	5	1.4	0.9	3.6	0.6

Sources:

[1] Stable isotope values (Collins 2008); Fractionation (Becker et al. 2007)

[2] Stable isotope values (USGS 2006); Fractionation (Schoeller et al. 1986, O'Connell et al. 2001, Becker et al. 2007)

[3] Stable isotope values (Newsome et al. 2009); relative percent cover (PISCO, unpublished data), Fractionation (Becker et al. 2007)

[4] Stable isotope values (this study), Fractionation-standard deviation only (Becker et al. 2007)

[5] Stable isotope values (Sydeman et al. 1997); Fractionation (Becker et al. 2007)

3.7. Figures

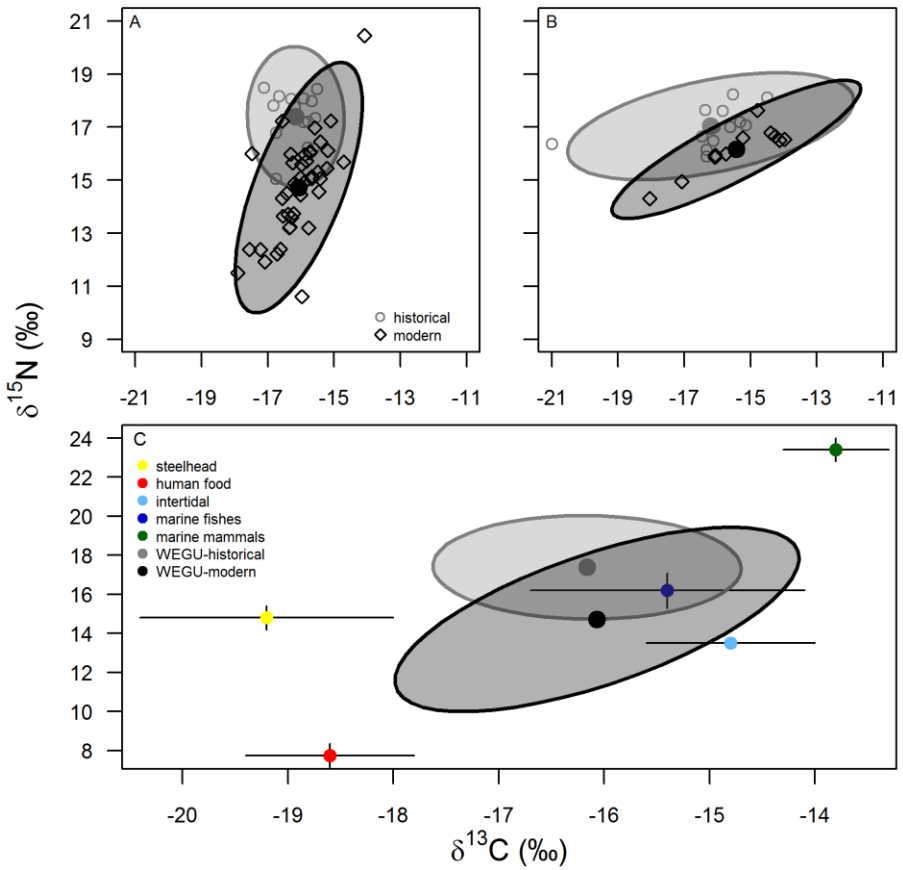


Figure 3-1. Isotope signatures of δ13C and of δ15N of breast feathers from historical and modern adult Western Gulls (A), historical and modern adult Brandt's Cormorants (B), and isotope signatures of δ13C and of δ15N of breast feathers from historical and modern Western Gulls (mean ± 95% CI) with isotope signatures of potential prey sources, after accounting for fractionation (mean ± SD; Table 3-1) (C). Note the ellipses in 1A and 1C contain identical data, but axes are at different scales. Individual feather samples are indicated by open symbols, means are indicated by filled symbols, and 95% CI are represented by ellipses. $\delta^{13}C$ isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007).

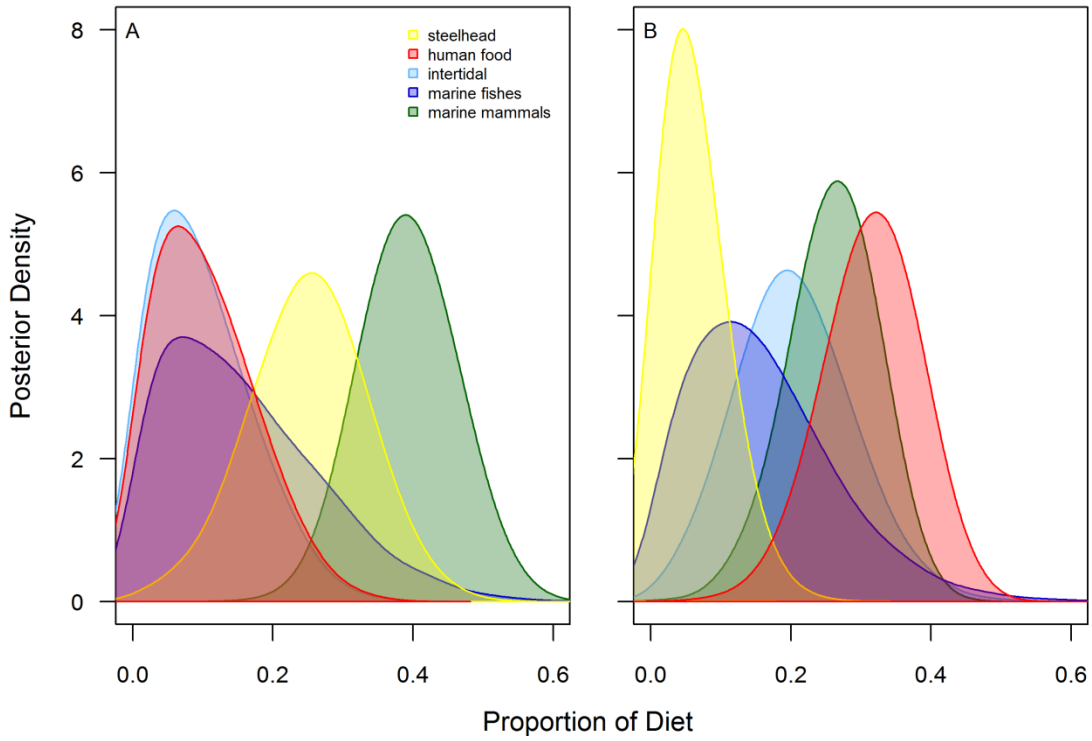


Figure 3-2. Proportion of diet sources that contribute to historical (A) and modern (B) Western Gulls. Data are represented as posterior densities from the mixing model output from MixSIAR, using potential prey sources from Table 3-1. $\delta^{13}C$ isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). Note that posterior densities less than 0.0 result from a smoother function to create this graphic.

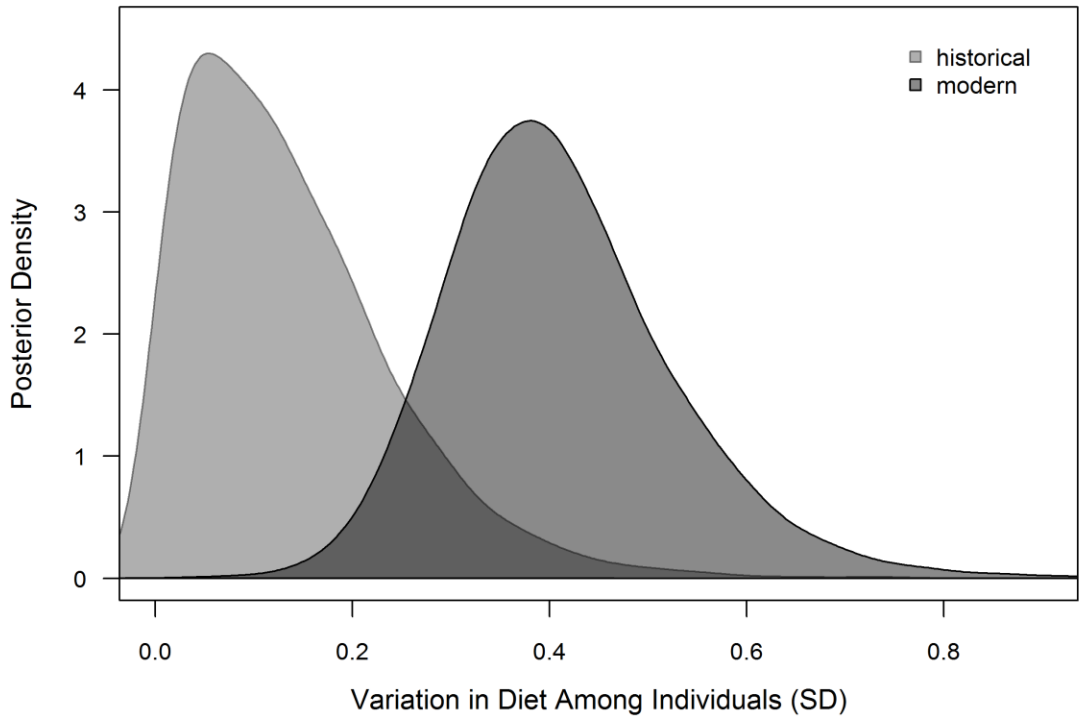


Figure 3-3. Variation in isotopic signatures among individuals from historical (A) and modern (B) Western Gulls. Data are represented as posterior densities from the mixing model output from MixSIAR. $\delta^{13}C$ isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). Note that posterior densities less than 0.0 result from a smoother function to create this graphic.

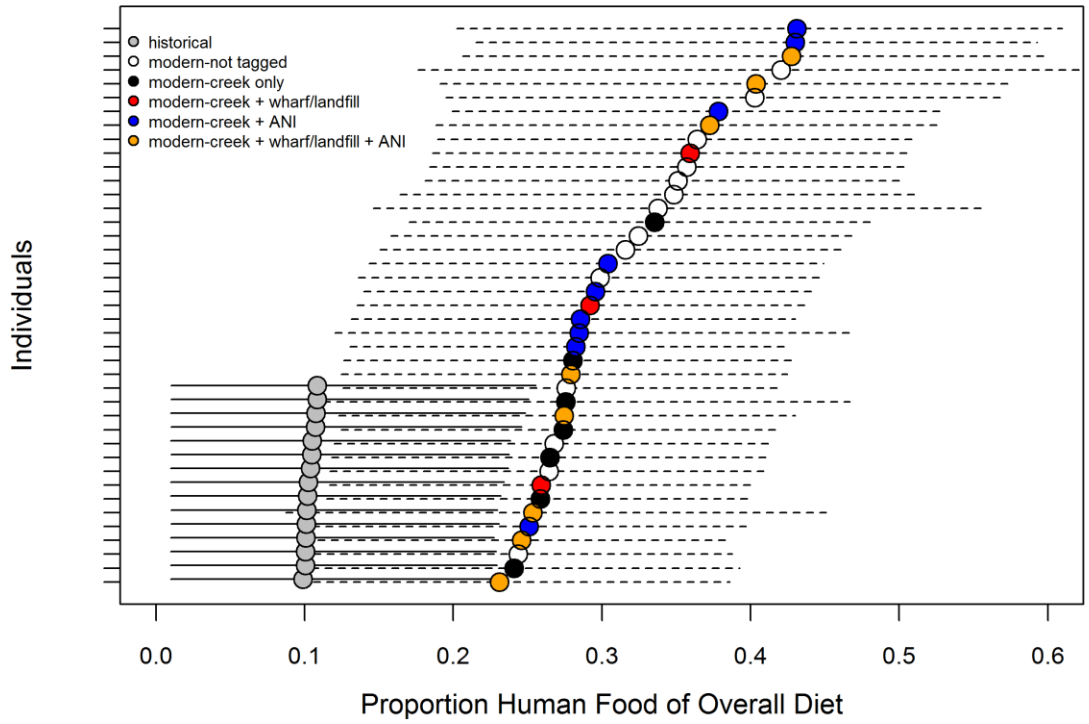


Figure 3-4. The proportion of human food that contributes to individual gull diet for historical and modern Western Gulls. Data are represented as mean posteriors (points) and 90% credible intervals (lines) for prey source of human food from the mixing model output from MixSIAR. Of the 41 modern gulls with isotopic data, 27 of them were radio-tracked and their presence in different foraging locations are indicated in the legend. $\delta^{13}C$ isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007).

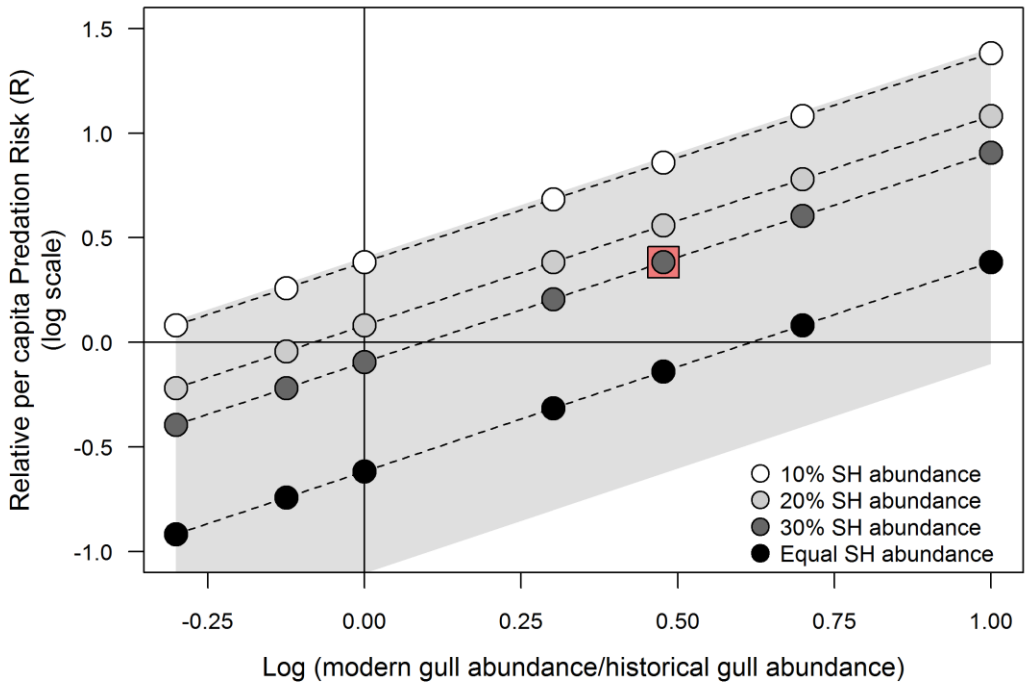


Figure 3-5. The relative per capita predation risk (R) of modern verses historical juvenile steelhead (SH) based on the ratio of modern to historical proportion of steelhead to gull diet across a suite of relative increases in gull population size. Relative predation risk was also evaluated across a suite of proportional population decline in steelhead, where different lines denote where modern steelhead abundance is equal (black circle), 30% (dark grey circle), 20% (light grey circle), or 10% (white circle) of historical abundance. The grey shaded region represents the 90% confidence intervals of the proportion of steelhead to gull diet assuming modern steelhead abundance is 30% of the historical abundance. The red square denotes our hypotheses of relative gull and salmonid abundance. Note data are presented on a log scale, such that where x=0 denotes zero change in gull population size, and where y=0 denotes zero change in relative per capita predation risk of salmonids.

4. Appendix A – Assumptions of the Model (Chapter 1)

This study likely provides the most robust accounting to date of potential sources of uncertainty to estimate avian predation rates on salmon. Through propagating uncertainty of the various processes, we generated realistic posterior probability estimates of predation. Below we present and discuss assumptions.

4.1. Detection Probability

We held the probability of detection constant across all years for the consumption model even though detection probability was somewhat variable among years. We investigated the sensitivity of model results to changes in the tag detection rate and found predation rates varied minimally (<0.002 change in median probability of predation) with fairly substantial changes (±0.23) to the published estimates for detection probability (0.644 ± 0.083 SE, reported by Frechette et al (2012)). The marginal effect of detection probabilities on estimated predation rates is primarily driven by low transportation rates, such that increases in detection rate have little impact on transportation rates, and subsequently have minimal effects on estimates of predation. In the following two paragraphs, we discuss how detection rates varied depending on the year, however given the results of the model sensitivity analysis such slight differences in detection probabilities among years likely have little to no effect on our estimated predation rates.

The model assumed scanning effort on Año Nuevo Island (ANI) was constant among years. Although standardized scanning effort resulted in constant detection probabilities for most years (i.e., 2006 through spring 2009; Frechette et al. 2012),

deviations from typical scanning effort in 2005, 2010, and 2011 likely affected the true detection probabilities during those years. Detection probability was likely lower for PIT tags deposited in 2005 because tags may have been washed away or buried before the first full scan of ANI in November 2006. In contrast, detection probability was higher in 2010 and 2011 when scanning effort increased to ensure tag detections from the transportation experiment. As a result, these variations in detection effort may result in slightly under-estimated predation rates in 2005 (due to reduced scanning effort) and over-estimated predation rates for 2010 and 2011 (due to increased scanning effort).

Because the transportation experiment was conducted during a year with increased detection probability (i.e., 2010), our transportation estimates are inflated for years with less scanning effort (2006 through spring 2009) which would therefore under-estimate predation rates for those years. As a result, the accurate median predation rate may be higher than the estimated predation rates for watersheds with recapture data only prior to 2009 (Gazos Creek, Aptos Creek, and the San Lorenzo River), and may be less variable than the estimated predation rates for watersheds that spanned all years of scanning effort (Waddell Creek, Scott Creek, and Soquel Creek).

4.2. Transportation Probability

We assumed transportation probabilities were the same across years even though it is possible that annual differences in foraging patterns may differ among years, thereby influencing estimates of predation. Since it is impossible to retrospectively quantify transportation rates, we are constrained by the reality of the system and applied 2010 transportation rates to all years of the study. This unaccounted for variation in

transportation probabilities among years may also be reflected in the coherent annual variation in predation rates between Scott and Waddell Creeks. For example, if transportation rates varied systematically across years, the assumption would generate greater variation in the estimated annual predation rates between both creeks.

Transportation estimates also assume PIT tagged hotdogs or Icelandic capelin are consumed, processed, and transported to ANI in a way that represents eating a PIT tagged steelhead. Results from the transportation experiment demonstrate that capelin were consistently transported to ANI at a higher rate than hotdogs. Although no paired experiment was possible to compare capelin and steelhead transportation rates due to the threatened status of steelhead, we assume the difference in transportation rates between capelin and steelhead is minimal. This is supported by a study of Herring Gulls that reported minimal differences in mean gut retention time (<7% difference) when fed three different species of fish prey (Hilton et al. 1998). Therefore, it is likely that fish species such as capelin and steelhead are processed similarly by gulls in our system, and we therefore assume capelin transportation rates are representative of steelhead transportation rates. Because we did not feed capelin at all six study watersheds, we were constrained in using hotdog data only to compare transportation rates among sites. We then multiplied the hotdog transportation rates by a capelin correction factor of 2.3 to result in transportation rate estimates more comparable of consumed steelhead. This multiplier increased the transportation rates, and therefore resulted in lower, and hence more conservative, estimated probabilities of predation at all study watersheds.

In our model, we assume the majority of steelhead PIT tags deposited on ANI were transported by adult Western Gulls, which was supported by the results of the

transportation experiment. Of the 3,141 PIT tagged hotdogs and Icelandic capelin fed to birds present at creek mouths, an overwhelming majority of these were consumed by Western Gulls, where 51.4%, 23.4%, and 17.1% were consumed by adult, subadult, and juvenile Western Gulls, respectively, and the remaining 8.2% were consumed by California Gulls and other gull species. Of these consumed tags, 59 tags were subsequently detected on ANI, mostly from adult Western Gulls (N=56) and a small number from subadult Western Gulls (N=3). However, two of the three tags eaten by subadults were likely eaten by the same individual because both tags were fed at the same location and day and were detected next to each other on ANI. These results suggest PIT tag transportation by other age classes of Western Gulls or other avian species is rare, therefore supporting our assumption that the majority of deposited PIT tags are from adult Western Gulls.

4.3. Recapture Probability: Steelhead Tagging

Our model assumptions include PIT tagged steelhead are representative of all out-migrating steelhead within each watershed. Although lethal and non-lethal effects of PIT tagging are of concern when applying results to a greater non-tagged population, mortality of juvenile salmonids from PIT tagging is considered to be low (less than 2%) and retention of PIT tags is considered to be high (95%; Sogard et al. 2009). Additionally, over 27% of all PIT tagged steelhead in Scott Creek steelhead were handled multiple times in the creek between the initial PIT tag event and their subsequent recapture on ANI, suggesting tagging was not the source of mortality for these

individuals. Therefore, it seems unlikely that tagging biases our estimates of predation rates.

The model estimates predation rates on the tagged population of steelhead, and it is important to note that the characteristics of the tagged population vary by watershed. Specifically, tagging location and time may have an effect on survival before individuals are exposed to gull predation, and therefore predation rates represent different subsets of the wild juvenile steelhead population depending on when and where fish were tagged for a given watershed. For example, individuals tagged in the lagoon are predominately age 0+ and age 1+ steelhead, whereas individuals tagged in the creek mainstem and upper watershed include the entire range of age classes, some of which may never attempt to out-migrate (Hayes et al. 2008). As a result, a smaller proportion of juveniles PIT tagged in the upper watershed may out-migrate to the ocean where they are ultimately exposed to gull predation. Therefore, predation rates may be diluted at watersheds where some juveniles were PIT tagged in the upper watershed (e.g. Waddell, Scott, and Soquel Creeks) when compared to watersheds where juveniles were tagged exclusively in lagoon habitat (Gazos Creek, San Lorenzo river, and Aptos Creek). Although survival of juvenile steelhead is typically higher in the upper watershed when compared to the lagoon environment (Satterthwaite et al. 2012), most out-migrating individuals eventually use the lagoon habitat to rear before entering the ocean (Hayes et al. 2011) and possibly experience greater cumulative mortality. These potential biases are difficult to correct for individual cases. Regardless, these biases result in conservative estimates of predation of out-migrating steelhead at some sites and likely do not affect

the overall magnitude nor the negative relationship between consumption rates and distance from ANI.

5. Appendix B – Evaluating the sensitivity of MixSIAR to input parameters (Chapter 3)

Stable isotope mixing models are sensitive to fractionation factors and the stable isotope values of potential prey (Bond and Jones 2009), which necessitates a thorough justification for which parameters are used. Here we examine how MixSIAR mixing model results are affected by altering two parameters of the mixing model: discrimination factors and prey isotope signatures. Our results suggest that although the different parameters used to populate the model yield different results, the overall trend remains qualitatively similar. Thus, the results of the model we present in the main manuscript are maintained across a suite of fractionation factors and adjustments to the stable isotope signature used to represent prey, such as marine fishes.

5.1. Fractionation Factors

Selecting appropriate fractionation factors is critical to the interpretation of stable isotope mixing models (Caut et al. 2009), however here we demonstrate qualitatively similar MixSIAR results despite using three different published literature values for diet-tissue fractionation (Figure 5-1). First, we re-introduce the mixing model results from Figure 3-2 (Figure 5-1A and Figure 5-1B), which used the fractionation factors summarized in Table 3-1 and was based on the diet-feather fractionation factor of 11 seabird studies (Becker et al. 2007) which we applied to both Western Gull and Brandt's cormorant feathers. We also incorporated fractionation factors between human diet and human fingernails to (Schoeller et al. 1986, O'Connell et al. 2001) to determine

the stable isotope signature of human food. This model is moderate in complexity, as it incorporates different fractionation factors between diet and humans verses birds, however uses an average diet-feather fractionation for both Western Gulls and Brandt's Cormorants.

Second, we re-ran MixSIAR using a slightly more complicated combination of fractionation factors, yet the model yielded very similar results (Figure 5-1C and Figure 5-1D), suggesting our results from this study are robust to a suite of possible fractionation factors. For this alternative model, we used the same fractionation factors between human diet and human fingernails as in the previous model (Schoeller et al. 1986, O'Connell et al. 2001), however we replaced the diet-feather fractionation factor with species-specific fractionation factors for Western Gulls and Brandt's Cormorants. A mean diet-feather fractionation factors for gulls (1.5 ± 1.1 $\delta^{13}C$, 4.2 ± 1.1 $\delta^{15}N$) was applied to a previous study that used stable isotope mixing models to determine the diet for Glaucous Gulls (*Larus hyperboreus*; Weiser and Powell 2011), and was calculated as the average fractionation factor between captive feeding studies of Ring-billed gulls (Hobson and Clark 1992) and Great Skua (Bearhop et al. 2002). For this more complicated model, we applied the fractionation factor calculated in Weiser and Powell (2011), before correcting for growing chicks, to Western Gulls in this study. For Brandt's Cormorants, we used the mean diet-feather fractionation estimated during a captive breeding study of *Great Cormorant* (*Phalacrocorax carbo*; Bearhop et al. 1999).

Lastly, we re-ran MixSIAR a third time using a general fractionation factor of 1.0 ± 0.5 $\Delta^{13}C_{food\text{-}consumer}$ and 3.0 ± 0.5 $\Delta^{15}N_{food\text{-}consumer}$ for all prey tissue to consumers (Figure 5-1E, Figure 5-1F). Generalized fractionation factors of ~ +1.0 $\delta^{13}C$ and +3.0 δ

^{15}N are commonly used in studies that lack species-specific fractionation factors (Kelly 2000, Nardoto et al. 2006, Newsome et al. 2010), and have also been used for the fractionation factor from diet-feather of Yellow-legged gulls (Pedro et al. 2013). The results of this simplified model with generalized fractionation factors (Figure 5-1E, Figure 5-1F) differ substantially from the moderate (Figure 5-1A and Figure 5-1B) and complex (Figure 5-1C and Figure 5-1D) models. When using different consumers as integrated signatures of their diet, care should be taken to use fractionation factors that reflect differences in taxon and tissue specific fractionation factors.

By comparing the mixing model results of these three models, we conclude the results of the first and second mixing models were indistinguishable from each other despite differences in fractionation factors, and thus we believe our model is not particularly sensitive to the fractionation factors used for this study. The third model, which used the same fractionation factor for all consumers was substantially different than the previous two models. Using generalized fractionation factors may be appropriate for studies where stable isotope values from all potential prey are estimated directly from prey tissue. However, when a variety of different consumers are fractionated out to represent prey of a different consumer, this will likely yield incorrect results.

We chose to apply the average seabird diet-consumer fractionation value for both Western Gulls and Brandt's Cormorants for this study (Figure 3-2, Figure 5-1A, Figure 5-1B), instead of specific fractionation factors developed for closely related species (Figure 5-1C, Figure 5-1D). Even closely related species can have large differences in fractionation factors, as is demonstrated with a 2 per mil difference in the

fractionation factors Ring-billed gulls (Hobson and Clark 1992) and Great Skua (Bearhop et al. 2002). Therefore, we assumed an average seabird fractionation factor would result in less biased results than those estimated for different species in different systems. Regardless, the average (Figure 5-1A, Figure 5-1B) and species-specific (Figure 5-1C, Figure 5-1D) mixing model results are indistinguishable from one-another such that either approach yields similar results.

5.2. Addressing shifts in prey isotope signatures in the marine environment

Here we examine the assumption that prey isotope values remained consistent over the last 100 years. This was a necessary assumption because we lack prey samples from the early 1900's in our study system. However, we documented a shift in the stable isotope signature for seabird prey in the marine environment through stable isotope analysis of Brandt's Cormorants over time. Here, we re-ran the mixing model for historical Western Gull diet but substituted the stable isotope signature for modern Brandt's Cormorant feathers (to represent marine prey) with the historical stable isotope signature for Brandt's Cormorant diet. We found no distinguishable difference between the Western Gull diet composition using modern Brandt's Cormorant diet (Figure 5-2A) to the model that used historical Brandt's cormorant diet (Figure 5-2B). Thus, we determined shifts in prey isotopes over time likely do not significantly influence the results of the mixing model in this study.

5.3. Figures

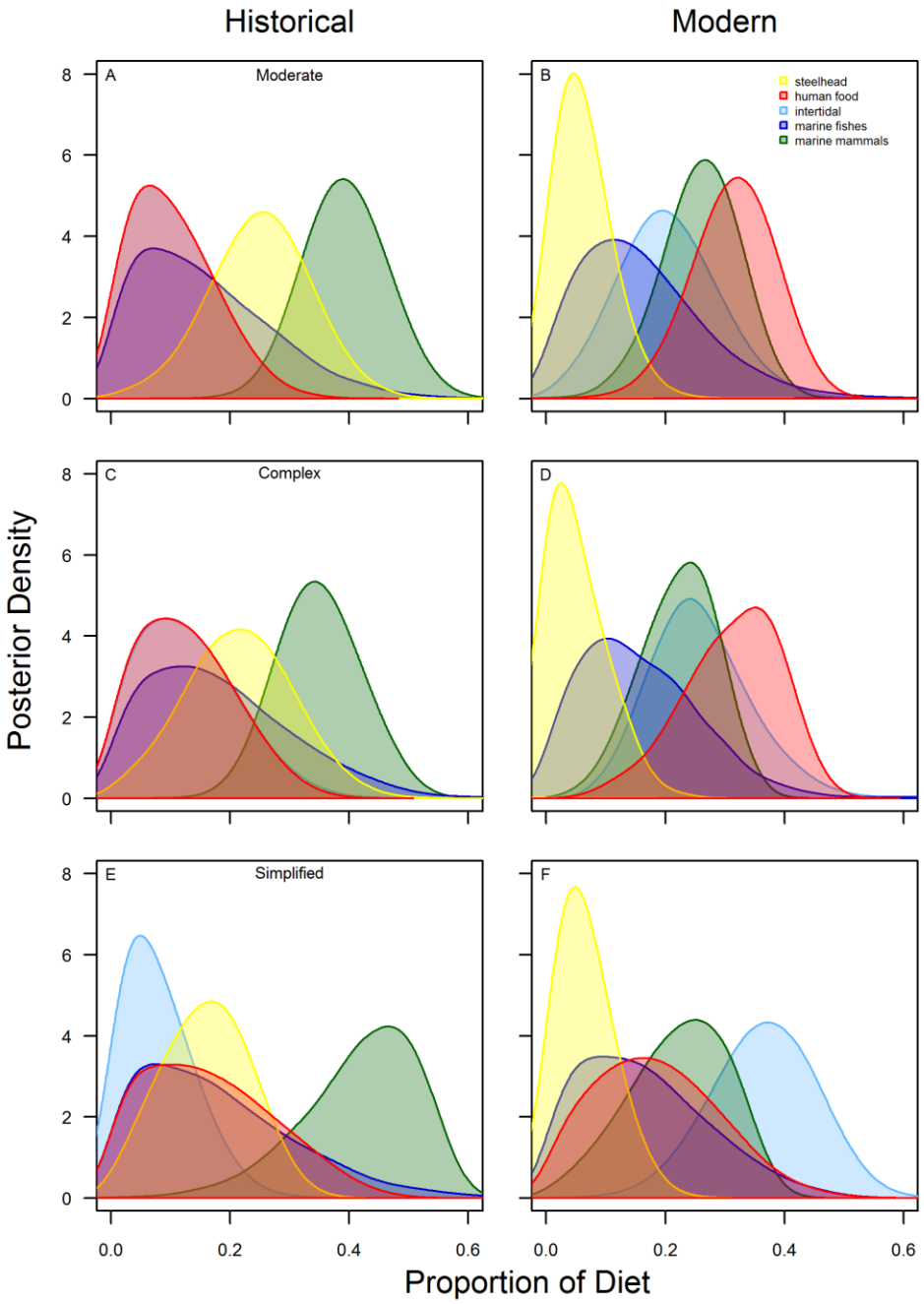


Figure 5-1. Comparing the proportion of diet sources that contribute to historical and modern Western Gull diet given three different fractionation scenarios: moderate (panels A,B), complex (panels C,D), and simplified (panels E,F). Data are represented as posterior densities from the mixing model output from MixSIAR and δ13C isotope

values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). Note that posterior densities less than 0.0 result from a smoother function to create this graphic and that panels A and B are identical to Figure 3-2 in the main manuscript and are re-introduced here for comparison. See text for details of the three different fractionation scenarios.

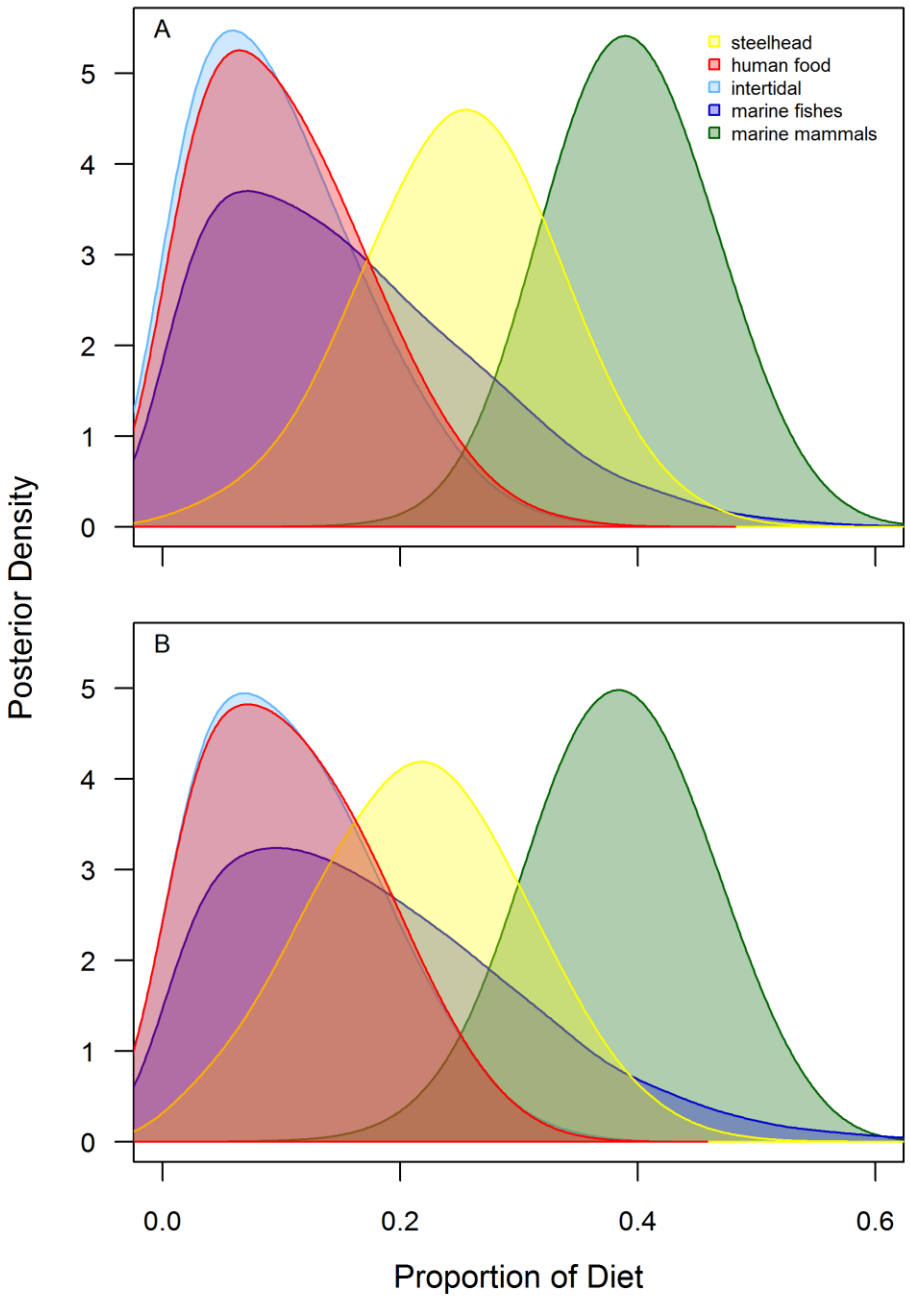


Figure 5-2. Comparing the proportion of diet sources that contribute to historical Western Gull diet given two different scenarios. Panel A uses the stable isotope signature for current Brandt's Cormorants to represent the stable isotope signature of historical marine fishes and therefore assumes the historical isotope signature of marine fishes is the same across time. Panel A is identical to Figure 3-2A in the main manuscript. Panel B uses the stable isotope signature for historical Brandt's Cormorants to represent marine diet in the early 1900's, whereas all other prey data are identical to Panel A and Table 3-1

in the main manuscript. Data are represented as posterior densities from the mixing model output from MixSIAR. δ13C isotope values from historical feathers were Suess-corrected to the reference year 2000 using equation 4 in Verburg (2007). Note that posterior densities less than 0.0 result from a smoother function to create this graphic.

Discussion

Humans have altered the coastal landscape in ways that can promote opportunistic generalist species and result in decline in native prey. My research has shown these patterns hold true along the central California coast where subsidized gull predators are contributing to predation risk of imperiled prey. Specifically, I demonstrated that Western Gulls consume approximately 30% of juvenile steelhead per year in some watersheds, thus contributing a significant source of mortality for salmonids along the central California coast (Chapter 1). Interestingly, even though gulls are not selecting juvenile steelhead based on body size, they are removing primarily wild steelhead, including large individuals that are important for population recovery. Thus, gulls are likely providing an additive source of predation for juvenile salmonids (Chapter 2). The impact of predation is likely exacerbated by humans as anthropogenic sources support increasing gull populations and thus indirectly contribute to predation risk of native steelhead. Even if gulls consume less steelhead per individual, predation risk of juvenile steelhead will likely increase if gull populations continue to rise and salmonid populations experience further decline (Chapter 3). Together, these chapters demonstrate that human activity can indirectly affect predator-prey dynamics and contribute to extinction risk of native prey.

This dissertation quantifies the increased predation risk steelhead experience as an indirect result of human activities and prompts the need to identify effective conservation actions to prevent extinction of steelhead populations along the central California coast. The predation risk model in Chapter 3 sets the stage for discussion of recovery action and predicts a reduction in predation risk if steelhead were to contribute

less to gull diet, if gull population size decreases, or if steelhead population sizes increases. Excluding gulls from steelhead-bearing creeks during juvenile steelhead outmigration may significantly reduce the contribution of steelhead to gull diet and alleviate predation risk. While deterring gulls may be successful at a watershed scale, this action may only concentrate predation risk in nearby watersheds, thereby affecting regional salmonid abundance. There is increasing emphasis in salmonid management to manage multiple salmon populations as a stock complex, which contributes to population resilience and persistence (Hilborn et al. 2003). Thus, gull deterrence measures should be considered at a regional scale. Reducing salmonid predation risk can also be achieved by decreasing gull population size. Managers have attempted to reduce the impacts of avian predators on native prey directly through selective culling (Sanz-Aguilar et al. 2009, Thiériot et al. 2012) or indirectly by banning fisheries discards to prohibit gulls access to reliable food sources (Bicknell et al. 2013). While some of these actions have been successful in recovering native prey, overall success remains unknown. Efforts that increase steelhead population numbers, especially the wild and large individuals important for population recovery (Chapter 2), will likely contribute to reduced predation risk by gulls. This may include restoring coastal lagoons to their original larger size to provide critical nursery habitat for these individuals (Bond et al. 2008). After considering all these options, it becomes clear that not just one action in isolation will reduce salmonid predation risk by gulls. Instead, all these actions should be pursued to maximize potential success for population recovery.

Predator-prey dynamics are ubiquitous in nature and define the structure of communities throughout the world. As human populations increase, the structure of

these natural communities is altered, often in ways that go undetected. While there has been growing appreciation of how human activities can directly alter communities and ecosystems (such as via harvest), there is arguably less appreciation of how anthropogenic subsidies can propagate through a food web, ultimately impacting imperiled species. Through understanding these pathways, we may gain insight into restoration or management activities for imperiled species. For example, instead of single predator management, can subsidies be managed? This research provides an example of how humans are agents of global change in biological communities, and how these impacts may be mitigated to protect imperiled species and foster healthy ecosystems.

Bibliography

Ackerman, J. T. 2002. Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. Oikos 99:469–480.

Adrean, L. J., D. D. Roby, D. E. Lyons, K. Collis, and A. F. Evans. 2012. Potential effects of management on Caspian Tern *Hydroprogne caspia* predation on juvenile salmonids at a colony in San Francisco Bay, California. Transactions of the American Fisheries Society 141:1682–1696.

Ainley, D., D. Anderson, and P. Kelly. 1981. Feeding ecology of marine cormorants in southwestern North America. The Condor 83:120–131.

Ainley, D., and T. Lewis. 1974. The history of Farallon Island marine bird populations, 1854-1972. The Condor 76:432–446.

Annett, C. A., and R. Pierotti. 1989. Chick hatching as a trigger for dietary switching in the Western Gull. Colonial Waterbirds 12:4–11.

Annett, C. A., and R. Pierotti. 1999. Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. Ecology 80:288–297.

Antolos, M., D. D. Roby, D. E. Lyons, K. Collis, A. F. Evans, M. Hawbecker, and B. A. Ryan. 2005. Caspian Tern predation on juvenile salmonids in the mid-Columbia River. Transactions of the American Fisheries Society 134:466–480.

Antonelis, G., and C. Fiscus. 1980. The pinnipeds of the California Current. California Cooperative Oceanic Fisheries Report 21:68–78.

Araki, H., B. A. Berejikian, M. J. Ford, and M. S. Blouin. 2008. Fitness of hatchery-reared salmonids in the wild. Evolutionary Applications 1:342–355.

Baltz, D., and G. Morejohn. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. The Auk 94:526–543.

Beakes, M. P., W. H. Satterthwaite, E. M. Collins, D. R. Swank, J. E. Merz, R. G. Titus, S. M. Sogard, and M. Mangel. 2010. Smolt transformation in two California steelhead populations: effects of temporal variability in growth. Transactions of the American Fisheries Society 139:1263–1275.

Beamish, R. J., R. M. Sweeting, C. M. Neville, K. L. Lange, T. D. Beacham, and D. Preikshot. 2012. Wild chinook salmon survive better than hatchery salmon in a period of poor production. Environmental Biology of Fishes 94:135–148.

Bearhop, S., D. Thompson, S. Waldron, I. C. Russell, G. Alexander, and R. W. Furness. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. Journal of Applied Ecology 36:75–84.

Bearhop, S., S. Waldron, S. C. Votier, and R. W. Furness. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiological and Biochemical Zoology 75:451–458.

Beck, N., E. Freund, and M. Mathias. 2006. Comparative lagoon ecological assessment project (CLEAP), Santa Cruz County, California. 2NDNATURE Ecosystem Science and Design, Santa Cruz, California.

Becker, B. H., and S. R. Beissinger. 2006. Centennial decline in the trophic level of an endangered seabird after fisheries decline. Conservation Biology 20:470–479.

Becker, B., S. Newman, S. Inglis, and S. Beissinger. 2007. Diet-feather stable isotope (δ15N and δ13C) fractionation in Common murres and other seabirds. The Condor 109:451–456.

Berejikian, B. A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. Canadian Journal of Fisheries and Aquatic Sciences 52:2476–2482.

Bicknell, A. W. J., D. Oro, K. C. J. Camphuysen, and S. C. Votier. 2013. Potential consequences of discard reform for seabird communities. Journal of Applied Ecology 50:649–658.

Blokpoel, H., and A. L. Spaans. 1991. Introductory remarks: superabundance in gulls: causes, problems and solutions. Pages 2361–2364 Acta Congressus Internationalis Ornithologici, Christchurch, New-Zealand.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in ecology & evolution 26:183–192.

Bolnick, D. I., R. Svanbäck, M. S. Araújo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proceedings of the National Academy of Sciences of the United States of America 104:10075–10079.

Bond, A., and I. Jones. 2009. A practical introduction to stable-isotope analysis for seabird biologists: approaches, cautions and caveats. Marine Ornithology 37:183–188.

Bond, A. L., and J. L. Lavers. 2014. Climate change alters the trophic niche of a declining apex marine predator. Global change biology. In Press.

Bond, M. H., C. V. Hanson, R. Baertsch, S. A. Hayes, and R. B. MacFarlane. 2007. A new low-cost instream antenna system for tracking passive integrated transponder (PIT)-tagged fish in small streams. Transactions of the American Fisheries Society 136:562–566.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2242–2252.

Bridge, E. 2006. Influences of morphology and behavior on wing-molt strategies in seabirds. Marine Ornithology 34:7–19.

Brodie, E. D., B. J. Ridenhour, and E. D. Brodie. 2002. The evolutionary response of predators to dangerous prey: hotspots and coldspots in the geographic mosaic of coevolution between garter snakes and newts. Evolution 56:2067–2082.

Brook, B. W., N. S. Sodhi, and C. J. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology and Evolution 23:453–460.

Burnham, K., and D. Anderson. 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. Ecology 65:105–112.

Burnham, K., and D. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second Edi. Springer-Verlag New York, Inc., New York, NY.

Capitolo, P. J., G. J. McChesney, H. R. Carter, and S. J. Rhoades. 2009. Breeding population estimates for sample colonies of Western Gulls, California Gulls, and Caspian Terns in northern and central California, 2006-2008. Unpublished report, Humboldt State University, Department of Wildlife, Arcata, California and U.S. Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex, Newark, California. 22 p.

Carter, H. R., G. J. McChesney, D. L. Jaques, C. S. Strong, M. W. Parker, J. E. Takekawa, D. L. Jory, and D. L. Whitworth. 1992. Breeding populations of seabirds in California, 1989-1991. Vols. 1 and 2. Unpublished report, U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Dixon, California and U.S. Fish

and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex, Newark, California.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors (Δ 15N and Δ 13C): the effect of diet isotopic values and applications for diet reconstruction. Journal of Applied Ecology 46:443–453.

Charrier, G., S. A. Hayes, J. C. Garza, and D. E. Pearse. (In Preparation). Patterns of reproductive success in wild steelhead (*Oncorhynchus mykiss*) in a small coastal stream.

Collins, A. L. 2008. Tracking the source of beneficial steelhead growth in coastal lagoons. Undergraduate Thesis, University of California Santa Cruz, USA.

Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, and R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River Estuary: vulnerability of different salmonid species, stocks, and rearing types. Transactions of the American Fisheries Society 130:385–396.

Connor, W. P., and K. F. Tiffan. 2012. Evidence for parr growth as a factor affecting parr-to-smolt survival. Transactions of the American Fisheries Society 141:1207–1218.

Conover, M. 1983. Recent changes in Ring-billed and California gull populations in the western United States. The Wilson Bulletin 95:362–383.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353–362.

Deevey, E. S. J. 1947. Life tables for natural populations of animals. The Quarterly Review of Biology 22:283–314.

Duhem, C., P. Roche, E. Vidal, and T. Tatoni. 2008. Effects of anthropogenic food resources on Yellow-legged Gull colony size on Mediterranean islands. Population Ecology 50:91–100.

Dulvy, N. K., Y. Sadovy, and J. D. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries 4:25–64.

Elton, C., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. The Journal of Animal Ecology 11:215–244.

Esque, T. C., K. E. Nussear, K. K. Drake, A. D. Walde, K. H. Berry, R. C. Averill-Murray, A. P. Woodman, W. I. Boarman, P. A. Medica, J. Mack, and J. S. Heaton. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endangered Species Research 12:167–177.

Essington, T. E., A. H. Beaudreau, and J. Wiedenmann. 2006. Fishing through marine food webs. Proceedings of the National Academy of Sciences of the United States of America 103:3171–3175.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476.

Evans, A. F., N. J. Hostetter, D. D. Roby, K. Collis, D. E. Lyons, B. P. Sandford, R. D. Ledgerwood, and S. Sebring. 2012. Systemwide evaluation of avian predation on juvenile salmonids from the Columbia River based on recoveries of passive integrated transponder tags. Transactions of the American Fisheries Society 141:975–989.

Evans, A. F., D. D. Roby, K. Collis, B. M. Cramer, J. A. Sheggeby, L. J. Adrean, D. S. Battaglia, and D. E. Lyons. 2011. Recovery of coded wire tags at a Caspian Tern colony in San Francisco Bay: a technique to evaluate impacts of avian predation on juvenile salmonids. North American Journal of Fisheries Management 31:79–87.

Farmer, R. G., and M. L. Leonard. 2011. Long-term feeding ecology of Great Black-backed Gulls (*Larus marinus*) in the northwest Atlantic: 110 years of feather isotope data. Canadian Journal of Zoology 89:123–133.

Federal Register. 2005. Endangered and threatened species: final listing determinations for 16 ESUs of west coast salmon, and final 4(d) protective regulations for threatened salmonid ESUs. Pages 37160–37204 Federal Register, Washington, D.C.

Federal Register. 2006. Endangered and Threatened Species : Final Listing Determinations for 10 Distinct Population Segments of West Coast. Federal Register, Washington, D.C.:833–862.

Fernández-Olalla, M., A. Martínez-Abraín, J. Canut, D. García-Ferré, I. Afonso, and L. M. González. 2012. Assessing different management scenarios to reverse the declining trend of a relict capercaillie population: a modelling approach within an adaptive management framework. Biological Conservation 148:79–87.

Festa-Bianchet, M., T. Coulson, J.-M. Gaillard, J. T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. Proceedings of the Royal Society B: Biological Sciences 273:1537–1543.

Fraser, D. 2013. The emerging synthesis of evolution with ecology in fisheries science. Canadian Journal of Fisheries and Aquatic Sciences 70:1417–1428.

Frechette, D. 2010. Impacts of avian predation on juvenile salmonids in central California watersheds. Master's thesis. San Jose State University, San Jose, California.

Frechette, D., A. L. Collins, J. T. Harvey, S. A. Hayes, D. D. Huff, A. W. Jones, N. A. Retford, A. E. Langford, J. W. Moore, A.-M. K. Osterback, William H. Satterthwaite, and S. A. Shaffer. 2013. A bioenergetics approach to assessing potential impacts of avian predation on juvenile steelhead during freshwater rearing. North American Journal of Fisheries Management 33:1024–1038.

Frechette, D. M., A.-M. K. Osterback, S. A. Hayes, J. W. Moore, S. A. Shaffer, M. Pavelka, C. Winchell, and J. T. Harvey. (In Review). Assessing the relationship between gulls and salmon in central California using radio telemetry. North American Journal of Fisheries Management.

Frechette, D., A.-M. K. Osterback, S. A. Hayes, M. H. Bond, J. W. Moore, S. A. Shaffer, and J. T. Harvey. 2012. Assessing avian predation on juvenile salmonids using passive integrated transponder tag recoveries and mark–recapture methods. North American Journal of Fisheries Management 32:1237–1250.

Fry, B., and E. Sherr. 1984. δ13C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science 27:13–47.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Good, T. P., M. M. Mcclure, B. P. Sandford, K. A. Barnas, D. M. Marsh, B. A. Ryan, and E. Casillas. 2007. Quantifying the effect of Caspian Tern predation on threatened and endangered Pacific salmon in the Columbia River estuary. Endangered Species Research 3:11–21.

Good, T. P., R. S. Waples, and P. Adams. 2005. Updated status of federally listed ESUs of west coast salmon and steelhead. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-66:1–598.

Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Myers, J. D. Raithel, M. Schlegel, B. L. Smith, C. White, and P. J. White.

2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. The Journal of Animal Ecology 80:1246–1257.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of evolutionary biology 24:699–711.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21:1009–1020.

Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. Small-rodent dynamics and predation. Ecology 82:1505–1520.

Harrington, R., N. Owen-Smith, P. C. Viljoen, H. C. Biggs, D. R. Mason, and P. Funston. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. Biological Conservation 90:69–78.

Hayes, S. A., M. H. Bond, C. V. Hanson, E. V. Freund, J. J. Smith, E. C. Anderson, A. J. Ammann, and R. B. MacFarlane. 2008. Steelhead growth in a small central California watershed: upstream and estuarine rearing patterns. Transactions of the American Fisheries Society 137:114–128.

Hayes, S. A., M. H. Bond, C. V. Hanson, A. W. Jones, A. J. Ammann, J. A. Harding, A. L. Collins, J. Perez, and R. B. MacFarlane. 2011. Down, up, down and "smolting" twice? Seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. Canadian Journal of Fisheries and Aquatic Sciences 68:1341–1350.

Hayes, S. A., M. H. Bond, C. V. Hanson, and R. B. MacFarlane. 2004. Interactions between endangered wild and hatchery salmonids: can the pitfalls of artificial propagation be avoided in small coastal streams? Journal of Fish Biology 65:101–121.

Hayes, S. A., M. H. Bond, B. K. Wells, C. V. Hanson, A. W. Jones, and R. B. MacFarlane. 2012. Using archival tags to infer habitat use of central California steelhead and coho salmon. Pages 471–492 *in* J. R. McKenzie, B. Parsons, A. C. Seitz, R. K. Kopf, M. G. Mesa, and Q. Phelps, editors. Proceedings of the 2nd International Symposium on Advances in Fish Tagging and Marking Technology. American Fisheries Society, Symposium 76, Bethesda, Maryland.

Hayes, S. A., A.-M. K. Osterback, E. A. Gilbert-Horvath, N. A. Retford, D. E. Pearse, J. C. Garza, and J. Kiernan. 2013. Monitoring life history traits of ESA-listed salmonids on the central California coast. Final Report submitted to the California

Department of Fish and Wildlife as part of the requirements of FRGP Award #P0930407.

Hedges, R., E. Rush, and W. Aalbersberg. 2009. Correspondence between human diet, body composition and stable isotopic composition of hair and breath in Fijian villagers. Isotopes in Environmental and Health Studies 45:1–17.

Henderson, M., and A. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 48:988–994.

Hester, M., R. Carle, J. Beck, and D. Calleri. 2013. Seabird conservation and habitat restoration: 2009 - 2012. Unpublished report to California Dept. of Parks and Recreation, Año Nuevo State Park.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences of the United States of America 100:6564–6568.

Hilton, G. M., D. C. Houston, and R. W. Furness. 1998. Which components of diet quality affect retention time of digesta in seabirds? Functional Ecology 12:929–939.

Hilton, G. M., D. R. Thompson, P. M. Sagar, R. J. Cuthbert, Y. Cherel, and S. J. Bury. 2006. A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. Global Change Biology 12:611–625.

Hinch, S. G., and P. S. Rand. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. Canadian Journal of Fisheries and Aquatic Sciences 55:1821–1831.

Hobson, K., and R. Clark. 1992. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. The Condor 94:189–197.

Holling, C. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91:293–320.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Hostetter, N. J., A. F. Evans, D. D. Roby, and K. Collis. 2012. Susceptibility of juvenile steelhead to avian predation: the influence of individual fish characteristics and river conditions. Transactions of the American Fisheries Society 141:1586–1599.

Howell, S., and C. Corben. 2000. Molt cycles and sequences in the Western Gull. Western Birds:38–49.

Hughes, T. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551.

Hunt, G. J., and M. Hunt. 1976. Exploitation of fluctuating food resources by Western Gulls. The Auk 93:301–307.

Huxel, G., and K. McCann. 1998. Food web stability: the influence of trophic flows across habitats. The American Naturalist 152:460–469.

Inger, R., and S. Bearhop. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:447–461.

Jackson, C. D., and G. E. Brown. 2011. Differences in antipredator behaviour between wild and hatchery-reared juvenile Atlantic salmon (*Salmo salar*) under seminatural conditions. Canadian Journal of Fisheries and Aquatic Sciences 68:2157–2165.

Jackson, J. 2008. Ecological extinction and evolution in the brave new ocean. Proceedings of the National Academy of Sciences of the United States of America 105:11458–11465.

Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Jonsson, N., B. Jonsson, and L. P. Hansen. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. Journal of Applied Ecology 40:900–911.

Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River Basin. Science 290:977–979.

Keefer, M. L., R. J. Stansell, S. C. Tackley, W. T. Nagy, K. M. Gibbons, C. A. Peery, and C. C. Caudill. 2012. Use of radiotelemetry and direct observations to evaluate sea lion predation on adult Pacific salmonids at Bonneville Dam. Transactions of the American Fisheries Society 141:1236–1251.

Kelly, J. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Canadian Journal of Zoology 78:1–27.

Kristan, W. B. I., and W. I. Boarman. 2007. Effects of anthropogenic developments on common raven nesting biology in the West Mojave Desert. Ecological Applications 17:1703–1713.

Kristan, W. B. I., W. I. Boarman, and J. J. Crayon. 2004. Diet composition of common ravens across the urban-wildland interface of the west Mojave Desert. Wildlife Society Bulletin 32:244–253.

Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. Researches on Population Ecology 40:259–269.

Lavoie, R., J. Rail, and D. Lean. 2012. Diet composition of seabirds from Corossol Island, Canada, using direct dietary and stable isotope analyses. Waterbirds 35:402–419.

Layman, C. A., J. P. Quattrochi, C. M. Peyer, and J. E. Allgeier. 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology Letters 10:937–944.

Levy, D., and T. Northcote. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. Canadian Journal of Fisheries and Aquatic Sciences 39:270–276.

Lindley, S. T., and M. S. Mohr. 2003. Modeling the effect of striped bass (Morone saxatilis) on the population viability of Sacramento River winter-run chinook salmon (Oncorhynchus tshawytscha). Fishery Bulletin 101:321–331.

Lowry, M. S., and O. Maravilla-Chavez. 2005. Recent abundance of California sea lions in western Baja California, Mexico and the United States. Pages 485–497 *in* D. K. Garcelon and C. A. Schwemm, editors. Proceedings of the Sixth California Islands Symposium, Ventura, California, December 1-3, 2003. National Park Service Technical Publication CHIS-05-01, Institute for Wildlife Studies, Arcata, California.

Lynch, M., and M. O'Hely. 2001. Captive breeding and the genetic fitness of natural populations. Conservation Genetics 2:363–378.

Magnusson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific Coast. Estuaries 26:1094–1103.

Mangel, M., and P. S. Levin. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. Philosophical Transactions: Biological Sciences 360:95–105.

Medica, P. A., K. E. Nussear, T. C. Esque, and M. B. Saethre. 2012. Long-term growth of desert tortoises (*Gopherus agassizii*) in a southern Nevada population. Journal of Herpetology 46:213–220.

Miller, G. 2010. In central California, coho salmon are on the brink. Science 327:512–513.

Moore, J. W., S. A. Hayes, W. Duffy, S. Gallagher, C. J. Michel, and D. Wright. 2011. Nutrient fluxes and the recent collapse of coastal California salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 68:1161–1170.

Moore, J. W., and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11:470–480.

Moyle, P. B., J. A. Israel, and S. E. Purdy. 2008. Salmon, steelhead, and trout in California: status of an emblematic fauna. Pages 1–316 Center for Watershed Sciences at University of California Davis. A report commissioned by California Trout, Davis, California.

Mudge, G. 1978. The gull increase, as illustrated by studies in the Bristol Channel. Ibis 120:115–116.

Mudge, G., and P. Ferns. 1982. The feeding ecology of five species of gulls (Aves: Larini) in the inner Bristol Channel. Journal of Zoology, London 197:497–510.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. Proceedings of the National Academy of Sciences 109:21201–21207.

Nardoto, G. B., S. Silva, C. Kendall, J. R. Ehleringer, L. A. Chesson, E. S. B. Ferraz, M. Z. Moreira, J. P. H. B. Ometto, and L. A. Martinelli. 2006. Geographical patterns of human diet derived from stable-isotope analysis of fingernails. American Journal of Physical Anthropology 131:137–146.

National Marine Fisheries Service. 2012. Final recovery plan for central California coast coho salmon Evolutionarily Significant Unit. National Marine Fisheries Service, Southwest Region, Santa Rosa, California.

Nevins, H. M., S. R. Benson, E. M. Phillips, J. DeMarignac, A. P. DeVogelaere, J. A. Ames, and J. T. Harvey. 2011. Coastal Ocean Mammal and Bird Education and Research Surveys (BeachCOMBERS), 1997 – 2007: ten years of monitoring beached marine birds and mammals in the Monterey Bay National Marine

Sanctuary. Marine Sanctuaries Conservation Series ONMS11-02. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD. 63 pp.

Newsome, S. D., M. T. Tinker, D. H. Monson, O. T. Oftedal, K. Ralls, M. M. Staedler, M. L. Fogel, and J. A. Estes. 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90:961–974.

Newsome, S., C. Martínez Del Rio, S. Bearhop, and D. Phillips. 2007. A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429–436.

Newsome, S., K. Ralls, C. Van Horn Job, M. L. Fogel, and B. L. Cypher. 2010. Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*). Journal of Mammalogy 91:1313–1321.

NMFS (National Marine Fisheries Service). 2011. California sea lion (*Zalophus californianus*): U.S. stock assessment.

O'Connell, T. C., R. E. M. Hedges, M. A. Healey, and A. H. R. W. Simpson. 2001. Isotopic comparison of hair, nail and bone: modern analyses. Journal of Archaeological Science 28:1247–1255.

Ohman, M. D., G. H. Rau, and P. M. Hull. 2012. Multi-decadal variations in stable N isotopes of California Current zooplankton. Deep Sea Research Part I 60:46–55.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514.

Osterback, A.-M. K., D. M. Frechette, S. A. Hayes, M. H. Bond, S. A. Shaffer, and J. W. Moore. (In Review.). Linking individual size and rearing history to survival and predation risk of threatened steelhead (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences.

Osterback, A.-M. K., D. M. Frechette, A. O. Shelton, S. A. Hayes, M. H. Bond, S. A. Shaffer, and J. W. Moore. 2013. High predation on small populations: avian predation on imperiled salmonids. Ecosphere 4(9):1–21.

Paine, R. 1966. Food web complexity and species diversity. The American Naturalist 100:65–75.

Palkovacs, E. P., and A. P. Hendry. 2010. Eco-evolutionary dynamics: intertwining ecological and evolutionary processes in contemporary time. F1000 biology reports 2:1–5.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology & Evolution 10:430.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. J. Torres. 1998. Fishing down marine food webs. Science 279:860–863.

Pedro, P. I., J. A. Ramos, V. C. Neves, and V. H. Paiva. 2013. Past and present trophic position and decadal changes in diet of Yellow-legged Gull in the Azores Archipelago, NE Atlantic. European Journal of Wildlife Research 59:833–845.

Peterson, B., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

Pettorelli, N., T. Coulson, S. M. Durant, and J.-M. Gaillard. 2011. Predation, individual variability and vertebrate population dynamics. Oecologia 167:305–314.

Phillis, C. C., J. W. Moore, M. Buoro, S. A. Hayes, J. C. Garza, and D. E. Pearse. 2014. Shifting thresholds: rapid evolution of migratory histories in steelhead/rainbow trout, *Oncorhynchus mykiss*. PeerJ PrePrints 2:e361v1.

Pierotti, R. 1981. Male and female parental roles in the Western Gull under different environmental conditions. The Auk 98:532–549.

Pierotti, R., and C. A. Annett. 1990. Diet and reproductive output in seabirds. BioScience 40:568–574.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rau, G. H., M. D. Ohman, and A. Pierrot-Bults. 2003. Linking nitrogen dynamics to climate variability off central California: a 51 year record based on 15N/14N in CalCOFI zooplankton. Deep Sea Research Part II 50:2431–2447.

Rayner, M. J., M. E. Hauber, T. E. Steeves, H. A. Lawrence, D. R. Thompson, P. M. Sagar, S. J. Bury, T. J. Landers, R. A. Phillips, L. Ranjard, and S. A. Shaffer. 2011. Contemporary and historical separation of transequatorial migration between genetically distinct seabird populations. Nature Communications 2:1–7.

Roby, D. D., D. E. Lyons, D. P. Craig, K. Collis, and G. H. Visser. 2003. Quantifying the effect of predators on endangered species using a bioenergetics approach:

Caspian Terns and juvenile salmonids in the Columbia River Estuary. Canadian Journal of Zoology 81:250–265.

Rogers, T. L., and J. K. Elliott. 2013. Differences in relative abundance and size structure of the sea stars Pisaster ochraceus and Evasterias troschelii among habitat types in Puget Sound, Washington, USA. Marine Biology 160:853–865.

Roni, P., and T. Quinn. 1995. Geographic variation in size and age of North American chinook salmon. North American Journal of Fisheries Management 15:325–345.

Ruckelshaus, M. H., P. S. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33:665–706.

Ryan, B., S. Smith, J. M. Butzerin, and J. W. Ferguson. 2003. Relative vulnerability to avian predation of juvenile salmonids tagged with passive integrated transponders in the Columbia River Estuary, 1998–2000. Transactions of the American Fisheries Society 132:275–288.

Sanz-Aguilar, A., A. Martínez-Abraín, G. Tavecchia, E. Mínguez, and D. Oro. 2009. Evidence-based culling of a facultative predator: Efficacy and efficiency components. Biological Conservation 142:424–431.

Satterthwaite, W. H., S. A. Hayes, J. E. Merz, S. M. Sogard, D. M. Frechette, and M. Mangel. 2012. State-dependent migration timing and use of multiple habitat types in anadromous salmonids. Transactions of the American Fisheries Society 141:781–794.

Scheuerell, M., and J. Williams. 2005. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*). Fisheries Oceanography:448–457.

Schmidt, S. N., M. J. Vander Zanden, and J. F. Kitchell. 2009. Long-term food web change in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 66:2118–2129.

Schoeller, D., M. Minagawa, R. Slater, and I. R. Kaplan. 1986. Stable isotopes of carbon, nitrogen and hydrogen in the contemporary North American human food web. Ecology of Food and Nutrition 18:159–170.

Schreiber, R. 1970. Breeding biology of Western Gulls (Larus occidentalis) on San Nicolas Island, California, 1968. The Condor 72:133–140.

SCPL (Santa Cruz Public Library). 2000. Population Statistics for Santa Cruz County and Cities, 1850-2000. Accessible online at: http://www.santacruzpl.org/history/articles/426/#no5.

Selbie, D. T., B. A. Lewis, J. P. Smol, and B. P. Finney. 2007. Long-term population dynamics of the endangered Snake River sockeye salmon: Evidence of past influences on stock decline and impediments to recovery. Transactions of the American Fisheries Society 136:800–821.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*salmo gairdneri gairdneri*) and Silver Salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game. Fish Bulletin:1–266.

Sharma, R., A. B. Cooper, and R. Hilborn. 2005. A quantitative framework for the analysis of habitat and hatchery practices on Pacific salmon. Ecological Modelling 183:231–250.

Sheer, M. B., and E. A. Steel. 2006. Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and lower Columbia River basins. Transactions of the American Fisheries Society 135:1654–1669.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269–311.

Snellen, C., P. J. Hodum, and E. Fernández-Juricic. 2007. Assessing Western Gull predation on purple sea urchins in the rocky intertidal using optimal foraging theory. Canadian Journal of Zoology 85:221–231.

Sogard, S. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60:1129–1157.

Sogard, S. M., J. E. Merz, W. H. Satterthwaite, M. P. Beakes, D. R. Swank, E. M. Collins, R. G. Titus, and M. Mangel. 2012. Contrasts in habitat characteristics and life history patterns of *Oncorhynchus mykiss* in California's central coast and central valley. Transactions of the American Fisheries Society 141:747–760.

Sogard, S. M., T. H. Williams, and H. Fish. 2009. Seasonal patterns of abundance, growth, and site fidelity of juvenile steelhead in a small coastal California stream. Transactions of the American Fisheries Society 138:549–563.

Spear, L. B. 1988. Dispersal patterns of Western Gulls from southeast Farallon Island. The Auk 105:128–141.

Spiller, D., and T. W. Schoener. 1998. Lizards reduce spider species richness by excluding rare species. Ecology 79:503–516.

Steenweg, R. J., R. A. Ronconi, and M. L. Leonard. 2011. Seasonal and age-dependent dietary partitioning between the Great Black-backed and Herring Gulls. The Condor 113:795–805.

Stock, B. C., and B. X. Semmens. 2013. MixSIAR GUI user manual, version 1.0. Accessible online at: http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR.

Stokstad, E. 2007. Can the Bald Eagle still soar after it is delisted? Science 316:1689–1690.

Sydeman, W., K. Hobson, P. Pyle, and E. McLaren. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. The Condor 99:327–336.

Sydeman, W., J. Penniman, T. Penniman, P. Pyle, and D. G. Ainley. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. The Journal of Animal Ecology 60:135–149.

Taylor, E., and J. McPhail. 1985. Burst swimming and size-related predation of newly emerged coho salmon *Oncorhynchus kisutch*. Transactions of the American Fisheries Society 114:546–551.

Thayer, J. A., and W. J. Sydeman. 2004. Long-term studies of seabirds on Año Nuevo Island and mainland, 2003. In: Final Report to the Monterey Bay National Marine Sanctuary – Sanctuary Integrated Monitoring Network. Point Reyes Bird Observatory, Stinson Beach, California.

Thiériot, E., P. Molina, and J.-F. Giroux. 2012. Rubber shots not as effective as selective culling in deterring gulls from landfill sites. Applied Animal Behaviour Science 142:109–115.

Thorpe, J. 2007. Maturation responses of salmonids to changing developmental opportunities. Marine Ecology Progress Series 335:285–288.

Twardochleb, L. A., M. Novak, and J. W. Moore. 2012. Using the functional response of a consumer to predict biotic resistance to invasive prey. Ecological Applications 22:1162–1171.

USEPA (United States Environmental Protection Agency). 2008. Municipal solid waste generation, recycling, and disposal in the United States: facts and figures for 2008.

Accessible online at:
http://www.epa.gov/waste/nonhaz/municipal/pubs/msw2008rpt.pdf.

USGS (United States Geological Survey). 2006. You are what you eat: food web isotope study using fingernails. Accessible online at:
http://wwwrcamnl.wr.usgs.gov/isoig/projects/fingernails/.

Verburg, P. 2007. The need to correct for the Suess effect in the application of δ13C in sediment of autotrophic Lake Tanganyika, as a productivity proxy in the Anthropocene. Journal of Paleolimnology 37:591–602.

Vickery, P. D., M. L. Hunter Jr, and J. V. Wells. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288.

Vidal, E., F. Medail, and T. Tatoni. 1998. Is the Yellow-legged Gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. Biodiversity and Conservation 7:1013–1026.

Voorbergen, A., W. F. De Boer, and L. G. Underhill. 2012. Natural and human-induced predation on Cape Cormorants at Dyer Island. Bird Conservation International 22:82–93.

Votier, S. C., S. Bearhop, M. J. Witt, R. Inger, D. Thompson, and J. Newton. 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. Journal of Applied Ecology 47:487–497.

Ward, B. R. 2000. Declivity in steelhead (*Oncorhynchus mykiss*) recruitment at the Keogh River over the past decade. Canadian Journal of Fisheries and Aquatic Sciences 57:298–306.

Ward, B., P. Slaney, A. R. Facchin, and R. W. Land. 1989. Size-biased survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46:1853–1858.

Ward, E. J., P. S. Levin, M. M. Lance, S. J. Jeffries, and A. Acevedo-Gutiérrez. 2012. Integrating diet and movement data to identify hot spots of predation risk and areas of conservation concern for endangered species. Conservation Letters 5:37–47.

Warzybok, P. M., R. W. Berger, and R. W. Bradley. 2012. Status of seabirds on Southeast Farallon Island during the 2012 breeding season. Unpublished report to the US Fish and Wildlife Service. PRBO Conservation Science, Petaluma, California. PRBO Contribution Number 1906.

Webb, L. 2013. Spatiotemporal variability in the diet of nonbreeding Brandt's Cormorant (*Phalacrocorax penicillatus*) in the Monterey Bay region. Master's thesis. San Jose State University, San Jose, California.

Weiser, E. L., and A. N. Powell. 2010. Does garbage in the diet improve reproductive output of Glaucous Gulls? The Condor 112:530–538.

Weiser, E., and A. Powell. 2011. Evaluating gull diets: a comparison of conventional methods and stable isotope analysis. Journal of Field Ornithology 82:297–310.

Wiley, A. E., P. H. Ostrom, A. J. Welch, R. C. Fleischer, H. Gandhi, J. R. Southon, T. W. J. Stafford, J. F. Penniman, D. Hu, F. P. Duvall, and H. F. James. 2013. Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs. Proceedings of the National Academy of Sciences of the United States of America 110:8972–8977.

Willette, T. M. 2001. Foraging behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha*) and size-dependent predation risk 10:110–131.

Williams, T. M., J. A. Estes, D. F. Doak, and A. M. Springer. 2004. Killer appetites: assessing the role of predators in ecological communities. Ecology 85:3373–3384.

Wittmer, H., A. Sinclair, and B. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144:257–267.

Yorio, P., and M. Giaccardi. 2002. Urban and fishery waste tips as food sources for birds in northern coastal Patagonia, Argentina. Ornitología Neotropical 13:283–292.

Zabel, R. W., and S. Achord. 2004. Relating size of juveniles to survival within and among populations of Chinook salmon. Ecology 85:795–806.