



A century of Chinook salmon consumption by marine mammal predators in the Northeast Pacific Ocean



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ABSTRACT

As many marine mammal populations have increased following bans on their harvest, there has been a growing need to understand potential impacts of these population changes on coastal marine ecosystems. Quantifying consumption of prey species, such as fish, is particularly important when those same prey are also targeted by commercial fisheries. Estimating the impact of marine mammal predators on prey fish depends upon knowledge of marine mammal diet composition; scientific advances over the last century have improved understanding of diets but have also led to inconsistent methods that challenge attempts at synthesis and comparison. Meta-analysis techniques offer the opportunity to overcome such challenges, yet have not been widely applied to synthesize marine mammal diets over space and time. As a case study, we focus on synthesizing diet studies of Chinook (king) salmon (*Oncorhynchus tshawytscha*) by four species of marine mammal predators in the Northeast Pacific Ocean: Steller sea lions (*Eumetopias jubatus*), California sea lions (*Zalophus californianus*), harbor seals (*Phoca vitulina*), and killer whales (*Orcinus orca*). We also highlight several simple meta-analyses for which these types of diet databases may be employed. Our assembled database consists of >330 records, spanning more than 100 years. Results indicate that the frequency of occurrence of Chinook salmon in killer whale studies is high (63%) relative to pinniped studies (<10%). They also suggest a strong increasing ability to discriminate Chinook salmon from other salmonids, which we attribute to switches in diet studies from lethal or observational sampling toward molecular methods (DNA, fatty acids). Our database and analysis code are published as supplementary material, which we hope will be useful for other researchers and will inspire more of these syntheses.

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1. Introduction

Marine mammals are important components of marine ecosystems. Around the globe, many marine mammal populations have increased following bans on their harvest, and many recoveries have occurred in coastal waters (Magera et al., 2013). These recoveries have largely been viewed as successful, but also highlight the need to quantify the impact that these recoveries have had on commercially and recreationally harvested fish species and fish populations that are depleted or protected (Marshall et al., 2015; Smith et al., 2015; Roman et al., 2015). Historically, marine mammal diet studies have been widely used to examine factors that are important to increased population growth rates, as well as to assess the impacts of marine mammals on lower trophic level prey (Laake et al., 2002). Understanding these

impacts is particularly important for prey populations and species that are at risk, such as Chinook salmon (*Oncorhynchus tshawytscha*) in the Northeast Pacific Ocean.

One of the challenges associated with assessing temporal changes in marine mammal diets is that the types of data collected have also changed, particularly in recent years. As many marine mammal populations have recovered from historically low levels, there has been an increased importance of understanding the top-down effects of marine mammals on food webs (Magera et al., 2013). Some changes in data collection through time have been necessitated by legal protection. In the United States, for example, researchers in the early 20th century could harvest marine mammals and collect stomachs for analysis until the passage of the Marine Mammal Protection Act in 1972. After 1972, stomach contents have not been used widely to quantify diet because they have only been available from stranded animals (Mintzer et al., 2008). Recently, scientific advances have enabled new types of individual-level data to quantify diet. Examples include the use of stable

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isotopes (Phillips and Gregg, 2003; Moore and Semmens, 2008; Bjorkland et al., 2015), quantitative fatty acid analyses (Iverson et al., 2004; Bromaghin et al., 2013), and next generation sequencing (Pompanon et al., 2012). Each of these different types of data may have inherent biases or represent different windows of dietary integration, and only recently have models become available that integrate across multiple data sources (Neubauer and Jensen, 2015).

A second challenge for reconstructing marine mammal diet is that many of the historical sampling programs were short-lived, focused on particular prey items or prey life stages, and sample sizes varied. For example, studies of consumption of salmonids by marine mammals have historically focused on predation of adult salmonids and not juveniles (Roffe and Mate, 1984; Wright et al., 2007). This focus has in part been a function of the diet data available — predation of adult salmon is easier to observe directly (Scordino, 2010), and hard parts are generally easier to identify in scat samples (Lance et al., 2012). Newer dietary reconstruction techniques, such as the use of fatty acids or genetics, incorporate consumption of juvenile fish, but don't allow researchers to quantify the size distribution of prey. Given the uncertainty associated with different types of data and different sampling programs, there is an increased need to synthesize existing datasets so that they can be combined in a larger meta-analysis.

Chinook salmon are both commercially valuable and important prey of top predators such as killer whales *Orcinus orca* (Ward et al., 2009). Hence, the objective of our study was to build a publicly-available database, and summarize the results via a hierarchical meta-analysis of marine mammal predation on Chinook salmon in the Northeast Pacific Ocean. Chinook salmon are an anadromous species, transitioning from natal streams to the ocean during their first or second year of life (Quinn, 2011). The majority of Chinook salmon in North America migrate northward, as far as Alaska (Weitkamp, 2010), where they mature over several years, before completing the return migration to their natal streams. At any point during their life in the ocean, juvenile or adult Chinook salmon may be consumed by marine mammals. Marine mammals included in this study are those that are thought to consume large quantities of Chinook salmon, including fish-eating 'resident' killer whales, and three species of pinnipeds: harbor seals (*Phoca vitulina*), California sea lions (*Zalophus californianus*), and Steller sea lions (*Eumetopias jubatus*). The database and code for this meta-analysis accompany this paper are available at https://github.com/eric-ward/marine_mammal_salmon_diet_database.

2. Methods

2.1. Marine mammal diet database

We assembled 344 studies from 76 peer-reviewed papers and reports detailing the diets of fish-eating 'resident' killer whales, harbor seals, California sea lions, and Steller sea lions. Study years ranged from 1915 through 2015, but over 85% of studies were from the last 30 years of this period. Study sites ranged from Monterey Bay, California, to the Aleutian Islands, Alaska, with over 90% of studies spanning California through southeast Alaska. From each study we recorded information about salmon in the diets and, when reported, we included specific information about consumption of Chinook salmon. The broader ecological literature reports disparate metrics of diet composition, such as frequency of occurrence or percent diet by mass or volume (Hyslop, 1980) and this is particularly true for marine mammals. We therefore recorded all reported diet metrics, but in the analysis focus on the most common one: frequency of occurrence (FO). Frequency of occurrence is defined as the proportion of total samples (e.g. scat or non-empty stomachs) in a study that contain a prey item of interest, in our case salmon or Chinook salmon. Details of the methods are below, and in the database associated with this paper.

From each paper or report, we defined a study as the diet composition of a predator species at a location, with a sample type (e.g. scat

sample, stomach content, observation) (Tables 1–2). To facilitate combining data into geographically distinct regions, each record included spatial information delineating study location by state or province, and a sub-region field defining a study collection's specific geographic location (e.g., Puget Sound). We then grouped studies into one of 6 distinct regions (geographic cells) — from central California to the Gulf of Alaska and Aleutian Islands — assigning a region code to each record. We delineated our spatial areas by aggregating a map of geographic distributions of Chinook salmon along the coast of North America (Weitkamp, 2010), as those represent statistical areas for salmon management. For each study we recorded the type of diet metric or "count type", which included frequency of occurrence, percent volume, percent diet estimate or model output. Each study was assigned a unique study number and comprises a unique database record. Many articles or reports included multiple predator species or locations, therefore we enumerated on average five studies per article or report.

The geographic distribution of studies within the database reflects the distribution of these four marine mammal species (Fig. 1). Harbor seals range along the entire Northeast Pacific from central Baja California to the end of the Aleutian Island chain (Caretta et al., 2013). Consequently, we found diet studies for harbor seals in every one of the six geographic cells in our analysis. Steller sea lion studies were conducted from Alaska to southern Oregon and northern California; this species is less abundant in central and southern California (Allen and Angliss, 2013). California sea lion studies occur from central California up to the inland water of Puget Sound and the Salish Sea, capturing the core range of this species (Caretta et al., 2013), though adult males in particular may have a broader range in offshore Canadian waters. The killer whale diet studies are restricted to resident populations only (fish eating), and therefore the studies are distributed only among the resident pods in the Salish Sea and British Columbia (Ford et al., 1995). Resident killer whale populations exist in southeast Alaska, however diet studies for that region were not available in the literature.

Due to co-occurrence of similar predators like California sea lions and Steller sea lions, in a small number of cases there was ambiguity about the identity of predator species. In these cases we recorded qualitative information about predator species present during sample collections. Of all studies, only two records existed of mixed predator diet samples that could not be attributed to one predator species (Table 1).

Additional diet data included the age and size of prey, the total number of prey items present (individual fish), and the percent of both Chinook salmon and total salmon. When available, we recorded estimates of uncertainty (standard errors or confidence intervals) and sample sizes. It is important to note that the numerical proportion of Chinook and total salmon recorded for a predator's diet was a relative measure and a function of the count type. For example, many studies recorded frequency of occurrence (FO) data, which is a measure of presence/absence in samples (usually scats), but is not the same as the percent contribution to the total diet (Reynolds and Aebischer, 1991; Klare et al., 2011). In contrast, the percent of diet may represent a mass or volume proportion of predator diet (e.g. the percent volume of one prey species in a stomach sample).

Many studies did not differentiate between salmonid species, and instead only reported total salmonid consumption. For instance, many

Table 1

Summary of marine mammal — salmon diet database entries by predator species. The database records indicate the number of studies, and the total samples indicate the number of samples across all studies.

Predator species	Studies	Total samples
Harbor seal	167	30,466
Steller sea lion	78	58,016
California sea lion	50	57,943
Steller/CA sea lion	2	166
Steller/CA sea lion or harbor seal	2	4881
Killer whale	40	4756

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