FORAGING TACTICS OF HUMPBACK WHALES FEEDING NEAR SALMON HATCHERY-RELEASE SITES IN SOUTHEAST ALASKA

By

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Abstract

Increases in the humpback whale (*Megaptera novaeangliae*) population have generated considerable interest in understanding the foraging habits of these large marine predators in the Gulf of Alaska. Globally, humpback whales are classified as generalist predators but are known to exhibit localized differences in diet. Intensified predation pressure is of particular concern to resource managers, who have observed whales feeding at juvenile hatchery salmon release sites in Southeast Alaska. We assessed the diets and behavioral tactics of humpback whales foraging near Hidden Falls Hatchery release sites (in Chatham Strait, 2016 to 2018) to better understand their predatory effects on juvenile hatchery-reared salmon. We used skin biopsies, prey sampling, and stable isotope analysis to estimate whales' diet composition. Aerial footage and photographic sequences were used to assess the foraging tactics used on this prey source. We observed three individual whales repeatedly feeding on juvenile hatchery-reared salmon, and we were able to sample them multiple times over a period spanning shifts in diet. Overall, the diets of these whales were higher trophically than other humpback whales foraging in the area, even before feeding on juvenile hatchery salmon started. These hatchery-feeding whales may be generally more piscivorous than other whales, which focused on planktivorous prey. Our repeat sampling, in conjunction with scheduled introductions of a novel prey source, provided a semi-controlled feeding experiment that allowed for incorporation and turnover rate estimates from humpback whale tissue in a way that was not previously possible for large, free-ranging cetaceans. Finally, during the course of this study we discovered an undescribed feeding tactic employed by hatchery-associated whales. We observed the use of solo bubble-nets to initially corral prey, followed by calculated movements to establish a secondary boundary with the pectoral fins that further condensed prey and increased foraging efficiency. Our study provided the first empirical evidence for what we describe as

"pectoral herding". This work deepens our knowledge about humpback whale foraging ecology, how this innovative species is able to exploit newly available prey, and to what extent they feed on commercially valuable hatchery salmon.

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As A. Brazier Howell once dedicated his work,

"to those who are endeavoring to

save from commercial extinction the great whales,

the largest animals that have ever lived".

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General Introduction

Since the termination of commercial whaling, the humpback whale (*Megaptera novaeangliae*) population has increased in the Gulf of Alaska (Hendrix *et al.* 2012). In 2016, the distinct population segment that breeds in Hawai'i and primarily feeds in Alaska was removed from the Endangered Species List (U.S. Department of Commerce 2016). Though this policy change is seen by some humpback whale biologist as a win, increased population size has caused controversy over this large marine mammal's impact on commercial fisheries. Humpback whales are known to feed on commercially valuable species as well as the prey those species consume (Moran *et al.* 2018; Straley *et al.* 2017). Recent increases in population, in combination with large body size and high metabolic rates, has generated concern about exactly how much biomass humpback whales are removing from valuable fish populations.

Pacific salmon (*Oncorhynchus spp.*) comprise one of the most lucrative fisheries managed by the State of Alaska (Alaska Department of Fish and Game 2019). Salmon populations have been largely exploited and salmon hatcheries in Alaska were established to enhance fish productions for commercial and recreational catch by supplementing wild stocks (Araki and Schmid 2010). Salmon hatcheries provide approximately one third of the commercial salmon catch in Alaskan waters (Vercessi 2015). In the past several decades, humpback whales have been observed feeding on hatchery-released juvenile salmon in Southeast Alaska (Chenoweth *et al.* 2017). This additional predation mortality from humpback whales is thought to have reduced the number of fish that return to spawn. Given that recruitment of Pacific salmon is often determined at a 'critical period' early in marine life (Beamish and Mahnken 2001; Hartt 1980), additional juvenile mortality from such a large predator during this period could have economic consequences for the fisheries that rely on hatchery production (Chenoweth and Criddle 2019). A better understanding of humpback

whale foraging behavior and diet compositions will enhance our knowledge about predation pressure on released juvenile salmon and help managers make informed decisions about future hatchery operations.

Humpback whales are known for their diverse feeding behaviors (Fleming *et al.* 2016; Jurasz and Jurasz 1979; McMillan *et al.* 2018; Parks *et al.* 2014; Weinrich *et al.* 1992) and localized foraging specializations (Sharpe 2001; Witteveen 2008; Ware *et al.* 2014; McMillan *et al.* 2018; Kosma e*t al.* 2019). Various foraging strategies include lunge feeding (Jurasz and Jurasz 1979; Watkins and Schevill 1979), bubble-net feeding (Goldbogen *et al.* 2017; Hain *et al.* 1982; Ingebrigtsen 1929; Jurasz and Jurasz 1979; Sharpe and Dill 1997), flick feeding (Jurasz and Jurasz 1979), cooperative feeding (Sharpe 2001), lobtail feeding (Weinrich *et al.* 1991) and other idiosyncratic tactics (Baker 1985; D'Vincent *et al.* 1985; Hain *et al.* 1982; McMillan *et al.* 2018). These techniques are innovative methods used to increase feeding efficiency. Humpback whales feeding on anthropogenically sourced prey at hatchery release sites is an excellent example of the foraging flexibility of this species. Though efforts have been made to document whales feeding at hatchery release sites (Chenoweth *et al.* 2017) and estimate the economic impact to fisheries (Chenoweth and Criddle 2019), little is known about individual foraging tactics or the relative importance of hatchery salmon in the diets of whales feeding at hatchery sites.

The goal of this thesis was to increase our understanding of the foraging ecology and feeding tactics of humpback whales targeting hatchery-release juvenile salmon in Southeast Alaska. Direct observations of humpback whales feeding are challenging to obtain and represent a single moment in time. Stable carbon and nitrogen isotope analysis (expressed as $\delta^{13}C$ and $\delta^{15}N$ values, respectively) can be useful in quantifying diet compositions of these large marine mammals over longer time frames. In chapter one, we used stable

isotope analyses to estimate the proportional contribution of different prey, including hatchery-reared juvenile salmon, to the diets of humpback whales. We also used repeated sampling of individual whales and a semi-controlled feeding experiment provided by scheduled hatchery releases to estimate stable isotope incorporation rate in humpback whale skin. In chapter two, we described specialized humpback whale foraging tactics to herd prey when feeding near hatchery release sites, including a novel tactic we termed 'pectoral herding'. We accomplished this by using emerging technology such as small cameras and unoccupied aerial vehicles to gain the necessary aerial perspective. The information provided herein furthers our understanding about the potential impacts of humpback whales on hatchery-released juvenile salmon in Southeast Alaska and more broadly expands upon the scientific literature regarding foraging ecology of humpback whales.

Chapter 1 Individual specialization among humpback whales in Southeast Alaska[1]

1.1 Abstract

Globally, humpback whales (*Megaptera novaeangliae*) are classified as generalist predators with a diverse diet, but regionally, these animals are known for phenotypic plasticity in foraging behavior and variable prey selection. In Southeast Alaska, humpback whales have been observed feeding on juvenile Pacific salmon (*Oncorhynchus* spp.) at hatchery release sites. Here we documented three individuals returning to repeatedly target this prey source over two years (2016 and 2017), and we combined feeding observations of these hatchery-associated whales with stable isotope analysis to expand our understanding of the foraging strategies and impact humpback whales have on this important marine resource. Generally, these three whales were found to be feeding at a higher trophic level than other humpback whales that were in the area but not targeting this anthropogenically derived food source. Trophic position was consistent over the two years, suggesting that hatchery-associated whales specialized on forage fish, whereas other whales in the area were targeting prey at lower trophic levels. Additionally, we obtained multiple tissue samples from the same free-ranging humpback whales over an extended period of time including times of known hatchery salmon releases, which allowed us to examine isotopic incorporation rate in humpback whale skin. The hatchery-associated whale that was sampled over the longest time period displayed an isotopic shift between 74 and 85 days after hatchery releases, believed to be due to the incorporation of hatchery-released juvenile salmon into its diet. Ultimately, isotopic characteristics of these unique whales

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deepens our understanding of individual specialization and foraging ecology of humpback whales.

1.2 Introduction

Humpback whales (*Megaptera novaeangliae*) generally spend the winter months in warmer, low-latitude waters where they breed and then migrate to cooler, higher latitude waters to forage in early spring, summer, and fall. These animals are top predators that can have an influence on the structure of marine ecosystems (Croll *et al.* 1998; Trites *et al.* 1997; Witteveen *et al.* 2012) through the consumption of substantial amounts of prey (Witteveen *et al.* 2015; Witteveen *et al.* 2006). Humpback whales are considered to be generalist predators with a diverse diet, feeding seasonally on krill (*Thysanoessa* spp. and *Euphausia pacifica*) and pelagic schooling fish, including capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), juvenile walleye pollock (*Gadus chalcogrammus*), and Pacific sand lance (*Ammodytes hexapterus*). Despite their generalist food habits, there are variations between the specific diets of feeding aggregations of humpback whales, where some groups target forage fish and others euphausiids (Witteveen *et al.* 2011). These cetaceans are known for their flexibility in foraging behavior (Chenoweth *et al.* 2017; Fleming *et al.* 2016; Parks *et al.* 2014; Weinrich *et al.* 1992) which can be an advantage in a changing environment (Pigliucci 2005). Furthermore, there is evidence of local foraging specialization in humpback whales according to prey availability (Kosma *et al.* 2019; McMillan *et al.* 2018; Sharpe 2001; Ware *et al.* 2014; Witteveen 2008).

In Southeast Alaska, humpback whales have been observed feeding on hatchery-reared juvenile Pacific salmon (*Oncorhynchus* spp., Chenoweth *et al.* 2017). High densities of hatchery salmon at release sites can attract predators such as harbor seals, eagles, gulls, river otters, minks, and piscivorous fishes (Scheel and Hough 1997); consequently,

hatchery managers often release young salmon *en masse* as a predator-swamping tactic (Chenoweth *et al.* 2017; Furey *et al.* 2016). However, this strategy can generate dense prey aggregations that are consumable by humpback whales (Piatt and Methven 1992). The presence of humpback whales has coincided with historically poor returns of chum salmon (*O. keta)* at the Hidden Falls Hatchery (located in Chatham Strait) in 2011, 2015, and 2016 (Chenoweth *et al.* 2017). Thus, humpback whales are suspected of causing high predation mortality and reducing the number of salmon that return as adults. This is cause for concern among hatchery managers (Chenoweth and Criddle 2019), given that recruitment of Pacific salmon is often determined early in marine life (Beamish and Mahnken 2001; McNeil and Himsworth 1980). Hatcheries produce salmon to provide economic opportunities for fishermen and to decrease fishing pressure on wild salmon populations (Heard 2001; Heard 2012). Understanding sources of predation mortality for juvenile hatchery salmon is crucial for assessing the success of hatcheries in supplementing fisheries catches and also provides information for ecosystem-based fisheries management in Alaska waters.

Estimating predation mortality by cetaceans is challenging, and conventional foraging studies (*e.g.*, stomach content analysis, fecal sampling) are rarely feasible for these animals (Pierce *et al.* 2007). Analyses of the stable carbon and nitrogen isotope composition (expressed as $\delta^{13}C$ and $\delta^{15}N$ values, respectively) of organisms is a well-established method for quantifying food habits and is commonly used to estimate foraging strategies for marine mammals (Bowen and Iverson 2013; Nelson *et al.* 2018; Newsome *et al.* 2010; Todd *et al.* 1997; Witteveen *et al.* 2012). While direct feeding observations have temporal and spatial restrictions, stable isotopes provide dietary information through time, providing a more comprehensive understanding about an animal's foraging habits (Bowen and Iverson 2013). Stable nitrogen isotope values are typically used as an index of trophic level, with

increases in $\delta^{15}N$ values representing increases in trophic level (Fry 2006). In marine mammal studies, $\delta^{15}N$ values typically increase ~2 - 4 ‰ per trophic level (Borrell *et al.* 2012; Wild *et al.* 2018; Witteveen *et al.* 2011). Stable carbon isotope values typically reflect the source of primary production (Rau *et al.* 2016) and can be used as a proxy for foraging habitat. For example, consumers in marine benthic and nearshore areas tend to exhibit higher $\delta^{13}C$ values than those in pelagic and offshore areas (Burton and Koch 1999; Hobson *et al.* 1994; Miller *et al.* 2010). Although stable isotopes are generally limited in the degree to which they distinguish individual prey items, wheat-based fish feed should be easily distinguishable from marine prey (Tomida *et al.* 2014). This suggests that hatchery salmon predation could hypothetically leave an identifiable stable isotope signature in the tissues of humpback whales. Isotopic mixing models (Monteiro *et al.* 2015; Parnell *et al.* 2013; Phillips and Gregg 2001; Phillips *et al.* 2014; Witteveen *et al.* 2012; Witteveen and Wynne 2016) could then be used to quantify the proportional contribution of hatchery salmon to humpback whale diets.

Understanding the rates of tissue incorporation and turnover are necessary for interpretation of isotopic mixing models, but these rates are not well known for cetaceans. Incorporation rate refers to the amount of time between prey ingestion and when the isotopic signature of that prey enters the tissue of a predator (Busquets-Vass *et al.* 2017; Thomas and Crowther 2015). Turnover rate refers to the rate of replacement of a tissue (Reiner 1953; Zilversmit *et al.* 1943). Stable isotope values from predator tissue reflect those of their prey over a time period relative to tissue turnover rate, and differences in turnover rate are one cause for variation in stable isotope signatures within and between tissues (Tieszen *et al.* 1983; Hobson and Clark 1992; Wild *et al.* 2018).

To estimate tissue incorporation rate, controlled feeding studies typically switch between two isotopically distinct preys items and analyze a time series of tissue samples (Tieszen *et al.* 1983; Voigt *et al.* 2003; Busquets-Vass *et al.* 2017). Controlled feeding experiments are not feasible in large cetaceans, which cannot be held in captivity unlike species such as bottlenose dolphins (*Tursiops truncates*) and beluga whales (*Delphinapterus leucas*) (St. Aubin *et al.* 1990; Hicks *et al.* 1985). However, in our study the release dates for juvenile hatchery salmon from Hidden Falls Hatchery are known for each year, and this prey item should be distinct from all others because it is not available in the marine realm before releases occur. This unique situation of timed release of juvenile hatchery salmon is the closest circumstance to a controlled feeding study on free-ranging humpback whales. Additionally, the discrepancy between marine origin prey and a unique anthropogenically sourced prey with a terrestrially based (*i.e.,* wheat-based, hatchery feed) signature, such as wheat-based hatchery feed, should represent a distinct and measurable shift in diets. Repeat sampling of the same individual whales before, during, and after fish releases should provide a time series of tissue samples to estimate incorporation and turnover rate. Biopsy sampling of humpback whales is a minimally invasive technique that provides skin tissue for isotopic assessment of diet (Palsboll *et al.* 1991; Todd *et al.* 1997; Weinrich *et al.* 1991).

The overarching goal of this study was to use stable isotopes to better understand the foraging ecology of humpback whales feeding on a novel prey source, juvenile hatchery salmon. We used stable isotope signatures to quantify the diet compositions of humpback whales foraging in nearshore waters of Southeast Alaska (2016 and 2017), including whales observed feeding at hatchery release sites and other whales presumed to have fed primarily on marine prey. We also estimated changes in $\delta^{13}C$ signatures from repeatedly

sampled whales to understand temporal effects of feeding on hatchery-released juvenile salmon. Our objectives were to 1) use stable isotope values to characterize the potential for individual specialization on novel prey sources (*i.e.,* hatchery salmon); 2) estimate the relative importance of hatchery-released juvenile salmon on humpback whale diets in Southeast Alaska, and 3) use repeated sampling of the same whales feeding on hatchery-released juvenile salmon to better understand incorporation rate and turnover rate in humpback whales. This study provides the first attempt at repeat sampling of the same free-ranging humpback whales over an extended period, allowing for isotope analysis to be used in longitudinal studies of foraging behavior.

1.3 Methods

1.3.1 Data Collection

This study was conducted in Chatham Strait, along the eastern shore of Baranof Island in Southeast Alaska (Fig. 1.1). We conducted systematic surveys from Warm Springs Bay north to Kelp Bay, with an emphasis on salmon hatchery release sites in Takatz Bay and Kasnyku Bay in 2016 (mid-May through the end of June) and 2017 (mid-April through end of July). All effort was timed to overlap with releases of juvenile salmon from Hidden Falls Hatchery (managed by the Northern Southeast Regional Aquaculture Association). In 2016, Hidden Falls Hatchery had two primary release sites (*i.e.,* Takatz Bay and Kasnyku Bay) and released an estimated 90,613,267 juvenile chum and coho (*O. kisutch*) salmon. In 2017 only Kasnyku Bay was used as a primary release site and 68,750,169 juvenile chum and coho salmon were released. Sampling effort in 2016 was over a 48-day period with 31 boat survey days and 2017 was over a 101-day period with 42 boat survey days.

We documented the behavior of each whale observed. Behavioral categories included feeding, milling (*i.e.*, remaining in the same location and potentially diving on prey),

traveling, or resting. If the whale was feeding, we visually identified prey. When possible, during feeding events we used a cast net and herring jigs to sample prey for greater taxonomic specificity. Separate sampling efforts were conducted to collect krill (*Euphausiids* spp.*)* with a tucker trawl (90 cm x 70 cm, 1000 μm) at variable depth. In the laboratory, we removed juvenile salmon otoliths and used thermal markings (Volk *et al.* 1999) to distinguish hatchery-reared from wild-origin fish. Primary consumers (*Mytilus* spp.*)* were collected from docks in Warm Springs Bay and Kasnyku Bay and were used as isotopic baselines for trophic level calculations.

During systematic surveys, we took photographs with digital SLR cameras (focal lengths from 70 to 300 mm) to identify humpback whales. Individual whales were identified based on the pigmentation and trailing edges of their flukes and/or the shape and marking on their dorsal fins (Katona *et al.* 1979). We cross-referenced with the Southeast Alaska Humpback Whale Catalog (Straley and Gabriele 2000). This catalog included all whale sightings through 2012 and continues to be updated with more recent observations (Straley and Gabriele, unpublished data).

Whales repeatedly feeding on hatchery-released juvenile salmon were identified and targeted for continued biological sampling throughout the season to monitor changes in stable isotope signatures. Samples from whales not observed feeding on hatchery-released juvenile salmon (termed “other whales”) were used as the basis for comparing stable isotope values. For all whales observed, we used a Barnett crossbow (68 kg draw weight) to collect shallow (*i.e.*, 40 mm in length and 7 mm in diameter) tissue samples from the flank of the animal. Photographs of both the flukes and the dorsal fin were taken to confirm the identity of each whale sampled. This research was conducted under National Marine Fisheries Service (NMFS) permit 14122 and 18529, University of Alaska Institutional Animal

Care and Use Committee (IACUC) permit 907314-3, and State of Alaska Department of Fish and Game permit CF-18-049.

1.3.2 Sample Preparation and Stable Isotope Analysis

Cetacean skin is made up of multiple layers and it has been suggested that directed sampling of specific layers allow for more nuanced analysis of dietary trends (Busquets-Vass *et al.* 2017; Wild *et al.* 2018). For this reason, we subsampled the "inner" and "outer" layer to assess potential differences between more recent diets (inner) and diets from earlier time periods (outer) (Fig. 1.2). Samples were prepared for stable isotope analysis through a multi-step process that included subsampling, oven drying, lipid extraction, and homogenization. We separated the skin from the blubber and cut it into three equally thick layers (Fig. 1.2). All subsamples were oven-dried for 24 hours at 60°C. Lipids tend to be depleted in ^{13}C relative to ^{12}C compared with other tissues (*e.g.,* muscle), causing samples with high lipid content to show relatively low $\delta^{13}C$ values (Deniro and Epstein 1978). Therefore, to account for differences in lipid content, samples were lipid-extracted prior to analysis. Duplicate samples were run without lipid extraction as a check for any changes to $\delta^{15}N$ values caused by the process (Logan and Lutcavage 2008; Murry *et al.* 2006; Post *et al.* 2007; Ryan *et al.* 2012). Lipid extraction was carried out by soaking the tissue in a 2:1 chloroform-methanol solution for 20 min in an ultrasonic bath (Folch *et al.* 1956; Logan *et al.* 2008; Sweeting *et al.* 2006). This process was repeated three times. Following lipid extraction, we oven-dried samples at 60°C for 24 hours to evaporate off any remaining solution. Dried, lipid-extracted and non-lipid-extracted samples were ground into a powder to ensure homogenization using a Wig-L-Bug Grinding Mill (International Crystal Laboratories). Whole prey samples were ground with a mortar and pestle. Aliquots of

homogenized whale and prey samples (0.2-0.4 mg) were sealed in 5 mm tin capsules and sent to the University of Alaska Fairbanks, Alaska Stable Isotope Facility (ASIF). ASIF used an elemental analyzer attached to an isotope ratio mass spectrometer (EA-IRMS) for bulk carbon and nitrogen isotope analyses and results are expressed in the δ notation, which indicates the ratio of the heavy isotope to the light isotope (relative to a standard). We used standard δ notation, defined as:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000,$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio of $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Stable isotope ratios are expressed in units of parts per million, 'per mil' (‰) relative to international standards (Vienna Pee Dee Belemnite for carbon and atmospheric nitrogen for nitrogen). Analytical precision was $\pm$0.2‰ for both $\delta^{13}C$ values and $\delta^{15}N$ values, which was determined by analyzing a peptone standard throughout the sample run.

We used multivariate analyses to test for differences in stable isotope signatures between hatchery-associated whales and other whales ('vegan' package in R; Oksanen *et al.* 2019). We calculated Bray-Curtis dissimilarity indices (Clarke *et al.* 1993) on the raw isotopic data. We then used a permutational multivariate analysis of variance (PERMANOVA) with Type III sums of squares (Number of permutations = 9999; $\alpha = 0.1$) to test for differences between groups. Any factor that produced a p-value > 0.1 was not included in the final model. We also calculated trophic level (TL) for each individual and group using the following equation:

$$TL = 2 \pm \frac{(\delta^{15}N_{specimen} - \delta^{15}N_{primary\ consumer})}{2.4},$$

where 2 is the trophic position of the primary consumer (*i.e.*, mussels collected from study area, both years) and 2.4 is the average enrichment factor per trophic level (Hobson *et al.* 1994).

1.3.3 Diet Compositions

We estimated diet compositions using the Bayesian stable isotope mixing model SIMMR (Stable Isotope Mixing Models in R; Parnell *et al.* 2010). We elected to use SIMMR over other mixing models because it allows for multiple dietary sources as well as associated uncertainties in both isotopic values and enrichment factors (Parnell *et al.* 2010); however, like any other mixing model, they are sensitive to lack of data from unsampled prey times (Phillips *et al.* 2014). Bayesian mixing models tend to generate more robust results than other modeling approaches and display diet compositions as probability distributions (Inger and Bearhop 2008; Moore and Semmens 2008; Parnell *et al.* 2010). We used stable isotope ratios for each whale and means with standard deviations for each prey species or group as input data. Currently, there are few available estimates for enrichment factors of $\delta^{13}C$ and $\delta^{15}N$ values pertaining to marine mammals, and no published enrichment factors specific to humpback whales (Witteveen 2008). Thus, we used enrichment factor estimates from Witteveen *et al.* (2012): 0.9 ‰ for $\delta^{13}C$ values and 3.2 ‰ for $\delta^{15}N$ values. We used mixing models (posterior probabilities from four chains of length after a burn-in of 10,000 iterations and thinned by subsampling every hundredth iteration) to estimate diet compositions for all hatchery-associated whales, all other whales, and each individual hatchery-associated whale (whale # 2227, # 2571, and # 2360), by year (2016 and 2017) and layer (inner and outer). In both years, hatchery-associated and other whale samples were divided into biweekly periods after the first release (Table S1.2) for comparison of the proportional consumption of hatchery salmon over time. We did not test for differences over time due to limited sample size within biweekly periods.

1.3.4 Temporal Shifts in $\delta^{13}C$

Salmon were released from Hidden Falls Hatchery on known dates, so we were able to use releases as a semi-controlled feeding experiment to analyze incorporation and turnover rate. We hypothesized that consumption of hatchery-released juvenile salmon would result in a reduction of $\delta^{13}C$ for hatchery-associated whales through time. We used generalized additive models (GAMs; 'mgcv' package in R, Wood 2011) with a Gaussian distribution and identity link to model changes in $\delta^{13}C$ values within the inner and outer layers. $\delta^{13}C$ values were modeled separately for each hatchery-associated whale (to account for individual foraging patterns) as a function of year and the number of days following hatchery release ('post-release days'). We treated year as a factor. The amount of smoothing for our nonparametric variable (*i.e.,* number of post-release days) was determined by generalized cross validation (GCV) (Wood 2006) and limited to eight knots to allow for complex changes in $\delta^{13}C$ values through time without overfitting. The full model formulation was:

$$\delta^{13}C_{i,j} = y_i \pm f(PR_i) \pm \varepsilon_{i,j},$$

where y is year and f is the smoothing function for the number of post release days (PR) for each sample. $\varepsilon_{i,j}$ denotes residual error.

1.4 Results

A total of 15 and 30 individual humpback whales were sampled in 2016 and 2017, respectively. In both years, three whales (#2227, #2571, and #2360) repeatedly foraged on juvenile chum and coho salmon near Hidden Falls Hatchery. We biopsied 12 other whales in 2016 and 27 other whales in 2017. Prey samples were comprised of juvenile hatchery-released chum salmon (n=99), juvenile hatchery-released coho salmon (n=27), wild juvenile salmon (n=19), Pacific herring (n=30), and krill (n=3) (Table 1.1; Table S1). Hatchery-

released juvenile salmon were found in Warm Springs Bay, Takatz Bay, Kasnyku Bay, and Kelp Bay in 2016 and Kasnyku Bay and Kelp Bay in 2017. Furthermore, otolith analysis (n = 103 juvenile salmon) revealed that wild-origin juvenile salmon coincided with large aggregations of hatchery-released juvenile salmon (83% of fish had thermal markings) being targeted by humpback whales. Coho salmon are not thermal-marked at Hidden Falls Hatchery so were not included in otolith analysis. Due to limited prey sampling in 2016, we used prey information from both years (2016 and 2017) as input data for 2016 mixing models.

1.4.1 Hatchery-Associated vs. Other Whales

We found no difference in mean $\delta^{13}C$ values between hatchery and other whales, but we did find that tissue from hatchery-associated whales exhibited statistically higher mean $\delta^{15}N$ than those of other whales (Table 1.2; Fig. 1.4). The mean trophic level for hatchery-associated whales was 5.3 $\pm$ 0.4 SD (inner skin layer) and 5.5 $\pm$ 0.6 SD (outer skin layer). Other whales showed a mean trophic level of 5.0 $\pm$ 0.3 SD (inner) and 5.0 $\pm$ 0.3 SD (outer) (Table 1.2). Results from the PERMANOVA showed a significant effect of whale type on stable isotope signatures in the inner ($F_{1,56}$ = 8.410, R^2 = 0.131, p = 0.002) and outer ($F_{1,54}$ = 12.781, R^2 = 0.191, p < 0.001) layers, but no effect of year.

Inferred diets of both hatchery-associated and other whales were comprised of a large portion of hatchery salmon, regardless of when the sample was collected. Notably, hatchery salmon were estimated in the diets of all whales prior to Hidden Falls Hatchery's first release (*i.e.*, when no juvenile hatchery-released salmon were available). Mixing model results for 2016 showed no trends through time, reflecting low variability in diet compositions (Fig. 1.3). In 2017, mixing model results showed some shifts in diet

composition for both hatchery-associated and other whales, reflecting some degree of variability in diet composition over time. Krill surpassed hatchery salmon consumption proportion in the inner layer of hatchery-associated whales for the 58-71 post-release day timeframe (n=1) and in the inner layer of other whales for the 16-29 post-release day period (n=9). In both years, other whales showed hatchery salmon in their diets before any Hidden Falls Hatchery releases. We were unsuccessful in sampling hatchery-associated whales before the day of first release in either year. Hatchery-associated whales showed a large contribution of hatchery salmon within the first biweekly period (1-15 d) in both 2016 and 2017.

1.4.2 Foraging Patterns of Hatchery-Associated Whales

In 2016, we observed hatchery-associated whale #2227 in Warm Springs Bay, two hatchery release sites (Takatz and Kasnyku bays), and Kelp Bay (n = 11 d; Table S1.3). This whale fed at hatchery release sites between 9 and 37 days post-release. However, we recorded this individual feeding on schools of juvenile salmon (within the broader study area) until 55 days post-release. All surface feeding observations (7 d) involved foraging on juvenile salmon. No notable increase or decrease was shown in the proportions of prey consumption for hatchery salmon (Fig. 1.6). In 2017, we observed hatchery-associated whale #2227 in Takatz Bay, Kasnyku Bay (release site), and Kelp Bay (n = 9 d; Table S1.2). The whale was found foraging at release sites between 7 and 14 days post-release. The whale left the study area 16 days post-release and was not observed again. The biopsy tissue sample from 7 days post-release was not an ideal sample (perpendicular penetration into whale skin) so the inner layer could not be analyzed. We found no temporal patterns in the proportions of hatchery salmon; however, in both years whale #2227 was feeding at a

higher trophic level than the other two hatchery-associated whales reflecting more consumption of hatchery coho salmon and/or Pacific herring.

Hatchery-associated whale #2571 was observed in Warm Springs Bay, Takatz Bay (release site), Kasnyku Bay (release site), and Kelp Bay in 2016 (n = 14 d; Table S1.4). This whale fed at hatchery releases sites between 18 days and 37 days post-release but was recorded feeding on schools of juvenile salmon within the study area 65 days post-release. All surface feeding events involved juvenile salmon. The outer layer exhibited variation in proportions of coho salmon, with a slight increase through time. There was no notable trend in the proportions of hatchery salmon from the inner or outer layer of the skin (Fig. 7). In 2017, hatchery-associated whale #2571 was only observed in Kelp Bay (n = 16 days). The whale was first observed feeding on juvenile hatchery salmon at 12 days post-release and last observed at 22 days post-release (Table S3). Half of all surface feeding targeted juvenile salmon. In the inner layer, there were spikes in proportions of krill consumed on 22 and 70 days post-release, which appeared to drive the greatest shifts in diet.

Finally, we observed hatchery-associated whale #2360 in Warm Springs Bay, Takatz Bay (release site), Kasnyku Bay (release site), and Kelp Bay in 2016 (n = 15 d; Table S1.5). This whale was observed feeding at release sites from 9 days to 20 days post-release and seen feeding on schools of juvenile salmon until 58 days post-release. All surface feeding events targeted juvenile salmon. We found no notable trend in the proportions of prey consumption in the inner or outer layer (Fig. 9; Table 2). In 2017, hatchery-associated whale #2360 was observed in Kasnyku Bay (release site), Kelp Bay, and outside the study area in Wilson Cove (east side of Chatham Strait) (n = 13 d; Table S1.4). This whale fed on juvenile hatchery salmon between 14 and 37 days post-release. After 37 days post-release, hatchery-associated whale #2360 shifted from solo bubble-net feeding to group foraging on

herring. The outer layer showed a substantial amount of variation, primarily due to a larger proportion of krill reflected in the first sample (25 days post-release).

1.4.3 Isotopic Incorporation Rate

Hatchery-associated whale #2227 was sampled 4 times in both 2016 and 2017 over 47 and 11 days, respectively. We found no significant effect of year or number of post-release days on the $\delta^{13}C$ signature (Table 1.4). Whale #2571 was sampled 5 times over 48 days in 2016 and 6 samples were collected over 84 days in 2017. Of all hatchery-associated whales, whale #2571 was sampled over the longest period, with a sample collected at 85 days post-release. We found a significant effect of the number of post-release days on the $\delta^{13}C$ values in the inner layer and an effect of year in the outer layer (Table 1.5; Fig. 1.8). Whale #2360 was sampled 4 times in both 2016 and 2017 over 37 and 49 days, respectively. We found a significant effect of year on the $\delta^{13}C$ values in the inner layer for hatchery-associated whale #2360 (Table 1.6; Fig. 1.10).

1.5 Discussion

Stable nitrogen isotope signatures differed between hatchery-associated whales and other whales not observed feeding at release sites, suggesting disparate foraging strategies between the two groups. This study also demonstrates the unique ability to incorporate new, anthropogenically produced prey by whales. Although our study could not definitively estimate the contribution of hatchery-release juvenile salmon to the diets of humpback whales, pairing direct observations with stable isotope analysis suggests some degree of individual specialization among humpback-associated whales, which are largely considered generalist predators. We identified three hatchery-associated whales (#2227, #2571, and

#2360) that regularly fed on hatchery-released juvenile salmon in Southeast Alaska (2016 to 2017). These three whales exhibited significantly higher trophic levels than other humpback whales found in the study area, revealing differences in prey selectivity between the two groups (Witteveen *et al.* 2011) even with no obvious differences in foraging habitat. This work highlights isotopic differences, persisting over a two-year period, in diets as a result of varied foraging strategies of humpback whales.

Previous studies at Hidden Falls Hatchery have documented consumption of hatchery-released salmon by humpback whales at release sites, but the extent (*i.e.*, number of whales, length of time, frequency, location of predation) to which humpback whales targeted wild or hatchery-released salmon after outmigration was not determined (Chenoweth *et al.* 2017). We found that as hatchery salmon move into surrounding bays (*i.e.*, Warm Springs Bay and Kelp Bay) they school with wild salmon, and some whales continue to feed on salmon in these adjacent areas resulting in the consumption of both hatchery-reared and wild (chum and pink) juvenile salmon. The presence of wild juvenile pink and chum salmon in Warm Springs Bay, Takatz Bay, Kasnyku Bay, and Kelp Bay is consistent with species composition reports from local anadromous streams (ADFG 2019a).

1.5.1 Hatchery-associated vs. Other Whales

Hatchery-associated whales #2227, #2571, and #2360 were repeatedly observed feeding on hatchery-released juvenile salmon from Warm Springs Bay to Kelp Bay. We found a difference in diet between these whales and other whales in Chatham Strait based on their stable isotope composition. However, we observed no concerted temporal shift in stable isotope signatures of hatchery-associated whales that would reflect hatchery salmon isotopically becoming incorporated into their skin. Stable isotope values indicative of higher trophic levels of the three hatchery-associated whales were present in the whales' skin

before, during, and after releases, indicating a cause that seem to be independent of consuming juvenile salmon from Hidden Falls Hatchery. Additionally, our mixing models inferred the presence of hatchery salmon in the diets of all whales during the first week of releases and, in some cases, before releases even occurred. The inferred proportion of hatchery salmon in the diets was never below 22.5% throughout the sampling period. This suggests that foraging behavior differentiates hatchery-associated whales from other whales, but that differences in diets were not uniquely due to consumption of hatchery-reared salmon. Different stable isotope ratios were evident in both the inner and outer layers of skin, indicating an isotopic distinction at a broader temporal scales (Busquets-Vass *et al.* 2017; Wild *et al.* 2018).

In nature, generalist populations are often composed of ecologically diverse individuals that use different subsets of available resources (Hoelzel *et al.* 1989), which can lead to specialization at the individual level (Bolnick *et al.* 2003). Intraspecific competition and environmental fluctuation are among the many causes of individual specialization. In 2006, the population of North Pacific humpback whales was well over 21,800 individuals (Barlow *et al.* 2011) and the annual population growth rate was 4 to 7% (Calambokidis *et al.* 2008). This increase in population size could have prompted feeding on hatchery-released juvenile salmon as a means of reducing the negative effects of intraspecific competition. Additionally, climate change has impacted the North Pacific (Di Lorenzo and Mantua 2016), influencing prey availability. Decreased access to preferred prey may have also triggered these individuals to expand their prey repertoire. A consumer population's response to spatial and temporal variation in the abundance and quality of prey will vary greatly with the degree of individual variation in diet (Pintor and Byers 2015). Another plausible explanation for differences in stable isotope ratios and trophic levels is that hatchery-associated whales simply demonstrate more exploratory behavior than other whales (Pintor and Byers 2015).

A greater tendency to exploit new resources would explain location and incorporation of hatchery-released salmon into their diets. Regardless of the mechanism, our direct observations and stable isotope results suggest that individual humpback whales exhibit specialized foraging strategies that differentiate their diets from one another. We found that hatchery-associated whales were consuming higher trophic level prey (*i.e.*, consuming more fish). Either hatchery-associated whales have recently developed the skills necessary to feed on hatchery-released salmon, allowing for greater specialization on forage fishes during early spring, or hatchery-associated whales already were forage fish specialists, which facilitated the consumption of hatchery-released salmon. During late spring and early summer, other whales seemed to feed primarily on krill (*i.e.*, a lower trophic level prey). Such behavior may have narrowed their focus or foraging areas, thereby preventing the utilization of hatchery salmon when highly abundant.

Half-life turnover rates for bottlenose dolphins (measurable in the inner but not the outer layer) are 24.2 $\pm$ 8.2 d for carbon and 47.6 $\pm$ 19 d for nitrogen. With this, we hypothesize that tissue samples from humpback whales would reflect foraging activity from at minimum one month prior. It is reasonable to believe that humpback whales would have turnover rates that are similar (or longer) than bottlenose dolphins (Giménez *et al.* 2016). However, the lack of measurable change in stable isotope ratios from hatchery-associated whale skin provided no indicator with which to estimate the time period represented. Thus, it is completely possible that all samples collected represented a period before any hatchery salmon consumption. Continued biopsy sampling of these whales, throughout their northward migration, would certainly help elucidate turnover rates for humpback whales.

That the stable isotope results suggested humpback whales had consumed hatchery-released salmon before salmon were in our study area is plausible, but seems unlikely. Port Armstrong Hatchery (operated by Armstrong-Keta, Inc.) is approximately 104 km south of

Kasnyku Bay. Port Armstrong released approximately 2.9 x 10^8 juvenile salmon (pink and chum) in the spring of 2016 and 6.7 x 10^7 (coho, chum, and pink) juvenile salmon in the spring of 2017 (ADFG 2019b), weeks prior to releases conducted by Hidden Falls Hatchery. These earlier releases and more southern locations may have provided an opportunity for whales to feed on hatchery-released salmon before entering our study area. However, the substantial amount of hatchery salmon estimated in the diets of all whales does not seem probable since only three were observed to be a 'hatchery salmon specialist' during the releases at Hidden Falls Hatchery and given the local, ephemeral availability of hatchery salmon. We believe the most logical explanation for a consistent "hatchery salmon" signature in the tissues of all whales is that we were possibly missing a wild prey source(s) with similar isotopic signatures to the hatchery salmon. Not accounting for all major prey items is problematic when using mixing models to estimate diet compositions. Doing so can bias model results in favor of known prey because proportions must sum to one (Phillips *et al.* 2014). The possibility of hatchery salmon having a similar isotopic composition to an unknown prey taxon makes it difficult to tease out the proportional contributions of hatchery salmon alone. Additionally, without specific incorporation rates for humpback whale skin, we cannot identify the specific time periods the stable isotope data represents.

Identifying all major prey sources was difficult due to little information on where humpback whales were feeding before entering our study area. There is also limited information about the movements of humpback whales in Southeast Alaska. Satellite-monitored radio tags have shown equal probability that observed whales could have entered our study area from the north or south (Mate *et al.* 2007; Witteveen *et al.* 2011). Mean δ^{15}N and δ^{13}C values from our hatchery-associated whales are closest to whales occupying the northern Gulf of Alaska (-17.6‰ ± 0.1, 13.5‰ ± 0.1; Witteveen *et al.* 2009)

and northern British Columbia (-17.6‰ ± 0.1, 12.9‰ ± 0.1; Witteveen *et al.* 2009), further supporting the idea that whales could have traveled into our study area through a northern or southern passage. Stable isotopic signatures of other whales were similar to those residing in Southeast Alaska (-17.1‰ ± 0.1, 12.7‰ ± 0.1; Witteveen *et al.* 2009), providing little information on previous foraging locations. Without fully understanding the location of individual whales before they moved into our given study area, we cannot speculate about feeding areas or prey sources before they were first observed. If we assume that whales observed as part of this study were migrating northward from their breeding grounds in Hawai'i, we could infer that the unknown prey source was potentially offshore krill or some species of forage fish. Offshore prey items tend to have low $\delta^{13}C$ values, which could potentially mask the stable isotopic signature of hatchery salmon, and may account for the missing source in our mixing models (Burton and Koch 1999; Hobson *et al.* 1994; Miller *et al.* 2010). Prey surveys in Southeast Alaska during late winter and early spring would fill this informational void.

1.5.2 Individual Specialization among Hatchery-Associated Whales

We analyzed the stable isotopic composition of humpback whale skin in order to characterize variation within and among individual humpback whale diets in Southeast Alaska. Minimal temporal variability in stable isotopic composition suggested relatively constant diets through the study period or that skin incorporation rates are longer than our sampling period. However, observations of individual hatchery-associated whales illustrated that, even though they share a preference for feeding on hatchery-released juvenile salmon, these whales vary in the degree to which they consume this unique prey source. Each whale arrived at the study area at different times, exhibited different proportions of prey, and

took different approaches on where (release site or surrounding area) they consumed hatchery-reared juvenile salmon.

Of all three hatchery-associated whales, whale #2227 was observed the most at release sites, spending 45% of all observation days at primary release sites. However, in 2017 there was a short observation period of this whale in the study area during the release period, resulting in a relatively short sampling period. This is potentially why we did not see much variation in this animal's diet and there was no evident diet composition shift due to the hatchery-released salmon consumed. Conversely, whale #2571 was only observed feeding at release sites during 10% of all observations. All observations from 2017 took place in Kelp Bay, where large schools of juvenile salmon (hatchery and wild) were consistently present. Whale #2571 appeared to forage on hatchery-released salmon while in adjacent bays and less so at source locations. However, this whales site residency was the highest of all three whales potentially allowing for more consistent consumption of hatchery-released salmon over the study period and resulting in more variation in the whale's diet composition. Whale #2360 was the only whale observed to switch from solo bubble-net feeding on juvenile salmon to group bubble-net feeding on Pacific herring. This behavior change in Whale #2360 is consistent with the isotopic evidence that hatchery-associated whales are forage fish specialist.

1.5.3 Isotopic Incorporation Rate

We attribute variable stable isotope results when measuring for incorporation and turnover rate to differences in sampling time periods among individuals. We found no effect of days post-release on the $\delta^{13}C$ signatures for whale #2227, likely resulting from short observation periods (number of days post-release) in both years. Whale #2360 was

sampled over a much longer time period (45 d post-release in 2016 and 73 d post-release in 2017) and displayed a significant effect of year within the inner layer. Whale #2571 had the longest sampling period (85 d post-release in 2017) and was the only whale to show a significant effect of post-release days (in the inner layer). Significant δ^{13}C-increase occurred between 74 and 85 days post-release. The only published value for humpback whale skin incorporation rate suggests 7 to 14 days (Todd 1997), however there are many discrepancies with this study (*e.g.*, based on anecdotal foraging behavior) and our more rigorous method of repeat sampling the same individual in conjunction with prey data provides a better estimation. Additionally, turnover rate from 74 to 85 days would be closer to turnover rates estimated by Hicks *et al.* (1985) and St. Aubin *et al.* (1990): 73 days for bottlenose dolphins and 70-75 days for beluga whales (70 to 75 d), respectively. Although we sampled whale #2360 on 73 days post-release, the whale did not enter the study area until 14 days post-release. Thus, this whale was observed to only have up to 59 days to consume hatchery-release salmon, whereas whale #2571 was in the study area and presumable able to consume hatchery-reared salmon within the study area for a full 85 days. With this, we conclude that previous incorporation rates for humpback whales (7 to14 d; Todd 1997) were vastly underestimated. We believe that the significant δ^{13}C-increase from whale #2571 between 74 to 85 days is a much closer approximation of incorporation rate for humpback whale skin; however, continued tissue collection beyond this timeframe would provide corroboration.

1.5.4 Conclusions

Three whales were found to incorporate hatchery-released juvenile salmon into their diets in Chatham Strait, though individuals varied in the degree to which they consumed this

particular prey type. Even though we were not able to provide an estimate of the proportion contribution of hatchery salmon to these individuals' diet, we were able to observe and document a substantial amount of predation on salmon occurring beyond the release sites. This provides more insight into the impact this predator is having on this important marine resource. Overall, we found that hatchery-associated whales fed at higher trophic levels than other whales in the area, suggesting some level of specialization in foraging behavior. The hatchery-associated whale that was sampled over the longest time period displayed an isotopic shift, potentially indicating a stable isotope incorporation rate of 74 to 85 days in humpback whale skin. Continued sampling of the same individual (and multiple individuals) over a broader temporal scale would increase our confidence in this effort and provide a better understanding about the temporal movement of stable isotopes through cetacean tissue. Our direct observations of forage behavior paired with repeated sampling provided further insight into the foraging ecology of humpback whales.

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1.7 References

ADFG. 2019a. Anadromous waters catalog: interactive mapping. Retrieved from: https://www.adfg.alaska.gov/sf/SARR/AWC/index.cfm?ADFG=main.interactive.

ADFG. 2019b. Hatchery release report form. Retrieved from: https://mtalab.adfg.alaska.gov/CWT/reports/hatcheryrelease.aspx.

Barlow, J., Calambokidis, J., Baker, S. C., Burdin, A. M., Clapham, P. J., Ford, J. K. B., *et al.* Yamaguchi, M. 2011. Humpback whale abundance in the North Pacific estimated by photographic capture-recapture with bias correction from simulation studies. Marine Mammal Science. 27(October):793–818.

Beamish, R. J. and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography. 49(1–4):423–437.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., and Forister, M. L. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist. 161(1):1–28.

Borrell, A., Abad-Oliva, N., Gõmez-Campos, E., Giménez, J., and Aguilar, A. 2012. Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. Rapid Communications in Mass Spectrometry. 26(14):1596–1602.

Bowen, W. D., and Iverson, S. J. 2013. Methods of estimating marine mammal diets: a review of validation experiments and sources of bias and uncertainty. Marine Mammal Science. 29(4):719–754.

Burton, R. K., and Koch, P. L. 1999. Isotopic tracking of foraging and long-distance Migration in Northeastern Pacific Pinnipeds. 119:578–585.

Busquets-Vass, G., Newsome, S. D., Calambokidis, J., Serra-Valente, G., Jacobsen, J. K., Aguíñiga-García, S., and Gendron, D. 2017. Estimating blue whale skin isotopic incorporation rates and baleen growth rates: implications for assessing diet and movement patterns in Mysticetes. PLoS ONE. 12(5). doi: 10.1371/journal.pone.0177880

Chenoweth, E. M. and Criddle, K. R. 2019. The Economic impacts of humpback whale depredation on hatchery-released juvenile Pacific salmon in Southeast Alaska. Marine and Coastal Fisheries. 11(1),:62–75.

Chenoweth, E. M., Straley, J. M., McPhee, M. V., Atkinson, S., and Reifenstuhl, S. 2017. Humpback whales feed on hatchery-released juvenile salmon. Royal Society Open Science. 4(7):170180.

Clarke, K. R., Warwick, R. M., and Brown, B. E. 1993. An index showing breakdown of seriation, related to disturbance, in a coral-reef assemblage. Marine Ecology Progress Series. 102(1–2):153–160.

Croll, D. A., Tershy, B. R., Hewitt, R. P., Demer, D. A., Fiedler, P. C., Smith, S. E., *et al.* Gendron, D. 1998. An integrated approach to the foraging ecology of marine birds and mammals. Deep-Sea Research Part II: Topical Studies in Oceanography. 45(7):1353–1371.

Deniro, M. J. and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta. 42:495–506.

Di Lorenzo, E. and Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nature Climate Change. 6(11):1042–1047.

Fleming, A. H., Clark, C. T., Calambokidis, J., and Barlow, J. 2016. Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. Global Change Biology. 22(3):1214–1224.

Folch, J., Less, M., and Stanley, S. G. H. 1956. A simple method for the isolation and purification of total lipids from animal tissues. Journal of Biological Chemistry. 226(1):497–509.

Fry, B. 2006. Stable Isotope Ecology. New York, NY. Springer. 308 pp.

Furey, N. B., Hinch, S. G., Bass, A. L., Middleton, C. T., Minke-Martin, V., and Lotto, A. G. 2016. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. Journal of Animal Ecology. 85:948–959.

Giménez, J., Ramírez, F., Almunia, J., Forero, M. G., and de Stephanis, R. 2016. From the pool to the sea: applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). Journal of Experimental Marine Biology and Ecology. 475:54–61.

Hartt, A. 1980. Juvenile salmonids in the oceanic ecosystem: the critical first summer. In W. J. McNeil and D. C. Himsworth (eds.). Salmonid Ecosystems of the North Pacific. Corvallis, OR. Oregon State University Press. 25–57.

Heard, W. 2001. Alaska salmon enhancement: a successful program for hatchery and wild stocks. In 30th Joint Meeting of the United States-Japan Cooperative Program in Natural Resources. January 2001:149–169.

Heard, W. R. 2012. Overview of salmon stock enhancement in southeast Alaska and compatibility with maintenance of hatchery and wild stocks. Environmental Biology of Fishes. 94(1):273–283.

Hicks, B. D., St. Aubin, D. J., Geraci, J. R., and Brown, W. R. 1985. Epidermal growth in the bottlenose dolphin, *Tursiops truncatus*. The Journal of Investigative Dermatology. 85(1):60–63.

Hobson, K. A. and Clark, R. G. 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. The Condor. 94(1):181–188.

Hobson, K. A., Piattt, J. F., and Pitocchellij, J. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology. 63(4):786–798.

Ingebrigtsen, A. 1929. Whales caught in the North Atlantic and other seas. Rapports et Process-Verbaux Des Réunion Conseil International Exploration de La Mer. 56:1–26.

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

Katona, S., Baxter, B., Brazier, O., Kraus, S., Perkins, J., and Whitehead, H. 1979. Identification of humpback whales by fluke photographs. *In* H. E. Winn and B. L. Olla (eds.). Behavior of Marine Animals. New York, NY. Plenum Press. 33–44.

Kosma, M. M., Werth, A. J., Szabo, A. R., and Straley, J. M. 2019. 2019. Pectoral herding: an innovative tactic for humpback whale foraging. Royal Society Open Science. 6(10):191104. doi:10.1098/rsos.191104.

Logan, J. M., Jardine, T. D., Miller, T. J., Bunn, S. E., Cunjak, R. A., and Lutcavage, M. E. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. Journal of Animal Ecology. 77(4):838–846.

Logan, J. M. and Lutcavage, M. E. 2008. A comparison of carbon and nitrogen stable isotope ratios of fish tissues following lipid extractions with non-polar and traditional chloroform/methanol solvent systems. Rapid Communications in Mass Spectrometry. 22(7):1081–1086.

McMillan, C. J., Towers, J. R., and Hildering, J. 2018. The innovation and diffusion of “trap-feeding”, a novel humpback whale foraging strategy. Marine Mammal Science. 35(3):779–796.

McNeil, W. J. and Himsworth, D. C. 1980. Salmonid ecosystems of the North Pacific. Corvallis, OR. Oregon State University Press. 331 pp.

Miller, T. W., Brodeur, R. D., Rau, G., and Omori, K. 2010. Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Marine Ecology Progress Series. 420:15–26.

Monteiro, S., Ferreira, M., Vingada, J. V., López, A., Brownlow, A., and Méndez-Fernandez, P. 2015. Application of stable isotopes to assess the feeding ecology of long-finned pilot whale (*Globicephala melas*) in the Northeast Atlantic Ocean. Journal of Experimental Marine Biology and Ecology. 465:56–63.

Moore, J. W. and Semmens, B. X. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters. 11(5):470–480.

Murry, B. A., Farrell, J. M., Teece, M. A., and Smyntek, P. M. 2006. Effect of lipid extraction on the interpretation of fish community trophic relationships determined by stable carbon and nitrogen isotopes. Canadian Journal of Fisheries and Aquatic Sciences. 63(10):2167–2172.

Nelson, M. A., Quakenbush, L. T., Mahoney, B. A., Taras, B. D., and Wooller, M. J. (2018). Fifty years of Cook Inlet beluga whale feeding ecology from isotopes in bone and teeth. Endangered Species Research. NOAA. 36(2000):77–87.

Newsome, S. D., Clementz, M. T., and Koch, P. L. 2010. Using stable isotope biogeochemistry to study marine mammal ecology. Marine Mammal Science. 26(3):509–572.

Palsboll, P. J., Larsen, F., and Hansen, E. S. 1991. Sampling of skin biopsies from free-ranging large cetaceans in West Greenland: development of new biopsy tips and bolt designs. Report of the International Whaling Commission, Special Issue. 13:71–79.

Parks, S. E., Cusano, D. A., Stimpert, A. K., Weinrich, M. T., Friedlaender, A. S., and Wiley, D. N. 2014. Evidence for acoustic communication among bottom foraging humpback whales. Scientific Reports. 4:1–7.

Phillips, D. L. and Gregg, J. W. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia. 127(2):171–179.

Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., *et al.* Ward, E. J. 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology. 92:823–835.

Piatt, J. F. and Methven, D. A. 1992. Threshold foraging behavior of baleen whales. Marine Ecology Progress Series. 84(3):205–210.

Pierce, G. J., Santos, M. B., and Cerviño, S. 2007. Assessing sources of variation underlying estimates of cetacean diet composition: a simulation study on analysis of harbour porpoise diet in Scottish (UK) waters. Journal of the Marine Biological Association of the United Kingdom, 87(1):213–221.

Pigliucci, M. 2005. Evolution of phenotypic plasticity: Where are we going now? Trends in Ecology and Evolution. 20(9):481–486.

Pintor, L. M. and Byers, J. E. 2015. Individual variation in predator behavior and demographics affects consumption of non-native prey. Behavioral Ecology. 26(3):797–804.

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., and Montaña, C. G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia. 152(1):179–189.

Rau, A. G. H., Mearns, A. J., Young, D. R., Olson, R. J., and Schafer, H. A. 2016. Animal 13C/ 3C correlates with trophic level in pelagic food webs. Ecology. 64(5):1314–1318.

Reiner, J. M. 1953. The study of metabolic turnover rates by means of isotopic tracers. Archives of Biochemistry and Biophysics. 46(1):53–79.

Ryan, C., McHugh, B., Trueman, C. N., Harrod, C., Berrow, S. D., and O'Connor, I. 2012. Accounting for the effects of lipids in stable isotope ($\delta^{13}C$ and $\delta^{15}N$ values) analysis of skin and blubber of balaenopterid whales. Rapid Communications in Mass Spectrometry. 26(23):2745–2754.

Scheel, D. and Hough, K. R. 1997. Salmon fry predation by seabirds near an Alaskan hatchery. Marine Ecology Progress Series. 150:35–48.

Sharpe, F. A. 2001. Social foraging of the southeast Alaskan humpback whale, *Megaptera novaeangliae*. PhD Dissertation, Simon Fraser University. 129 pp.

St. Aubin, D. J., Smith, T. G., and Geraci, J. R. 1990. Seasonal epidermal molt in beluga whales, *Delphinapterus leucas*. Canadian Journal of Zoology. 68(2):359–367.

Straley, J. M. and Gabriele, C. M. 2000. Humpback whales of southeast Alaska. Humpback whale fluke identification catalog. Third printing. Gustavus, Alaska.

Sweeting, C. J., Polunin, N. V. C., and Jennings, S. 2006. Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rapid Communications in Mass Spectrometry. 20(4):595–601.

Thomas, S. M. and Crowther, T. W. 2015. Predicting rates of isotopic turnover across the animal kingdom: a synthesis of existing data. Journal of Animal Ecology. 84(3):861–870.

Tieszen, L. L., Boutton, T. W., Tesdahl, K. G., and Slade, N. A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ Analysis of Diet. Oecologia. 57:32–37.

Todd, S. K. 1997. Dietary patterns of humpback whales (*Megaptera novaeangliae*) in the northwest Atlantic: evidence from $\delta^{13}C$ and $\delta^{15}N$ stable isotopes. PhD Dissertation, Memorial University of Newfoundland. 175 pp.

Todd, S., Ostrom, P., Lien, J., and Abrajano, J. 1997. Use of biopsy samples of humpback whale (*Megaptera novaeangliae*) skin for stable isotope ($\delta^{13}C$) determination. Journal of Northwest Atlantic Fishery Science. 22(1997):71–76.

Tomida, Y., Suzuki, T., Yamada, T., Asami, R., Yaegashi, H., Iryu, Y., and Otake, T. 2014. Differences in oxygen and carbon stable isotope ratios between hatchery and wild pink salmon fry. Fisheries Science. 80:273–280.

Trites, A. W., Christensen, V., and Pauly, D. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. Journal of Northwest Atlantic Fishery Science. 22:173–187.

Voigt, C. C., Matt, F., Michener, R., and Kunz, T. H. 2003. Low turnover rates of carbon isotopes in tissues of two nectar-feeding bat species. Journal of Experimental Biology. 206(8):1419–1427.

Volk, E. C., Schroder, S. L., and Grimm, J. J. 1999. Otolith thermal marking. Fisheries Research. 43:205–219.

Ware, C., Wiley, D. N., Friedlaender, A. S., Weinrich, M., Hazen, E. L., Bocconcelli, A., *et al.* Abernathy, K. 2014. Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, U.S.A. Marine Mammal Science. 30(2):494–511.

Weinrich, M.T., Lambertsen, R. H., Baker, C. S., Schilling, M. R., and Belt, C. R. 1991. Behavioural responses of humpback whales (*Megaptera novaeangliae*) in the Southern Gulf of Maine to biopsy sampling. Report of the International Whaling Commission, Special Issue. 13:91–97.

Weinrich, Mason T., Schilling, M. R., and Belt, C. R. 1992. Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. Animal Behaviour. 44(6):1059–1072.

Wild, L. A., Chenoweth, E. M., Mueter, F. J., and Straley, J. M. 2018. Evidence for dietary time series in layers of cetacean skin using stable carbon and nitrogen isotope ratios. Rapid Communications in Mass Spectrometry. 32(16):1425–1438.

Witteveen, Briann H., Foy, R. J., and Wynne, K. M. 2006. The effect of predation (current and historical) on fish abundance near Kodiak Island , Alaska. Fishery Bulletin. 104:10–20.

Witteveen, B. H. 2008. Using stable isotopes to assess population structure and feeding ecology of North Pacific humpback whales (*Megaptera novaeangliae*). PhD Disseration, University of Central Florida. 144 pp.

Witteveen, B. H., Worthy, G. A. J., and Roth, J. D. 2009. Tracing migratory movements of breeding North Pacific humpback whales using stable isotope analysis. Marine Ecology Progress Series. 393:173–183.

Witteveen, Briana H., Worthy, G. A. J., Wynne, K. M., Hirons, A. C., Andrews, A. G., and Markel, R. W. 2011. Trophic levels of North Pacific Humpback whales (*Megaptera novaeangliae*) through analysis of stable isotopes: implications on prey and resource quality. Aquatic Mammals. 37(2):101–110.

Witteveen, Briana H., Worthy, G. A. J., Foy, R. J., and Wynne, K. M. 2012. Modeling the diet of humpback whales: An approach using stable carbon and nitrogen isotopes in a Bayesian mixing model. Marine Mammal Science. 28(3):233–250.

Witteveen, Briana H., De Robertis, A., Guo, L., and Wynne, K. M. 2015. Using dive behavior and active acoustics to assess prey use and partitioning by fin and humpback whales near Kodiak Island, Alaska. Marine Mammal Science. 31(1):255–278.

Witteveen, Briana H., and Wynne, K. M. 2016. Trophic niche partitioning and diet composition of sympatric fin (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*) in the Gulf of Alaska revealed through stable isotope analysis. Marine Mammal Scienc. 32(4):1319–1339.

Wood, S.N. 2006. Generalized additive models: an introduction with R. Second Edition. Boca Raton, Florida. CRC Press. 496 pp.

Wood, Simon N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society. Series B: Statistical Methodology. 73(1):3–36.

Zilversmit, D. B., Entenman, C., and Fishler, M. C. 1943. On the calculation of “turnover time” and “turnover rate” from experiments involving the use of labeling agents. The Journal of General Physiology. 26(3):325–331.

1.8 Figures

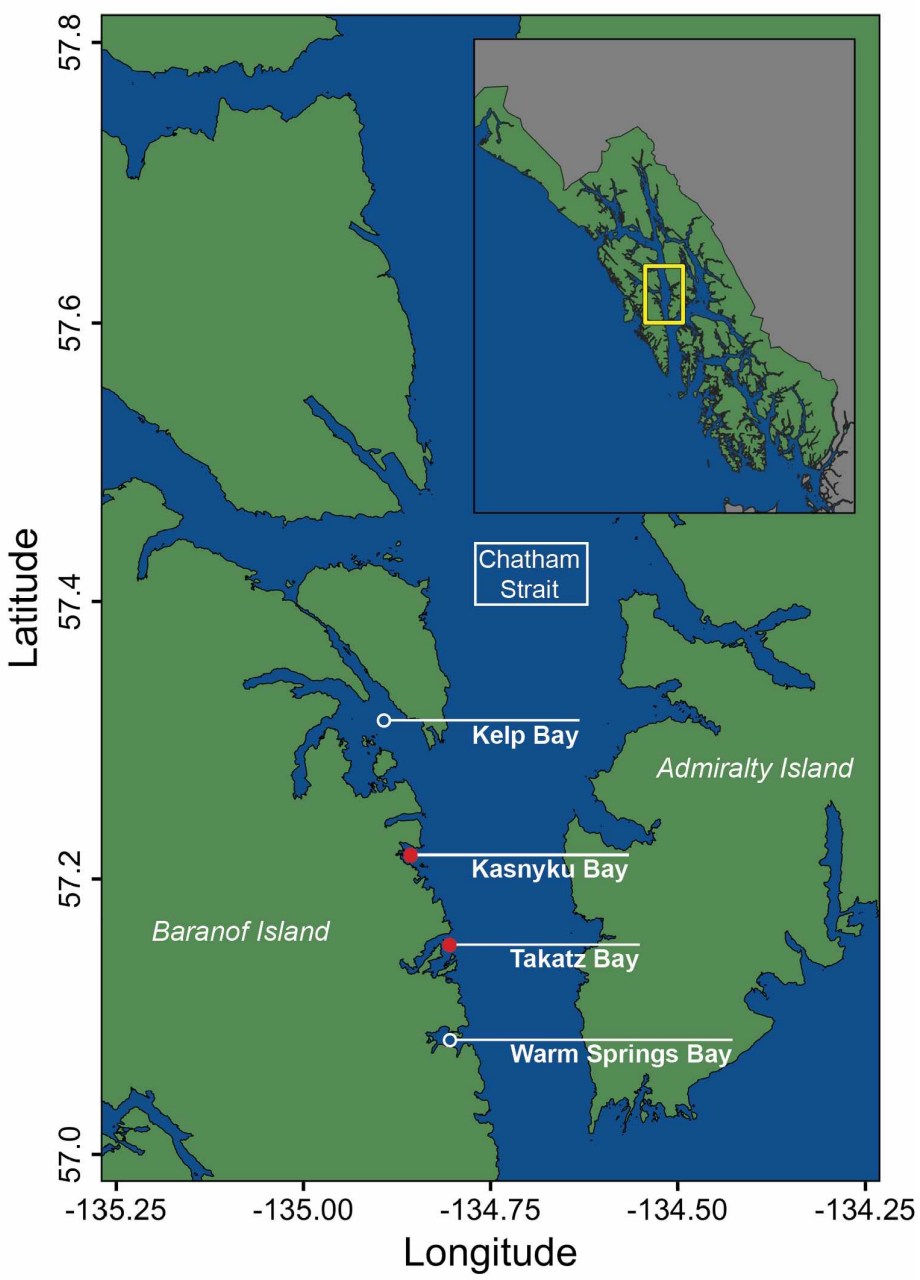

Figure 1.1. Map of study site (Southeast Alaska, 2016 to 2017). Red dots indicate release sites for Hidden Falls Hatchery.

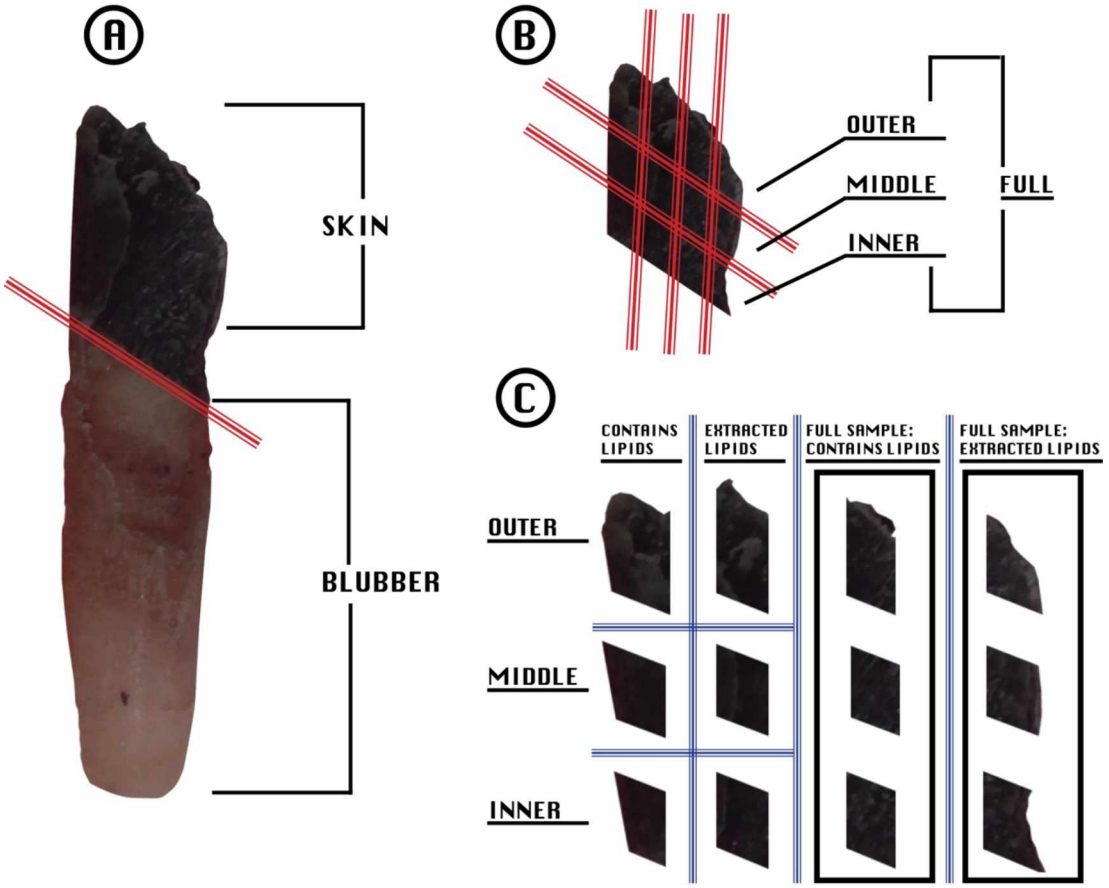

Figure 1.2. Diagram for sample processing of humpback whale biopsies. A: Complete biopsy sample, illustrating distinct skin and blubber components; B: Full skin sample, separated into outer, middle, and inner layers and subsamples for each layer (red lines denote locations where samples were sectioned), C: Subsampling scheme for stable isotope analysis, illustrating individual layers and sample types (*i.e.*, pre- and post-lipid extraction).

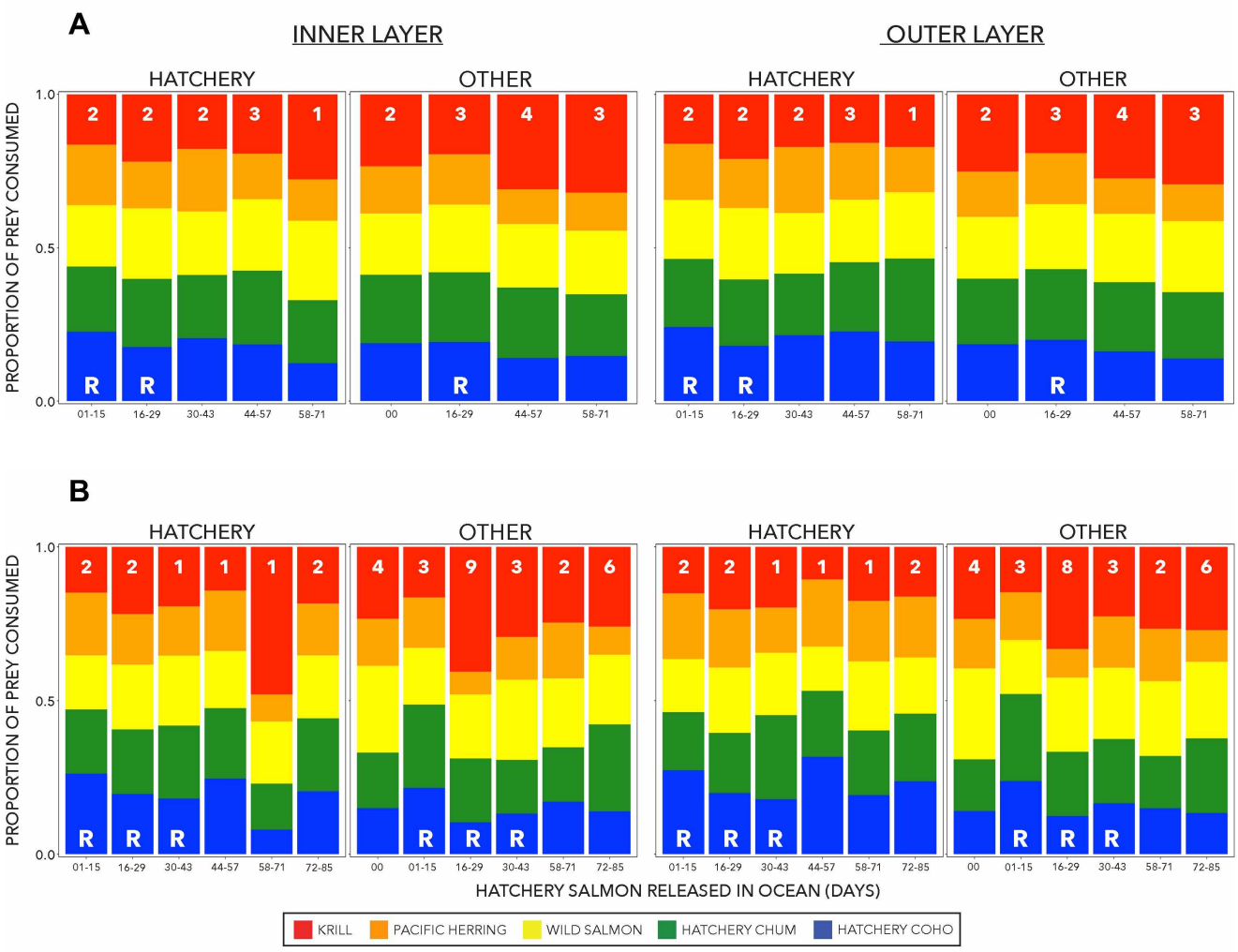

Figure 1.3. Proportions of prey estimated from Bayesian mixing models, by year (A: 2016 and B: 2017), layer (left: inner; right: outer), whale type (*i.e.*, hatchery-associated, 'hatchery' and other whales), and biweekly period. White numbers represent the number of whales (n) for each time period. "R" denotes time periods with active releases.

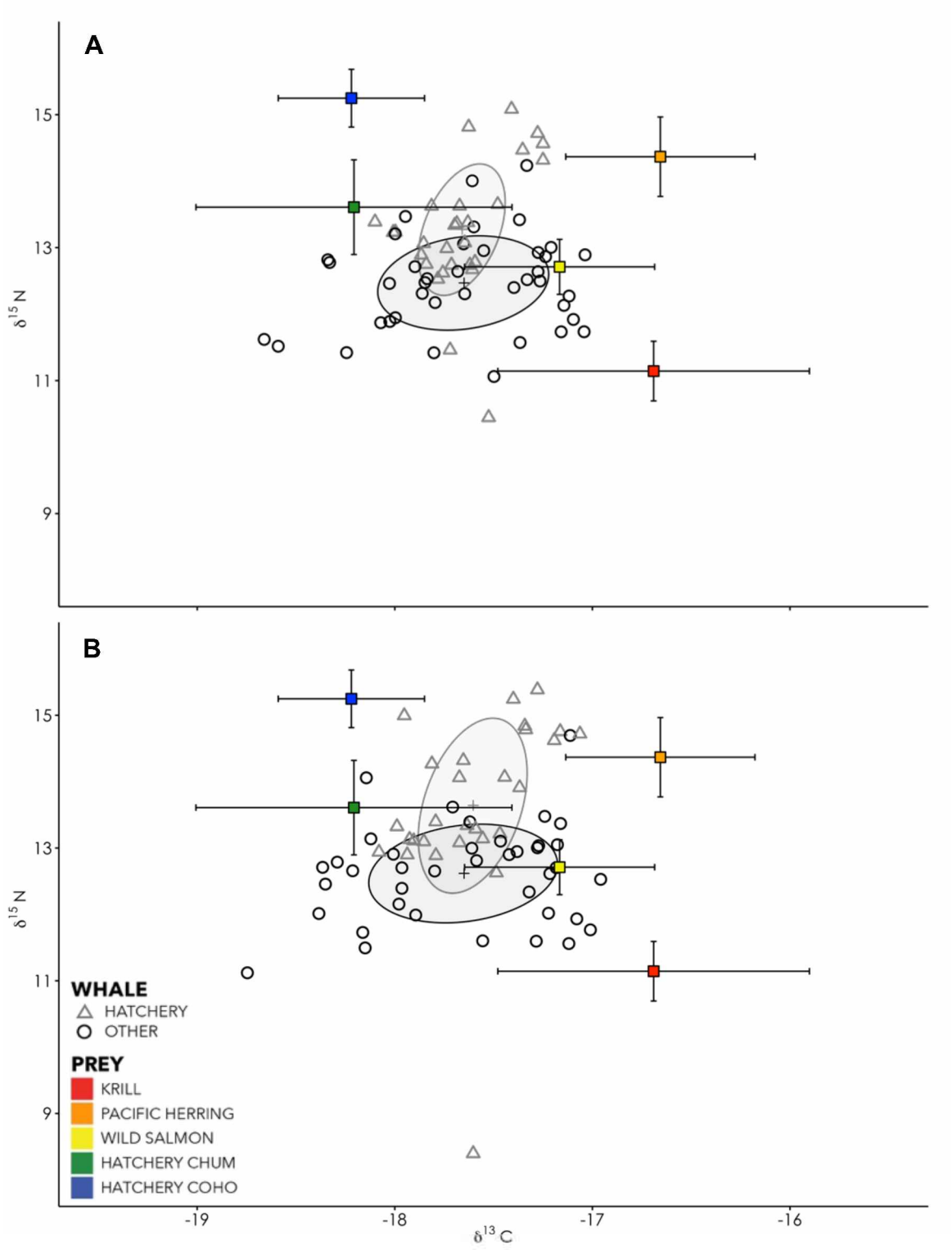

Figure 1.4. Bi-plot showing $\delta^{13}C$ and $\delta^{15}N$ values from the inner (A) and outer (B) layers of all humpback whale skin samples (Southeast Alaska, 2016 and 2017), by whale type (hatchery-associated, triangles; other, circles). Isotopic values for prey sources are also shown adjusted with trophic enrichment factors. Ellipses represent 95% confidence intervals.

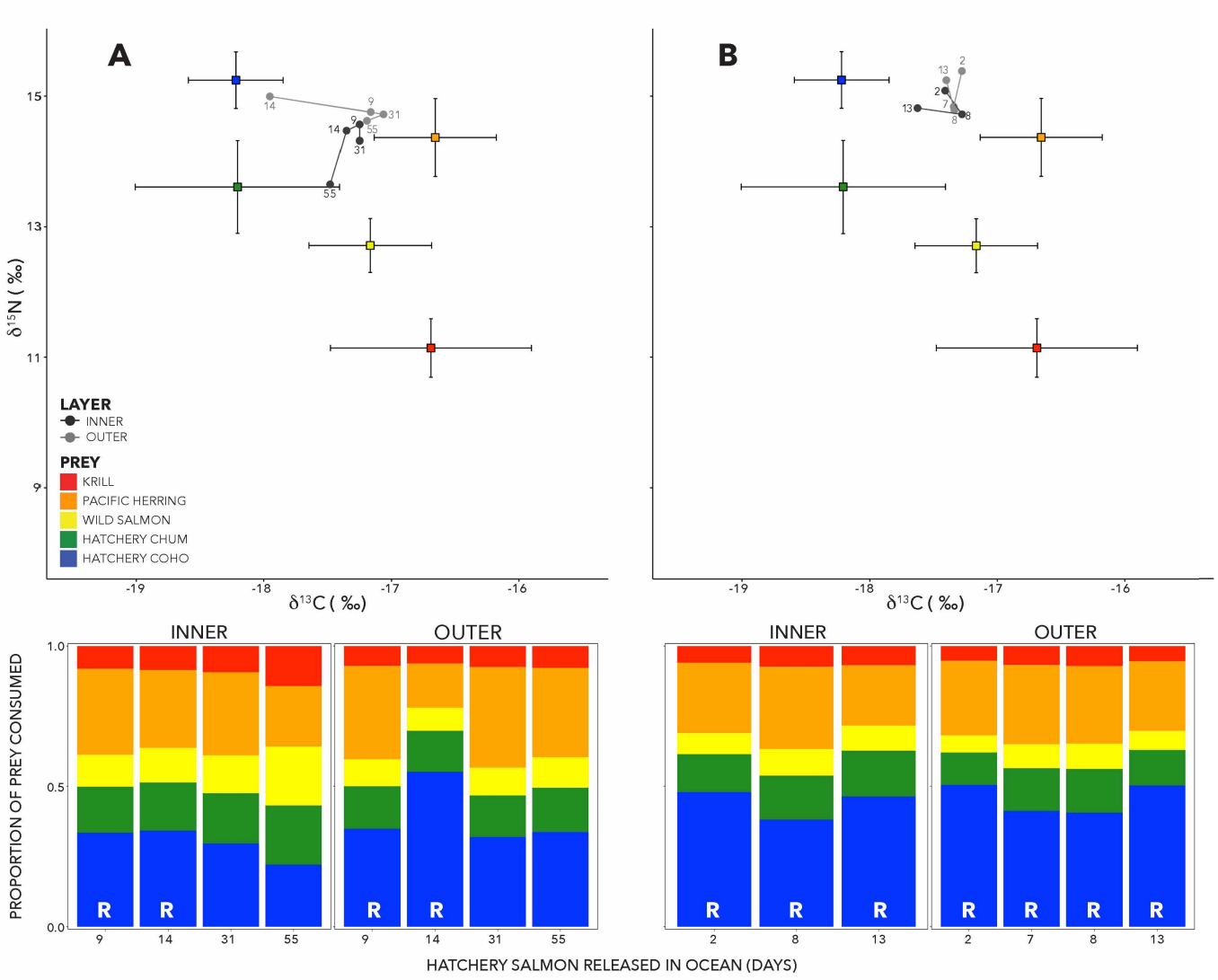

Figure 1.5. Stable isotope biplots (above) and proportions of prey consumed (as estimated from Bayesian mixing models; below) for hatchery-associated whale #2227, by year (A: 2016; B: 2017) and skin layer (*i.e.*, inner and outer). Numbers in biplots indicate the number of post-release days. "R" represents the active hatchery release window for each year. Prey sources are adjusted with trophic enrichment factors.

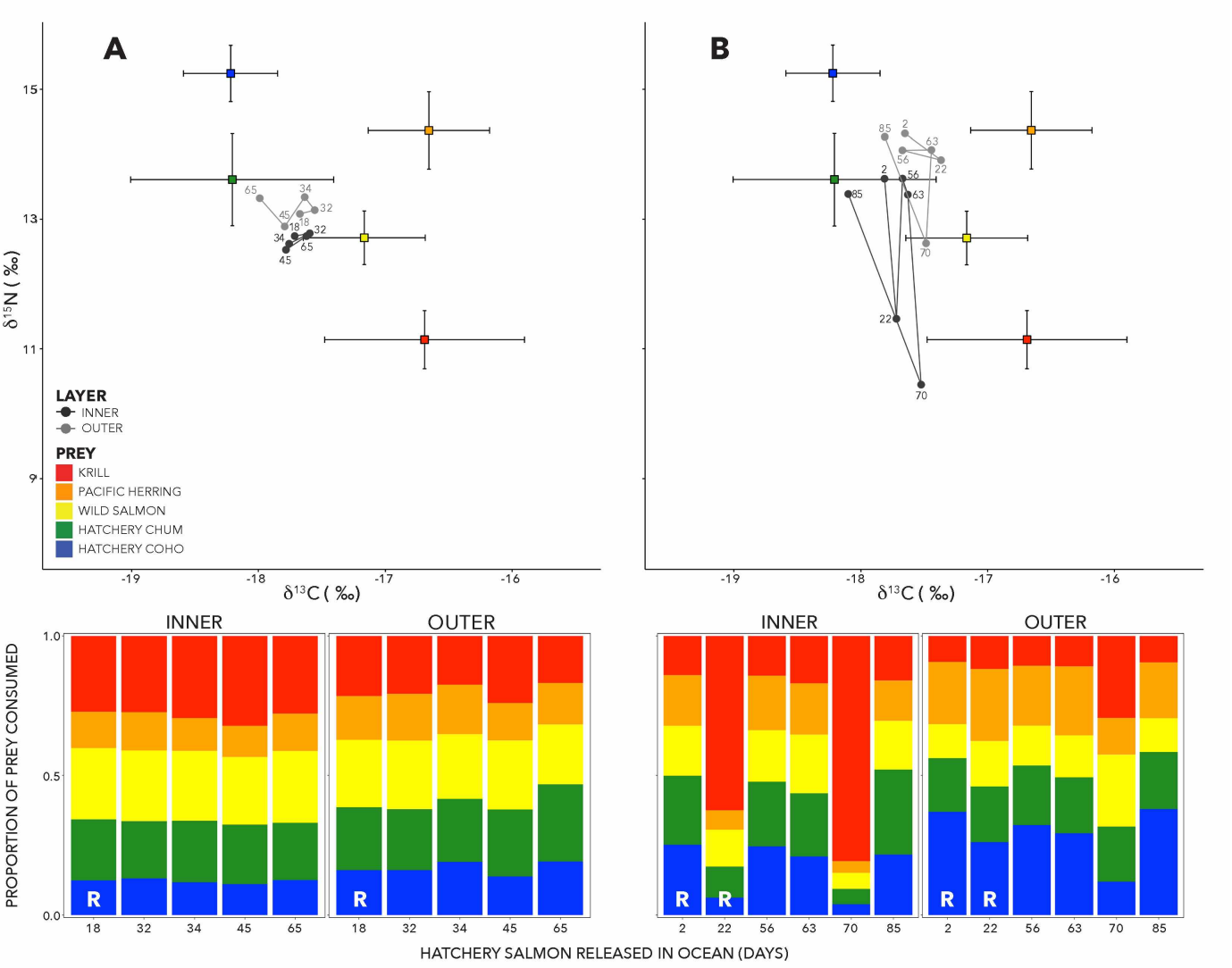

Figure 1.6. Stable isotope biplots (above) and proportions of prey consumed (as estimated from Bayesian mixing models; below) for hatchery-associated whale #2571, by year (A: 2016; B: 2017) and skin layer (*i.e.*, inner and outer). Numbers in biplots indicate the number of post-release days. "R" represents the active hatchery release window for each year. Prey sources are adjusted with trophic enrichment factors.

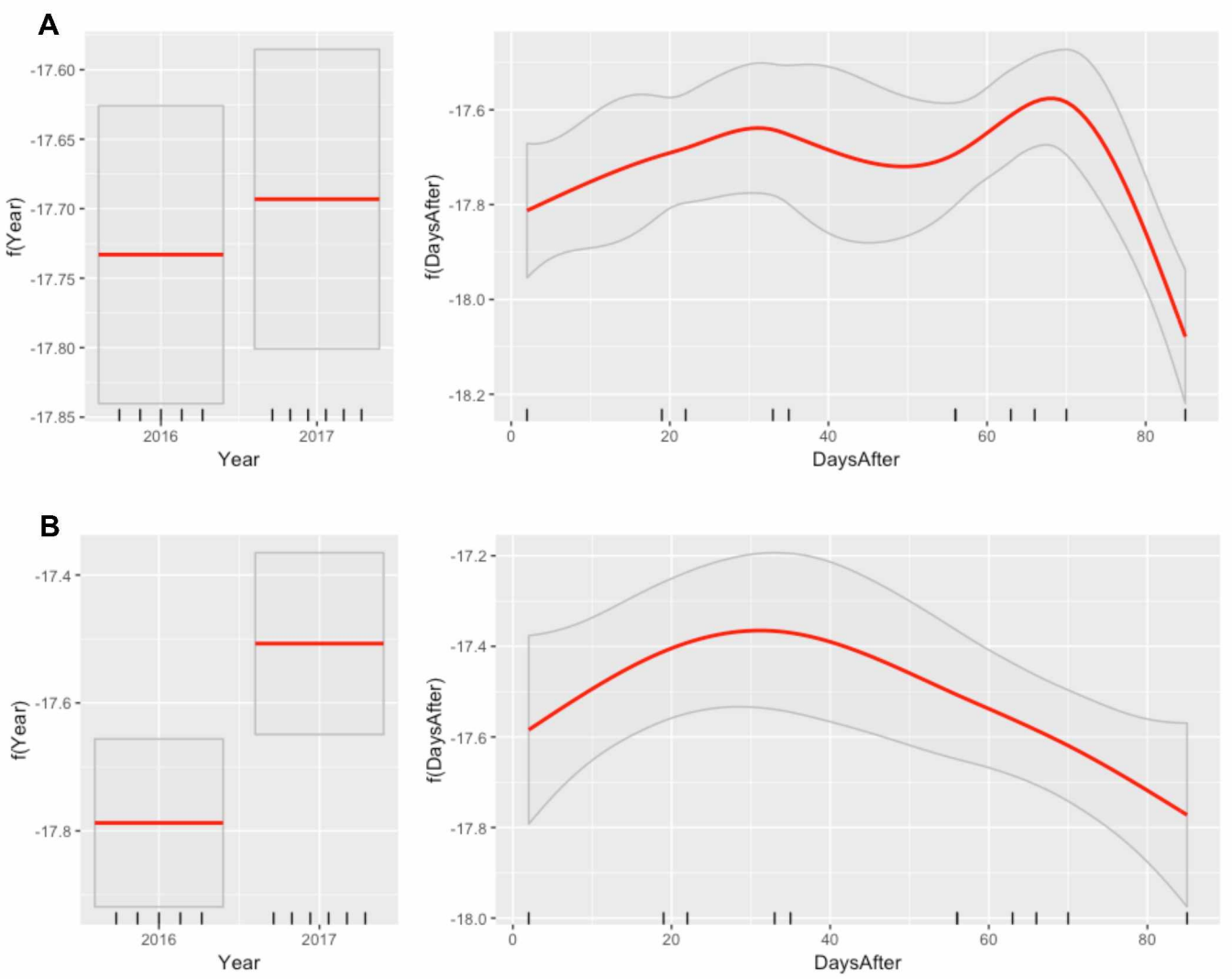

Figure 1.7. Partial effects of year and number of post-release days (*i.e.,* Days After) on $\delta^{13}C$ for hatchery-associated whale #2571. Generalized additive model results pertain to the inner (A) and outer (B) layers of the skin. There was a significant effect of number of post-released days in inner layer and year in the outer layer. Black tick marks denote the timing of each biopsy.

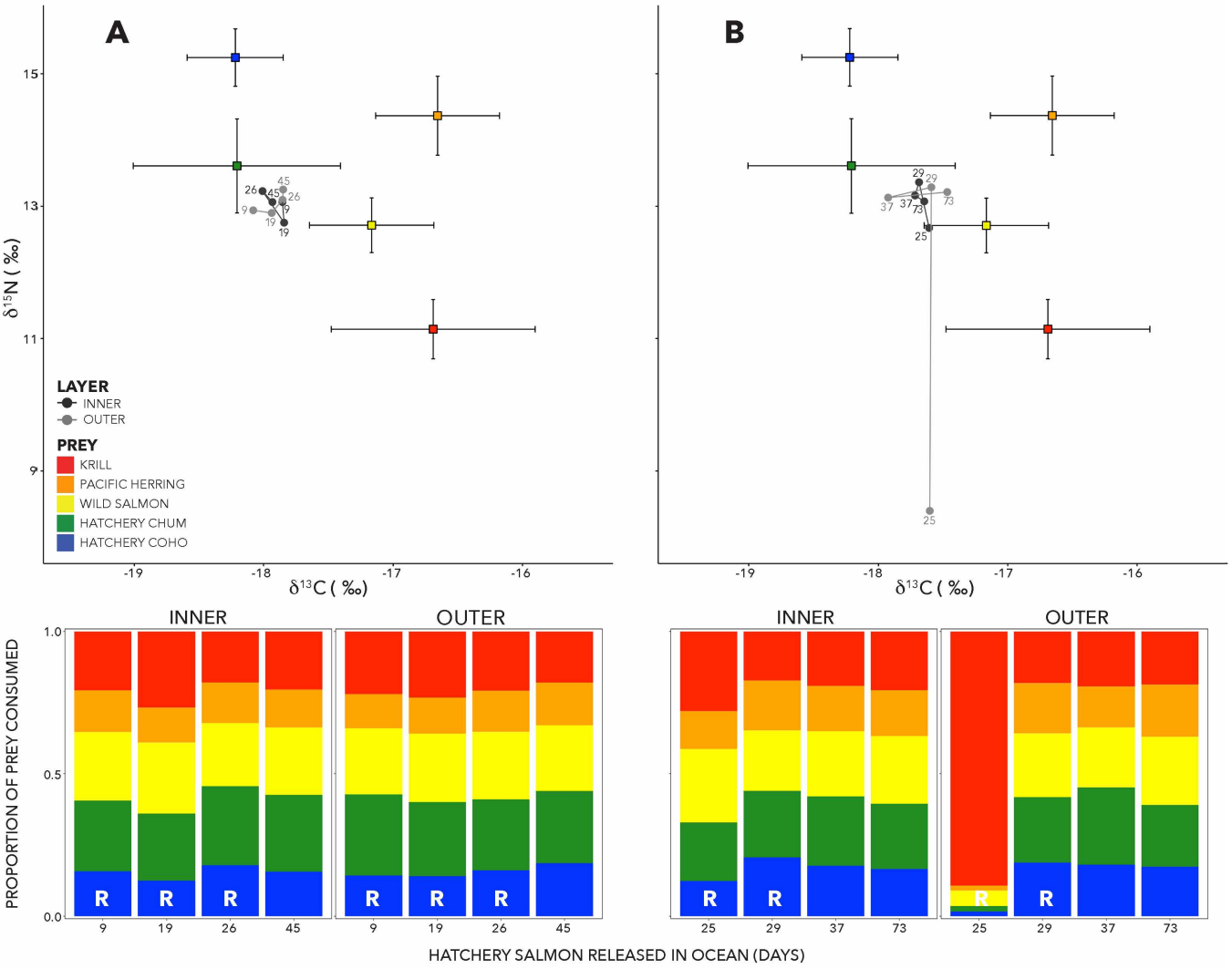

Figure 1.8. Stable isotope biplots (above) and proportions of prey consumed (as estimated from Bayesian mixing models; below) for hatchery-associated whale #2360, by year (A: 2016; B: 2017) and skin layer (*i.e.*, inner and outer). Numbers in biplots indicate the number of post-release days. "R" represents the active hatchery release window for each year. Prey sources are adjusted with trophic enrichment factors.

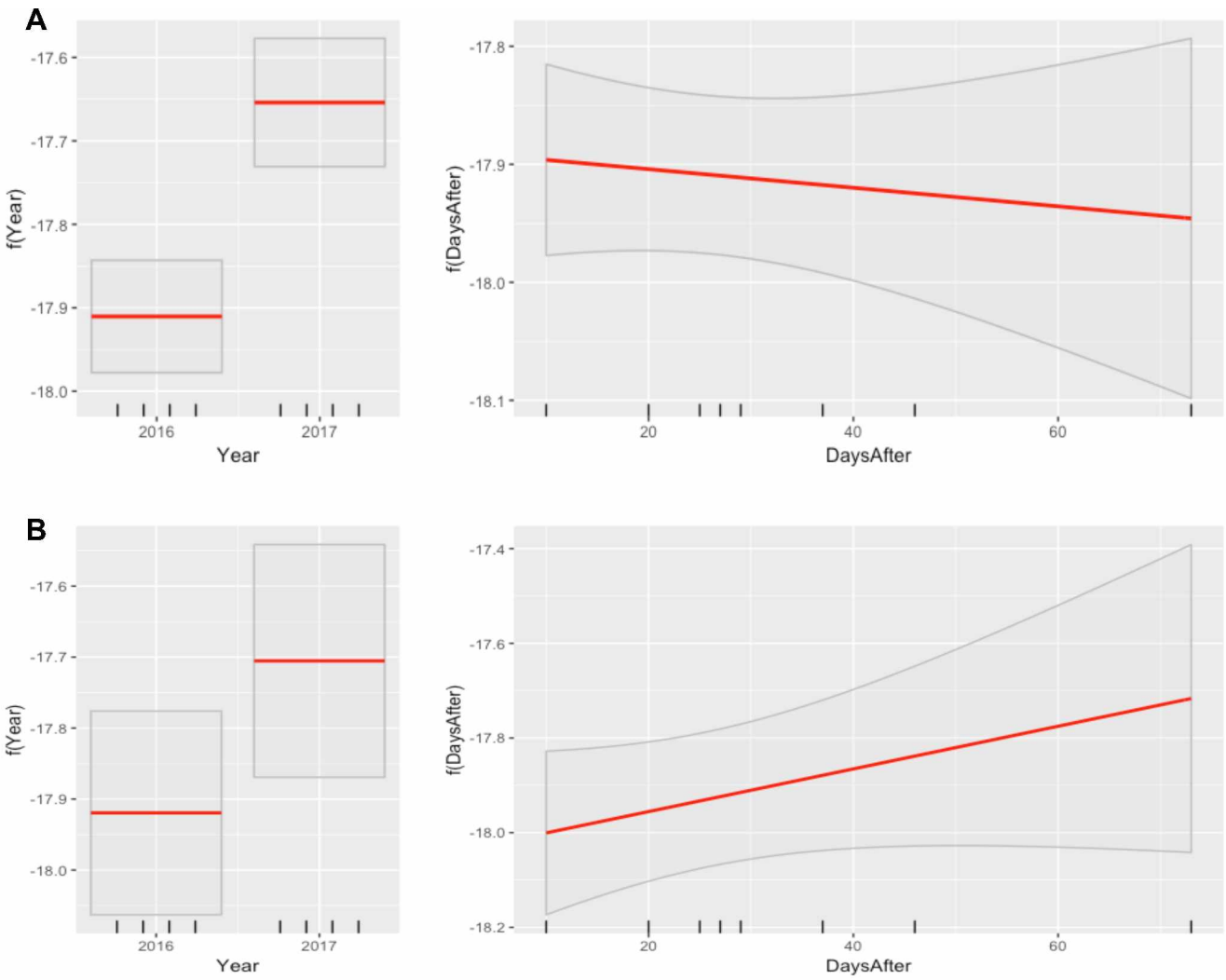

Figure 1.9. Partial effects of year and number of post-release days (*i.e.,* Days After) on $\delta^{13}C$ for hatchery-associated whale #2360. Generalized additive model results pertain to the inner (A) and outer (B) layers of the skin. There was a significant effect of year in the inner layer. Black tick marks denote the timing of each biopsy.

1.9 Tables

Table 1.1. Sample size and mean (± standard deviation) stable isotope ratios (‰) for each prey group sampled in Southeast Alaska (2016 to 2017).

Prey Group	n	$\delta^{13}C$ ± SD (‰)	$\delta^{15}N$ ± SD (‰)
Hatchery Chum Salmon (*Oncorhynchus keta*)	99	-19.1 ± 0.8	10.4 ± 0.7
Hatchery Coho Salmon (*Oncorhynchus kisutch*)	27	-19.1 ± 0.4	12.0 ± 0.4
Wild Salmon (*Oncorhynchus spp.)*	19	-18.1± 0.5	9.5 ± 0.4
Pacific Herring (*Clupea pallasii*)	30	-17.6 ± 0.5	11.2 ± 0.6
Krill (*Euphausiacea spp.)*	3	-17.6 ± 0.8	7.9 ± 0.4

Table 1.2. Sample size (n), mean (± standard deviation) stable isotope ratios (‰), mean (± standard deviation) trophic level (TL), and range of hatchery salmon in the diets of humpback whales, by year, group (*i.e.*, other and hatchery), and skin layer (A: inner; B: outer). Estimates are also shown for individual hatchery-associated whales #2227, 2571, and 2360.

A)

	Year	n	$\delta^{13}C$	$\delta^{15}N$	TL	Prop. of Hatchery Salmon Min	Prop. of Hatchery Salmon Max
Other	both	41	-17.7 ± 0.4	12.5 ± 0.7	5.0 ± 0.3	0.343 ± 0.3	0.413 ± 0.3
Hatchery	both	26	-17.7 ± 0.2	13.3 ± 1.0	5.3 ± 0.4	0.331 ± 0.2	0.437 ± 0.3
2227	2016	4	-17.3 ± 0.1	14.3 ± 0.4	5.7 ± 0.2	0.435 ± 0.3	0.509 ± 0.3
	2017	3	-17.4 ± 0.2	14.9 ± 0.2	6.0 ± 0.1	0.534 ± 0.4	0.614 ± 0.4
2571	2016	5	-17.7 ± 0.1	12.7 ± 0.1	5.1 ± 0.0	0.333 ± 0.2	0.377 ± 0.2
	2017	6	-17.7 ± 0.2	12.7 ± 1.4	5.1 ± 0.6	0.093 ± 0.1	0.522 ± 0.3
2360	2016	4	-17.9 ± 0.1	13.0 ± 0.2	5.2 ± 0.1	0.357 ± 0.2	0.457 ± 0.3
	2017	4	-17.7 ± 0.1	13.1 ± 0.3	5.2 ± 0.1	0.334 ± 0.2	0.437 ± 0.3

B)

Other	both	39	-17.7 ± 0.5	12.6 ± 0.7	5.0 ± 0.3	0.355 ± 0.3	0.428 ± 0.3
Hatchery	both	27	-17.6 ± 0.3	13.6 ± 1.3	5.5 ± 0.6	0.401 ± 0.3	0.471 ± 0.3
2227	2016	4	-17.3 ± 0.4	14.8 ± 0.2	5.9 ± 0.1	0.473 ± 0.4	0.691 ± 0.4
	2017	4	-17.3 ± 0.1	6.1 ± 0.1	6.1 ± 0.1	0.554 ± 0.4	0.628 ± 0.4
2571	2016	5	-17.7 ± 0.2	13.2 ± 0.2	5.3 ± 0.1	0.375 ± 0.3	0.463 ± 0.3
	2017	6	-17.6 ± 0.2	13.9 ± 0.6	5.6 ± 0.3	0.464 ± 0.3	0.586 ± 0.3
2360	2016	4	-17.9 ± 0.1	13.1 ± 0.2	5.2 ± 0.1	0.396 ± 0.3	0.437 ± 0.3
	2017	4	-17.6 ± 0.2	12.0 ± 2.4	4.8 ± 1.0	0.037 ± 0.0	0.452 ± 0.3

Table 1.3. Results from generalized additive models used to quantify effects of year and number of post-release days on $\delta^{13}C$ for samples obtained from both inner and outer layers of the skin from hatchery-associated whale #2227. Parameter estimates, standard errors (SE), t values, and p-values are indicated for factors (*i.e.,* year and whale type). Effective degrees of freedom (edf), Ref.df, F values, and p-values are shown for the smoothed variable (*i.e.,* number of post-release [PR] days). Deviance explained (Dev., %), adjusted R^2, and generalized cross validation (GCV) scores are also noted for each model. Non-significant terms (α = 0.1) are grayed out.

Model	Est. or edf	SE or Ref.df	t or F	p	Dev. (%)	adj. R^2	GCV
Inner Layer					39.7	0.096	0.031
Intercept	- 17.21	0.12	- 141.86	< 0.001			
Year	- 0.20	0.13	- 1.57	0.191			
* No. PR Days	- 0.0045	0.0036	- 1.25	0.278			
Outer Layer					12.6	- 0.224	0.14
Intercept	- 17.54	0.27	- 63.99	< 0.001			
Year	0.15	0.27	0.54	0.611			
* No. PR Days	0.0069	0.0081	0.85	0.435			

Table 1.4. Results from generalized additive models used to quantify effects of year and number of post-release days on $\delta^{13}C$ for samples obtained from both inner and outer layers of the skin from hatchery-associated whale #2571. Parameter estimates, standard errors (SE), t values, and p-values are indicated for factors (*i.e.,* year and whale type). Effective degrees of freedom (edf), Ref.df, F values, and p-values are shown for the smoothed variable (*i.e.,* number of post-release [PR] days). Deviance explained (Dev., %), adjusted R^2, and generalized cross validation (GCV) scores are also noted for each model. Non-significant terms (α = 0.1) are grayed out.

Model	Est. or edf	SE or Ref.df	t or F	p	Dev. (%)	adj. R^2	GCV
Inner Layer					91.0	0.772	0.015
Intercept	- 17.74	0.038	- 472.35	< 0.001			
Year	0.040	0.056	0.72	0.515			
No. PR Days	5.05	5.71	6.32	0.051			
Outer Layer					71.8	0.559	0.024
Intercept	- 17.80	0.058	- 305.35	< 0.001			
Year	0.28	0.084	3.33	0.0145			
No. PR Days	2.62	3.25	2.93	0.111			

Table 1.5. Results from generalized additive models used to quantify effects of year and number of post-release days on $\delta^{13}C$ for samples obtained from both inner and outer layers of the skin from hatchery-associated whale #2360. Parameter estimates, standard errors (SE), t values, and p-values are indicated for factors (*i.e.,* year and whale type). Effective degrees of freedom (edf), Ref.df, F values, and p-values are shown for the smoothed variable (*i.e.,* number of post-release [PR] days). Deviance explained (Dev., %), adjusted R^2, and generalized cross validation (GCV) scores are also noted for each model. Non-significant terms (α = 0.1) are grayed out.

Model	Est. or edf	SE or Ref.df	t or F	p	Dev. (%)	adj. R^2	GCV
Inner Layer					83.8	0.773	0.0075
Intercept	- 17.89	0.051	- 349.26	< 0.001			
Year	0.26	0.053	4.80	0.0049			
* No. PR Days	- 0.00079	0.0015	- 0.53	0.617			
Outer Layer					65.7	0.52	0.034
Intercept	- 18.05	0.11	- 165.34	< 0.001			
Year	0.21	0.11	1.88	0.118			
* No. PR Days	0.0045	0.0032	1.43	0.213			

1.10 Supplemental Tables

Table S1.1. Numbers of hatchery salmon released and whales observed for each biweekly period (A: 2016; B: 2017). Total number of fish released includes both chum and coho hatchery-released salmon.

A)

Biweekly Period	Start Date	End Date	No. Fish Released	Hatchery Whales (n)	Other Whales (n)
Before Releases	-	4/24/16	-	0	2
Week 1 & 2	4/25/16	5/8/16	62,973,648	2	0
Week 3 & 4	5/9/16	5/22/16	27,639,619	2	3
Week 5 & 6	5/23/16	6/5/16	-	2	0
Week 7 & 8	6/6/16	6/19/16	-	3	4
Week 9 & 10	6/20/16	7/3/16	-	1	3

Total fish released: 90,613,267

B)

Biweekly Period	Start Date	End Date	No. Fish Released	Hatchery Whales (n)	Other Whales (n)
Before Releases	-	5/3/17	-	0	4
Week 1 & 2	5/4/17	5/17/17	55,636,130	2	3
Week 3 & 4	5/18/17	5/31/17	8,451,591	2	9
Week 5 & 6	6/1/17	6/14/17	4,662,448	1	3
Week 7 & 8	6/15/17	6/28/17	-	1	0
Week 9 & 10	6/29/17	7/12/17	-	1	2
Week 11 & 12	7/13/17	7/27/17	-	2	6

Total fish released: 68,750,169

Table S1.2. Individual observations of hatchery-associated whale #2227. Asterisks (*) indicate that the whale was at a hatchery release site. Behaviors include surface feeding (SF), milling (M), and traveling (T). Areas were Warm Springs Bay (WSB), Takatz Bay (TB), Kasnyku Bay (KA), and Kelp Bay (KB). Prey types observed were juvenile salmon (S), hatchery-released juvenile salmon (HS), wild origin juvenile salmon (WS), herring (H), krill (K). Parentheses indicate some degree of uncertainty in prey identification.

Date	No. Post-Release Days	Behavior	Prey	Prey Identification Method	Approx. Date of Prey Sampling	Area	Biopsy
05/03/16	9	SF	HS	Visual	05/08 (HS ± WS)	WSB	X
05/08/16	14	T*	-	-	-	TB	X
05/13/16	19	SF*	HS	Visual	05/19 (HS ± WS)	KA	
05/14/16	20	SF	S	Visual	05/08 (HS ± WS)	WSB	
05/19/16	25	T	-	-	-	KB	
05/23/16	29	SF*	S	Visual	05/19 (HS ± WS)	KA	
05/24/16	30	M	S	Visual	05/08 (HS ± WS)	WSB	
05/25/16	31	M	(K)	Visual	-	KB	X
05/28/16	34	SF	S	Visual	05/08 (HS ± WS)	WSB	
05/31/16	37	SF*	S	Visual	05/19 (HS ± WS)	KA	
06/18/16	55	SF	S	Visual	-	KB	X
04/28/17	0	M	-	-	-	TB	
05/05/17	2	T	-	-	05/25 (HS ± WS)	KB	X
05/06/17	3	M	-	-	05/25 (HS ± WS)	KB	
05/10/17	7	SF*	S	Visual	05/15 (HS ± S)	KA	X
05/11/17	8	T	-	-	-	TB	X
05/15/17	12	T	-	-	05/15 (HS ± S)	KA	
05/16/17	13	SF*	S	Visual	05/16 (HS)	KA	X
05/17/17	14	SF*	S	Visual	05/16 (HS)	KA	
05/19/17	16	M*	-	Visual	05/16 (HS)	KA	

Table S1.3. Individual observations of hatchery-associated whale #2571. Asterisks (*) indicate that the whale was at a hatchery release site. Behaviors include surface feeding (SF), milling (M), and traveling (T). Areas were Warm Springs Bay (WSB), Takatz Bay (TB), Kasnyku Bay (KA), and Kelp Bay (KB). Prey types observed were juvenile salmon (S), hatchery-released juvenile salmon (HS), wild origin juvenile salmon (WS), herring (H), krill (K). Parentheses indicate some degree of uncertainty in prey identification.

Date	No. Post-Release Days	Behavior	Prey	Prey Identification Method	Approx. Date of Prey Sampling	Area	Biopsy
05/12/16	18	SF*	HS	Visual	05/19 (HS ± WS)	KA	X
05/13/16	19	SF*	HS	Visual	-	TB	
05/21/16	27	M	-	-	05/08 (HS ± WS)	WSB	
05/22/16	28	SF	S	Visual	05/08 (HS ± WS)	WSB	
05/26/16	32	SF	S	Visual	05/08 (HS ± WS)	WSB	X
05/28/16	34	SF	S	Visual	05/08 (HS ± WS)	WSB	X
05/31/16	37	SF*	HS	Visual	05/19 (HS ± WS)	KA	
06/06/16	43	SF	S	Visual	05/08 (HS ± WS)	WS	
06/08/16	45	SF	S	Visual	-	KB	X
06/18/16	55	SF	S	Visual	-	KB	
06/21/16	58	SF	S	Visual	-	KB	
06/22/16	59	SF	S	visual	05/08 (HS ± WS)	WSB	
06/27/16	64	M	-	-	-	KB	
06/28/16	65	SF	S	Visual	-	KB	X
04/23/17	0	M	(K)	Sounder	05/25 (HS ± WS)	KB	
05/04/17	1	T	-	-	05/25 (HS ± WS)	KB	
05/05/17	2	M	-	-	05/25 (HS ± WS)	KB	X
05/06/17	3	T	-	-	05/25 (HS ± WS)	KB	
05/15/17	12	SF	HS	Visual	05/25 (HS ± WS)	KB	
05/17/17	14	SF	S	Visual	05/25 (HS ± WS)	KB	
05/25/17	22	SF	HS±WS	Sampled	05/25 (HS ± WS)	KB	X
06/28/17	56	M	-	-	06/28 (H)	KB	X
07/03/17	61	SF	U	-	07/05 (H)	KB	
07/05/17	63	R	-	-	07/05 (H)	KB	X
07/06/17	64	M	-	-	07/05 (H)	KB	
07/08/17	66	M	-	-	07/05 (H)	KB	
07/12/17	70	SF	H	Visual	07/14 (H)	KB	X
07/14/17	72	T	-	-	07/14 (H)	KB	
07/15/17	73	T	-	-	07/14 (H)	KB	
07/27/17	85	SF	U	-	07/14 (H)	KB	X

Table S1.4. Individual observations of hatchery-associated whale #2360. Asterisks (*) indicate that the whale was at a hatchery release site. Behaviors include surface feeding (SF), milling (M), and traveling (T). Areas were Warm Springs Bay (WSB), Takatz Bay (TB), Kasnyku Bay (KA), and Kelp Bay (KB). Prey types observed were juvenile salmon (S), hatchery-released juvenile salmon (HS), wild origin juvenile salmon (WS), herring (H), krill (K). Parentheses indicate some degree of uncertainty in prey identification.

Date	No. Post-Release Days	Behavior	Prey	Prey Identification Method	Approx. Date of Prey Sampling	Area	Biopsy
05/03/16	9	SF*	HS	Visual	05/19 (HS ± WS)	KA	X
05/12/16	18	SF*	HS	Visual	05/19 (HS ± WS)	KA	
05/13/16	19	SF*	HS	Visual	-	TB	X
05/14/16	20	SF*	HS	Visual	-	TB	
05/20/16	26	SF	S	Visual	05/08 (HS ± WS)	WSB	X
05/21/16	27	M	-	-	05/08 (HS ± WS)	WSB	
05/22/16	28	SF	S	Visual	05/08 (HS ± WS)	WSB	
05/23/16	29	T	-	-	-	KB	
05/24/16	30	SF	S	Visual	05/08 (HS ± WS)	WSB	
05/25/16	31	M	-	-	-	KB	
05/28/16	34	T	-	-	-	KB	
05/30/16	36	SF	S	Visual	05/08 (HS ± WS)	WSB	
06/08/16	45	SF	S	Visual	-	KB	X
06/16/16	53	SF	S	Visual	05/08 (HS ± WS)	WSB	
06/21/16	58	SF	S	Visual	05/08 (HS ± WS)	WSB	
05/17/17	14	SF	S	Visual	05/25 (HS ± WS)	KB	
05/25/17	22	T	-	-	05/25 (HS ± WS)	KB	
05/28/17	25	T	-	-	05/25 (HS ± WS)	KB	X
05/30/17	27	T*	-	-	05/30 - HS	KA	
05/31/17	28	SF*	HS	Visual	05/30 - HS	KA	
06/01/17	29	SF*	HS	Visual	05/30 - HS	KA	X
06/06/17	34	SF*	HS	Visual	05/30 & 06/09 (HS)	KA	
06/09/17	37	SF*	HS	Sample	06/09 (HS) & 06/10 (HS ± WS)	KA	X
06/10/17	38	SF (BN Group)	H	Sample	06/10 (H)	KB	
06/12/17	40	SF (BN Group)	H	Visual	06/10 (H)	KB	
06/28/17	56	SF	H	Sample	06/28 (H)	KB	
07/08/17	66	M	-	-	07/05 (H)	KB	
07/15/17	73	SF (BN Group)	H	Visual	-	WC	X

Chapter 2 Pectoral herding: an innovative tactic for humpback whale foraging [2]

2.1 Abstract

Humpback whales (*Megaptera novaeangliae*) have exceptionally long pectorals (*i.e.*, flippers) that aid in shallow water navigation, rapid acceleration and increased manoeuvrability. The use of pectorals to herd or manipulate prey has been hypothesized since the 1930s. We combined new technology and a unique viewing platform to document the additional use of pectorals to aggregate prey during foraging events. Here, we provide a description of 'pectoral herding' and explore the conditions that may promote this innovative foraging behaviour. Specifically, we analysed aerial videos and photographic sequences to assess the function of pectorals during feeding events near salmon hatchery release sites in Southeast Alaska (2016–2018). We observed the use of solo bubble-nets to initially corral prey, followed by calculated movements to establish a secondary boundary with the pectorals—further condensing prey and increasing foraging efficiency. We found three ways in which humpback whales use pectorals to herd prey: (i) create a physical barrier to prevent evasion, (ii) cause water motion to guide prey towards the mouth, and (iii) position the ventral side to reflect light and alter prey movement. Our findings suggest that behavioural plasticity may aid foraging in changing environments and shifts in prey availability. Further study would clarify if 'pectoral herding' is used as a principal foraging tool by the broader humpback whale population and the conditions that promote its use.

[2] Kosma MM, Werth AJ, Szabo AR, and Straley JM. 2019. Pectoral herding: an innovative tactic for humpback whale foraging. Royal Society Open Science. **6**:191104. doi:10.1098/rsos.191104.

2.2 Background

Large body sizes of baleen whales generate high metabolic demands that require the consumption of sizable, dense patches of prey [1-3]. However, filter feeding is energetically demanding and requires effective methods for prey aggregation [2]. Behavioural plasticity and foraging innovations are common among rorquals [4,5]. Humpback whales (*Megaptera novaeangliae*) provide an excellent example of how individual changes in behaviour can lead to diverse foraging tactics that maximize feeding efficiency [6–9]. Such foraging includes lunge feeding [6,10], bubble-net feeding [6,11–14], flick feeding [6], cooperative feeding [15], lobtail feeding [7] and other idiosyncratic tactics [12,16–18].

Humpback whales are one of the world's largest filter-feeders and regularly use lunge feeding to capture prey. This particular technique is energetically costly [19] and requires a two-step process. The whale first uses a high-velocity lunge to engulf large volumes of prey-laden water. The whale then closes its mouth and the baleen acts as a sieve to filter prey [14,20]. The lunge can occur at depth [2,10,20–22] or on the surface [7,23,24]. In both situations, lunge feeding requires acceleration to high speeds [2,25] because the animal must overcome considerable drag from an open mouth. To counteract drag and increase speed, humpback whales open their mouths gradually, in synchrony with strong fluke strokes [20,22]. This acceleration maximizes the amount of water engulfed and aids in the capture of active prey [25]. Humpback whales feeding near the surface exhibit an array of lunge types [6,12,15] and some are in association with the creation of bubbles. A bubble-net is denoted by the formation of a ring of bubbles in a clockwise fashion to enclose prey [6,7,12,13,26] and this strategy can be employed by an individual or a group of whales. Bubble-nets serve as a physical barrier to increase lunge efficiencies and are most commonly used on naturally schooling fish (*i.e.,* Pacific herring).

Humpback whales have a distinctive body morphology that allows for the efficient capture of prey [27,28]. Notably, they have the longest pectorals (*i.e.,* flippers) of any cetacean, measuring from one- quarter to one-third of their body length [29,30]. The pectorals of other cetaceans typically do not exceed one-seventh the length of their bodies [31]. The exceptionally long appendages of humpback whales allow for effective navigation in shallower water [31,32], rapid acceleration, greater manoeuvrability and increased stability [6,33,34], thereby increasing capture abilities of small prey such as euphausiids, herring (*Clupea* spp.), capelin (*Mallotus villosus*) and sandlance (*Ammodytes* spp.) [31,35–37]. If not positioned effectively, however, larger pectorals may present a hydrodynamic disadvantage by increasing drag [38].

As the buccal cavity expands during a lunge, a hydrodynamically optimal position for the pectorals is for one or both to extend with the leading edge held at low angles of attack (α) [39]. Positioning the pectorals in this manner minimizes drag and provides the greatest amount of lift. The perpendicular position of extended pectorals also stabilizes the whale's body during a lunge [39]. Additionally, it has been hypothesized that rapid pectoral movement just prior to a lunge generates an upward pitching motion that counteracts the torque caused by rapidly engulfing water [34,39]. Segre *et al.* [40] defined four conditions for pectoral movement that would generate lift and increase propulsive thrust during an engulfment event: (i) both pectorals must move symmetrically, (ii) pectorals are angled into the path of the stroke, (iii) the stroke is oriented perpendicular to the whale's body, and (iv) the stroke is aligned with the direction of travel [40]. Lift is generated as pectorals are rotated at an angle to the water flow (angle of attack or α). However, this angle must be small relative to the direction of travel [41]. Above a critical α, the pectoral will impede lift, making the movement detrimental to acceleration. Miklosovic *et al.* [42] found that peak hydrodynamic efficiency of a humpback whale pectoral is around $\alpha = 7.5°$. Above this, drag

increases and lift decreases, with complete stall occurring at α~ 17.5°. These studies illustrate that there are strict hydrodynamic criteria for using pectorals efficiently during lunge feeding.

In addition to providing lift, decreasing drag and promoting acceleration, pectorals may be used to corral or concentrate prey during lunge-feeding events. Humpback whales have multiple foraging strategies to aggregate prey, but concentration of prey may be increased by herding techniques [31,43]. Howell [43] was the first to suggest that humpback whales use their pectorals to direct schools of fish into their mouths. Brodie [38] elaborated on this theory by describing the use of white coloration on the pectoral's ventral surface to 'flash' fish and herd prey towards the whale's mouth. He stated, 'if there are hydrodynamic disadvantages to such large flippers there must be selective compensation, one possibility being their role in concentrating prey' [38]. Both authors, however, reported reservations about their findings because they lacked the perspective necessary to document such behaviours [38]. Our objective was to use new technology (*e.g.,* unoccupied aerial vehicles (UAVs), small video cameras) to document and describe the distinctive role of humpback whale pectorals in herding and aggregating prey. We focused our efforts on whales feeding near salmon hatchery release sites [44] in Southeast Alaska (2016–2018). Hatchery structures allowed for close approaches with minimal behavioural disruption. Our results enhance our understanding of the complex and innovative foraging tactics that may be critical to humpback whale survival as population dynamics and environmental conditions continue to change [45,46].

2.3 Methods

2.3.1 Study Location and Timing

This study was conducted in Chatham Strait, along the eastern shore of Baranof Island in Southeast Alaska (figure 1). We conducted systematic surveys from Warm Springs Bay north to Kelp Bay, with an emphasis on salmon hatchery release sites in Takatz Bay and Kasnyku Bay in 2016 (mid-May to the end of June) and 2017 (mid-April to the end of July). We put forth a more directed effort to document foraging strategies by humpback whales in Kasnyku Bay in 2018 (May). All effort was timed to overlap with releases of juvenile salmon from Hidden Falls Hatchery (managed by the Northern Southeast Regional Aquaculture Association).

2.3.2 Data Collection

We recorded humpback whale sightings and behavioural observations as part of a 3-year study (2016– 2018) of humpback whale predation at Hidden Falls Hatchery and surrounding areas. We took identification photographs of each whale using digital SLR cameras with lenses ranging in focal lengths from 70 to 300 mm. Humpback whales were individually identified based on the pigmentation and trailing edges of their flukes and/or the shape and marks of their dorsal fins [47] and cross-referenced with the Southeast Alaska Humpback Whale Catalog [48]. This catalogue included all whale sightings through 2012 and additional observations from later time periods (JM Straley & CM Gabriele 2016, unpublished data). We made an effort to capture video and photographic sequences with a Nikon D7000 camera whenever whales were observed feeding at the surface. In 2017, we also used a GoPro Hero5 Black video camera affixed to the end of a 3.5 m pole to provide an aerial perspective while standing on walkway platforms attached to hatchery net pens. These platforms provided a unique and close-up perspective without disturbing whale

behaviour that enabled camera views directly above or within bubble-nets created by the feeding whales. In 2018, we used an UAV (DJI Mavic Pro with 4 k video at 24 fps) to capture footage of whales surface lunge feeding near the facility. In addition to visual prey identification, we used a cast net and herring jig to sample prey in foraging areas. We removed juvenile salmon otoliths to differentiate hatchery-reared and wild origin fish according to methods described by Volk *et al.* [49].

2.3.3 Data Analysis

We used Adobe Premiere Pro to analyse video footage and Adobe Lightroom to assess photographic sequences. Kinematic assessments of whale foraging behaviour were made, with particular focus on the use of pectorals. We recorded pectoral positions, movements and prey locations (when possible) using real-time and frame-by-frame processing. Whale foraging movements were then three- dimensionally modelled using Blender, with post-processing in Adobe Photoshop to accurately illustrate foraging behaviours seen in footage and photographs. Lunge durations were calculated from videos, when possible. All footage and photographic sequences were viewed and categorized based on surface foraging behaviour. Bubble-net feeding was denoted by the formation of a ring of bubbles followed by a lunge through the centre. A surface lunge was recorded as one of two commonly observed types: a vertical lunge, when the animal lunged upwards [24], and a lateral lunge, when the animal rotated approximately 90° while lunging [24]. Pectoral herding, a newly documented feeding strategy, was defined by directed movements of the pectorals to condense prey before a lunge. We identified three ways in which humpback whales used pectorals to herd prey: (i) create a physical barrier to prevent evasion by prey, (ii) cause water motion to direct prey movement, and (iii) position the white coloration on the ventral side to reflect light, causing prey to move in the opposite direction [12,38]. A feeding event

was defined as beginning with that start of a solo bubble-net and ending when the whale closed its mouth after a surface lunge. Multiple feeding events from one whale on the same prey, in the same general location, were defined as a foraging session. We calculated lunge duration when possible.

2.4 Results

We captured videos and photographic sequences of two humpback whales independently engaged in previously undocumented foraging techniques. Both whales (Whale A and Whale B) initiated feeding events with a solo bubble-net. Before lunging, these whales used their pectorals to manipulate and further condense prey. We defined this technique as 'pectoral herding', with two methods of execution: 'horizontal pectoral herding' and 'vertical pectoral herding'. More detailed information of Whale A and Whale B encounters are provided in supplementary material, S2.1 and S2.2. We captured footage of one additional whale using horizontal pectoral herding, though a limited number of observations precluded this whale from further analyses.

2.4.1 Horizontal Pectoral Herding

We encountered Whale A (#2360 in Southeast Alaska Humpback Whale Catalog) on 27 days from 2016 to 2018. We observed solo bubble-netting during 15 feeding sessions (135 feeding events). Each solo bubble- net involved what we describe as horizontal pectoral herding prior to the lunge. Video footage depicting horizontal pectoral herding can be viewed in electronic supplemental materials or in the published manuscript (https://doi.org/10.1098/rsos.191104). During horizontal pectoral herding, Whale A initiated the feeding event by deploying an upward-spiral bubble-net to corral prey (figures 2.2 and 2.3; Stage A). At the closure of the bubble-net, Whale A rotated its head parallel to the

surface of the water and towards the centre of the net. The whale then moved its left pectoral in and out of the water in a forward, sinusoidal motion along the initial edge of the bubble- net barrier (figures 2.2 and 2.3; Stage B). Whale A continued this pectoral movement while gradually opening its mouth and allowing the upper jaw to rise above the water line, while the lower jaw remained subsurface. The whale continued to open its mouth wider until it reached the opposite side of the bubble- net (figures 2.2 and 2.3; Stage C). Whale A's head rotated in the direction of the left pectoral 51.9% of all documented feeding events. In these cases, the lower jaw was tilted at an angle that exposed prey to the largest circumference of the buccal cavity (figure 2.4). For all other feeding events, the degree of head tilt was unknown or Whale A maintained a stationary head position, bringing its lower jaw up out of the water to meet the upper jaw. Whale A never rotated its head away from the herding pectoral. The mean lunge duration, defined as the start of pectoral movement to the close of the mouth, was 8 ± 1 s (calculated from 32 of 36 videos). Not all videos could be used to calculate lunge duration because they did not document the entire process.

We observed Whale A using horizontal pectoral herding in four locations that spanned approximately 21 km of coastline. This included Warm Springs Bay, Takatz Bay (2016 hatchery release site), Kasnyku Bay (2016 and 2017 hatchery release site) and Kelp Bay. In 2016, we observed Whale A lunge feeding in Warm Springs Bay, Takatz Bay and Kelp Bay. Although prey sampling was sparse and inconsistent, we observed juvenile salmon at all of these locations. In May 2016 and 2017, we collected juvenile hatchery salmon from Warm Springs Bay (within 12–44 days of feeding sessions) and visually identified juvenile salmon during all Warm Spring Bay foraging events. Feeding sessions in Takatz Bay coincided with a salmon release event and continued onto the day following. Juvenile salmon were only visually identified in Takatz Bay, but all feeding sessions were in the vicinity of hatchery salmon releases. In 2017, Whale A was observed horizontal pectoral herding in Kasnyku

Bay and Kelp Bay. The feeding sessions in Kasnyku Bay were associated with salmon releases (within 7 days of a release). Prey sampling and otolith marks from fish collected within 1–3 days of feeding sessions confirmed juvenile hatchery salmon in the area. We collected juvenile salmon (hatchery and wild) within 8 days of feeding sessions in Kelp Bay. Pacific herring (*Clupea pallasii*) were also sampled in Kelp Bay during nine different feeding sessions. We were unable to differentiate whether prey being consumed in Kelp Bay were juvenile salmon or herring. Of all feeding sessions involving horizontal pectoral herding, 94.1% were identified as having targeted juvenile (hatchery-released chum and coho, wild pink (*Oncorhynchus gorbuscha*) salmon.

2.4.2 Vertical Pectoral Herding

We documented Whale B (#2227 in Southeast Alaska Whale Catalog) solo bubble-net feeding at Hidden Falls Hatchery on 16 May 2017. During the 2.4 h observation period, we recorded 13 solo bubble-net feeding events, all of which were in the vicinity of newly released hatchery-reared juvenile coho salmon (figure 2.5). We observed two well-documented types of kinematic feeding behaviours for Whale B: vertical lunge and lateral lunge. We also documented vertical pectoral herding, which has not been previously documented in the scientific literature. Video footage depicting all three feeding types can be viewed in electronic supplemental materials or in the published manuscript (https://doi.org/10.1098/rsos.191104).

Vertical pectoral herding was used in 30.8% of all feeding events. We identified vertical pectoral herding when Whale B moved its pectorals from a neutral state (as in vertical lunge and lateral lunge) to a protraction–abduction posture (figure 2.6). After establishing this posture, the whale simultaneously moved both pectorals forward and into a V-shaped position on either side of its mouth, with pectorals curved ventrally (figure 2.7). A vertical

lunge was used during 23.1% of all feeding events. When employing this technique, the whale's pectorals first abducted with the tips curved up. Prior to closing its mouth, the pectorals adducted to a vertical lunge position, tight against the side of the body. Finally, the pectorals retracted and angled posteriorly as the whale lunged to the surface (figure 2.7). The distinguishing feature between vertical lunge and pectoral herding was a slight upward dorsal-oriented curve to the pectorals and less visibility of the pectorals as they were abducted with a swept-back configuration. A lateral lunge was used in 46.2% of the feeding events (figure 2.6). When using this technique, the whale pivoted on its left pectoral and rolled approximately 90° while lunging. The left pectoral was exposed and occasionally broke the surface of the water as the whale used it to manoeuvre.

When documenting Whale B's feeding events, we observed notable differences in light conditions. Both vertical lunge (3 of 3) and lateral lunge (5 of 6) occurred in shaded waters. All vertical pectoral herding events (4 of 4) occurred in sunlit water, which was easily identified from photographs due to a sun-induced green tint of the water (figure 2.6). Whale B employed different tactics in the same location only when light conditions varied. In general, Whale B appeared to use vertical pectoral herding in sunlit areas but switched to vertical lunge or lateral lunge when the same area became shaded. The single lateral lunge event in sunlight waters was located near a surface obstacle in the centre the bubble-net. Possible avoidance behaviour was documented as the whale lunged near the buoy. Prey movement in the direction opposite of vertical pectoral positioning was visible in 2 of 13 engulfment events (figure 2.8). In 'before' snapshots (*i.e.,* images taken prior to vertical pectoral positioning), we observed a dense aggregation of prey between the mouth and pectoral. In 'after' snapshots (*i.e.,* images taken once pectorals were placed in the V-shaped position), we observed less dense prey patches in the area between the mouth and pectoral. We also identified a greater relative density of prey that had moved towards the

whale's mouth. We could not calculate lunge duration for Whale B because the whale started to lunge in water too deep to see the entire process using aerial footage. The variation in light conditions also prevented the identification of consistent cues for the start of a lunge.

2.5 Discussion

It is well known that humpback whale pectorals aid in acceleration and manoeuvrability during feeding events [27,28]. Our study recognizes an alternative use of pectorals during foraging. Here, we have provided the first empirical evidence for a longstanding hypothesis that humpback whales use their pectorals to herd and aggregate prey [38,43,50]. Our study combined the use of new technology and a unique viewing opportunity at Hidden Falls Hatchery to provide the vantage points necessary for such documentation. Although the concept that humpback whales use their pectorals to manipulate prey is not new, the use of pectorals in conjunction with a bubble-net (as a secondary barrier) had never been documented. Using direct video footage and photographic sequences, we described this foraging technique as 'pectoral herding', with two methods of execution: horizontal pectoral herding and vertical pectoral herding. We observed two humpback whales using bubble-nets as a primary barrier to corral prey, proceeded by deliberate movements of the pectorals to establish a secondary barrier before the lunge. These observations suggest that pectorals are used to further condense prey inside the bubble-net, thereby increasing feeding efficiency for each event. From our results, we found three ways in which humpback whales use pectorals to herd prey: (i) create a physical barrier to prevent evasion by prey, (ii) cause water motion to direct prey movement, and (iii) position the white coloration on the ventral side to reflect light, causing prey to move in the opposite direction [12,38]. These

three methods of pectoral herding are not mutually exclusive and can be used in conjunction with one another.

2.5.1 Horizontal Pectoral Herding

The documented solo bubble-nets began and ended in the same general location. Thus, there is greater elapsed time for bubbles created near the beginning portion of the net, compared to the end. The greater dissipation of bubbles and possibility that fish are scared towards the beginning portion of the net (as a result of whale activity near the bubble-net closure site) suggests a potential weakness in the primary barrier. We hypothesize that Whale A uses horizontal pectoral herding to strengthen the beginning portion of the solo bubble-net and establish a secondary barrier to further condense prey, thereby increasing the amount of prey consumed during each lunge. Because the energetically costly movement of the left pectoral probably hinders the acceleration of the whale, we assert that an alternative use must be at play. We found that lunge durations of Whale A averaged 8 s, whereas Werth *et al.* [51] documented the mean engulfment rates from a solo humpback whale lunge to be closer to 2 s. This difference in engulfment rates with and without horizontal pectoral herding supports our hypothesis that any additional movement must substantially aid in prey capture. We conclude that Whale A used its pectorals in two of the three ways to herd prey: (i) create a physical barrier to prevent evasion by prey and (ii) cause water motion to direct prey movement. In addition, pectoral movements could create eddies and/or drag that increases the whale's capacity to alter prey movement. We note that our descriptions of horizontal pectoral herding rely upon observations from a single whale. However, we documented the use of this particular foraging technique by one additional whale, suggesting potential for cultural transmission of this foraging behaviour.

In over half of the documented events, Whale A rotated its head in the direction of the left pectoral before closing its mouth (during all other fully documented events, the head remained centred and never rotated in the opposite direction). This suggests that the left pectoral was herding prey and that the whale turned its mouth into the path of swimming prey, further increasing the amount of fish consumed per lunge. The lower jaw turned at an angle that exposed prey to the largest circumference of the buccal cavity, which probably prevented escape between the lower jaw and the surface of the water. The rostrum was also above the surface of the water to avoid blocking prey from entering the buccal cavity when the whale turned its head. When the whale's head remained central, the lower jaw surfaced to meet the upper jaw. During these events, the whale may have sensed that its buccal cavity was full of fish, making head rotation counterproductive [52].

2.5.2 Vertical Pectoral Herding

Our current understanding about lunge feeding revolves around the theory that whales use their pectorals to actively increase lift and/or stabilize their body during a lunge. The pectoral position used by Whale B suggests that the whale violated two out of the four criteria proposed for a hydrodynamic stroke [40]. First, the pectorals were not oriented at an efficient angle into the path of the stroke ($\alpha > 17.5°$). The stroke was also not oriented perpendicular to the body, which would inhibit stability during the lunge. Therefore, we claim that the pectoral movements of Whale B were not intended to increase hydrodynamic efficiency, stability or lift. Whale B's forward speed was probably hindered by a high angle of attack and V-shaped position of the pectorals around the mouth. During three of the four pectoral herding events, the rostrum and left pectoral broke the surface of the water at approximately the same time (within 1 s of each other). There is no hydrodynamic reason for the pectorals to be in line with or above the position of the mouth during a lunge. By

eliminating the use of pectorals for stabilization and thrust, we deduced that Whale B's pectorals were used to create a secondary barrier along the edges of the mouth during a lunge, manipulating prey movement towards the mouth and increasing foraging efficiency.

Light conditions and prey reactions also suggest that Whale B used its pectorals to herd prey. There were three main locations around the net pens that had recurring feeding events. During Whale B's feeding session, the eastern side of the net pens transitioned from sunlit waters to shade. In all three of these locations, Whale B used vertical pectoral herding when lunging in the sun. During the only sunlight feeding event without vertical pectoral herding, we hypothesize that Whale B was manoeuvring around a buoy and that the whale would have used vertical pectoral herding if the obstacle were not present. When waters transitioned from sunlight to shade in these three main locations, the whale used vertical or lateral lunges instead of vertical pectoral herding. This provides support for the hypothesis that behavioural shifts were based on light conditions rather than locational differences. Brodie [38] suggested that the ventral side of the pectorals can be used to 'flash' fish and cause them to move in the direction of the dark mouth, which functions as a deceptive refuge. When prey movement was visible in sunlit waters, we observed prey moving in the direction of the mouth, apparently in response to the position of the pectorals. This is convincing evidence that pectorals alter prey behaviour. The lack of vertical pectoral herding in shaded water suggests that the physical presence of the pectorals alone is not effective enough to cause fish to move towards the mouth. The combination of light reflection and a physical barrier probably provides a foraging benefit to justify the hydrodynamic detriment caused by vertical pectoral herding. Thus, it is probable that Whale B used pectorals in two of the three ways to herd prey: (i) create a physical barrier to prevent evasion by prey and (ii) position the white coloration on the ventral side to reflect light and cause prey to move in the opposite direction [12,38].

2.5.3 Prey and Behavioural Plasticity

Schooling fish cluster in response to predators or other startling disturbances [53–57], and humpback whales have been known to take advantage of this behaviour [26]. Sharpe [15] experimented with an artificial pectoral and found that herring respond to a rotating pectoral by fleeing in the opposite direction. It has also been suggested that humpback whales manipulate prey by slapping their pectoral fins or flukes on the surface of the water [7,26]. Whale A's pectoral movement makes a startling disturbance that could alter the direction of prey within the bubble-net barrier. We were unable to see prey in videos of Whale A foraging. However, the continued use of horizontal pectoral herding, in combination with its hydrodynamic disadvantages, is strong evidence for an increase in foraging efficiency. Additionally, a study on hatchery-reared juvenile salmon [58] showed that fish avoid light and seek out dark refugia when artificial lights were activated and/or flashing. We believe that light reflected off the ventral surface of Whale B's pectorals served as a stimulus to scare fish in the direction of the dark 'refuge' of the whale's mouth. We were able to directly observe prey movement towards the mouth in response to Whale B's pectoral placement in some of the videos. Pectoral movement and flashing may directly stun or disorient prey [7].

It is well known that humpback whales use bubble-nets to aggregate prey [12,26]; however, bubble-nets may not be as efficient when prey do not naturally aggregate into dense patches. This is because schooling fish would aggregate within a single area of the bubble-net, enabling the consumption of most fish in a single lunge. Non-schooling fish may very well distribute themselves throughout the bubble-net, resulting in fewer fish consumed per lunge. Acoustic prey surveys at our study site showed that groups of juvenile coho (Oncorhynchus kisutch) and chum (Oncorhynchus keta) salmon were small, patchy and short-lived compared to those formed by herring and krill [59]. Whales tend to moderate

their behaviour to efficiently exploit different prey types and respond to dynamic prey conditions [14,60]. It is possible that the two whales we observed have independently altered their foraging strategies to accommodate non-schooling fish and more effectively incorporate hatchery- released juvenile salmon into their diets. Because aerial documentation of solo bubble-netting whales has been limited, we cannot conclude whether or not pectoral herding is restricted to these whales and the unique prey resource of hatchery-reared juvenile salmon. Pectorals are an efficient secondary barrier and may be used by other whales lunging on different prey. For Whales A and B, 93.9% of pectoral herding events exclusively targeted juvenile salmon. The remaining events may have also targeted herring as prey. Additionally, a bubble-net may be substantially larger than the size of a whale's open mouth, restricting engulfment to only a portion of the prey enclosed within the net. A secondary barrier further condenses prey, conceivably enhancing the energy gained per lunge.

McMillan *et al.* [18] documented humpback whales using a feeding strategy called 'trap-feeding'. The authors inferred that whales use pectorals to manipulate prey by flicking fish into their mouth. The available footage of the pectoral movement in this study relies on a lateral perspective with poor visibility below the water's surface and no view of prey. This makes it difficult to connect pectoral movements to a specific behaviour or make inferences about prey responses. Additionally, lateral footage makes it difficult to differentiate between the use of pectorals as a stabilizing force during a lunge and pectoral movements to manipulate prey. In general, most whale observations are obtained from land or boat, yielding lateral views that limit the perspective and skew our perception of individual behaviours. With innovative technology (*e.g.,* UAVs, small video cameras), we can now gain the perspectives necessary for more accurate interpretations of marine mammal foraging tactics. Our observations, which relied on an aerial perspective, provide insight into

the position of humpback whales in relation to prey (above and below the water) as well as a more detailed depiction of the whale's movements and position during feeding events. Based on lateral–aerial comparisons of pectoral herding by humpback whales, we believe that conventional boat or land- based footage should be supplemented by aerial imagery in order to gain insight and avoid misinterpretations about marine mammal behaviour.

Despite the advantages of using advanced technology, our study is limited by small sample sizes and a lack of quantitative kinematics. Our findings depended on functional interpretations of movements made by two whales with only above-surface documentation. A more inclusive survey of solo feeding humpback whales (encompassing broader spatial scales and additional whales) would provide greater insight into how these animals are taking advantage of their lengthy appendages during foraging. Furthermore, future investigations should pair aerial footage of feeding whales with prey distribution data, and synchronous motion suction cup tags (*i.e.,* DTAGs) to better quantify kinematic behaviours and prey dynamics, both above and below the surface [61]. Notably, however, our study suggests a flaw with current tagging technology. Although tags are often deployed on the backs of whales to record movements (pitch, yaw and roll) of the entire whale, we found that prey aggregation and capture is not limited to movements of the head, caudal peduncle and tail flukes. Thus, tag sensors that also quantitatively record these movements of the pectorals would allow for a clearer understanding of how these appendages are kinematically being used. Finally, more accurate lunge durations (*e.g.,* starting when the whale's mouth opened) would help us compare acceleration rates between lunges with and without pectoral herding, furthering our understanding about the hydrodynamic impacts caused by pectoral movements.

In summary, our results provide empirical evidence of the use of pectorals to herd prey. They also illustrate considerable variation among individual humpback whale foraging

strategies. With our documentation of pectoral herding, we have provided support for plasticity in foraging behaviour of cetaceans. These animals are highly innovative, with individual whales successfully using different tactics to approach the same prey in the same situation [26]. Maintaining a suite of foraging strategies probably aids humpback whales in a changing environment, where food availability fluctuates and competition may impact population dynamics. Further investigation would enhance our understanding about whether humpback whales use pectoral herding as a principal foraging technique as well as the conditions that promote its use.

2.6 Ethics Statement

This research was conducted under National Marine Fisheries Service (NMFS) permits 14122 and 18529, University of Alaska Institutional Animal Care and Use Committee (IACUC) permit 907314-3 and State of Alaska Department of Fish and Game permit CF-18-049. The research reported in this publication was supported by the National Institute of General Medical Sciences of the National Institutes of Health, under award RL5GM118990. The content within this manuscript is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health.

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the authors and does not necessarily represent the official views of the National Institutes of Health.

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2.9 Author Contributions

M.M.K., A.J.W., A.R.S., and J.M.S. contributed to the experimental conception and design; M.M.K. was primarily responsible for data collection; M.M.K was primarily responsible for analysing and interpreting data with contributions from A.J.W., A.R.S. and J.M.S.; M.M.K. drafted the article. All authors revised the article and provided final approval for the version to be published.

2.10 References

1. Piatt JF, Methven DA. 1992 Threshold foraging behavior of baleen whales. *Mar. Ecol. Prog. Ser.* **84**, 205–210.

2. Goldbogen JA, Calambokidis J, Croll DA, Harvey JT, Newton KM, Oleson EM, Schorr GS, Shadwick RE. 2008 Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *J. Exp. Biol.* **211**, 3712–3719.
3. Werth AJ, Potvin J. 2016 Baleen hydrodynamics and morphology of cross-flow filtration in balaenid whale suspension feeding. *PLoS ONE* **11,** e0150106**.** **(**doi:10.1371/journal.pone.0150106)
4. Eisenberg J. 1981 The Mammalian Radiations. Chicago: University of Chicago Press.
5. Partridge L , Green P. 1985 Intraspecific feeding specializations and population dynamics. In: Behaviroral Ecology (Ed. by R.M. Silby & R. H. Smith), pp. 207-226. Oxford: Blackwell Scientific Publications.
6. Jurasz CM, Jurasz VP. 1979 Feeding modes of the humpback whale, *Megaptera novaeangliae*, in Southeast Alaska. *Sci. Rep. Whales Res. Inst.* **31**, 69–83.
7. Weinrich MT, Schilling MR, Belt CR. 1992 Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Anim. Behav.* **44**, 1059–1072. (doi:10.1016/S0003-3472(05)80318-5)
8. Parks SE, Cusano DA, Stimpert AK, Weinrich MT, Friedlaender AS, Wiley DN. 2014 Evidence for acoustic communication among bottom foraging humpback whales. *Sci. Rep.* **4**, 1–7.
9. Fleming AH, Clark CT, Calambokidis J, Barlow J. 2016 Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. *Glob. Chang. Biol.* **22**, 1214–1224.

10. Watkins WA, Schevill WE. 1979 Aerial observation of feeding behavior in four baleen whales: *Eubalaena glacialis, Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. *J. of Mammalogy* ***60***, 155–163. (doi:10.2307/1379766)
11. Ingebrigsten A. 1929 Whales caught in the North Atlantic and other seas. *Int. Council Explor. Sea, Rapp. P-V Reun.* **56**, 1–26.
12. Hain JHW, Carter GR, Krauss SD, Mayo CA, Winn HE. 1982 Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fish Bull.* **80**, 259–268.
13. Sharpe FA, Dill LM. 1997 The behavior of Pacific herring schools in response to artificial humpback whale bubbles. *Can. J. Zool.* **75**, 725–730. (doi: 10.1139/z97-093)
14. Goldbogen JA, Cade DE, Calambokidis J, Friedlaender AS, Potvin J, Segre PS, Werth AJ. 2017 How baleen whales feed: the biomechanics of engulfment and filtration. *Ann. Rev. Mar. Sci.* **9**, 367–386.
15. Sharpe FA. 2001 Social foraging of the southeast Alaskan humpback whale, *Megaptera novaeangliae* [dissertation]. Burnaby (BC): Simon Fraser University.
16. Baker CS. 1985 The population structure and social organization of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific [dissertation]. Honolulu (HI): University of Hawaii.
17. D'Vincent CG, Nilson RM, Hanna RE. 1985 Vocalization and coordinated feeding behavior of the humpback whale in Southeastern Alaska. *Scientific Reports of the Whale Research Institute*, **36**, 41–47.
18. McMillan CJ, Towers JR, Hildering J. 2018 The innovation and diffusion of "trap-feeding", a novel humpback whale foraging strategy. *Mar. Mamm. Sci.* ***9999***, 1–18. (doi:10.1111/mms.12557)

19. Potvin J, Goldbogen JA, Shadwick RE. 2009 Passive versus active engulfment: verdict from trajectory simulations of lunge-feeding fin whales *Balaenoptera physalus*. J. R. Soc. Interface **6**, 1005–1025. (doi: 10.1098/rsif.2008.0492)
20. Goldbogen JA, Pyenson ND, Shadwick RE. 2007 Big gulps require high drag for fin whale lunge feeding. *Mar. Ecol. Prog. Ser.* **349**, 289–301.
21. Croll DA, Acevedo-Guitierrez A, Tershy BR, Urban-Ramirez J. 2001 The diving behavior of blue and fin whales: is dive duration shorter than expected based on oxygen stores? Comparative Biochemistry and Physiology Part A **129**, 797-809.
22. Goldbogen JA. 2006 Kinematics of foraging dives and lunge-feeding in fin whales. *J. Exp. Biol.* **209**, 1231–1244.
23. Gill PC. 2002 A blue whale (*Balaenoptera musculus*) feeding ground in a southern Australian coastal upwelling zone. *J. Cetacean Res. Manag.* **4**, 179–184.
24. Ware C, Friedlaender AS, Nowacek DP. 2010 Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Mar. Mam. Sci.* **27**, 587–605. (doi:10.1111/j.1748-7692.2010.00427.x)
25. Simon M, Johnson M, Madsen PT. 2012 Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *J. Exp. Biol.* **215**, 3786–3798. (doi:10.1242/jeb.071092)
26. Wiley DN, Ware C, Bocconcelli A, Cholewiak D, Friedlaender A, Thompson M, Weinrich M. 2011 Underwater components of humpback whale bubble-net feeding behavior. *Behaviour* **148**, 575–602. (doi:10.1163/000579511X570893)
27. Woodward BL, Winn JP, Fish FE. 2006 Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *J Morphol* **267**, 1284–1294. (doi:10.1002/jmor. 10474).

28. Fish FE, Weber PW, Murray MM, Howle LE. 2011 The tubercles on humpback whales' flippers: application of bio-inspired technology. *Integr. Comp. Biol.* **51**, 203–213.
29. True FW. 1983 The whalebone whales of the western North Atlantic. Washington, DC: Smithsonian Institution Press.
30. Fish FE, Battle JM. 1995 Hydrodynamic design of the humpback whale flipper. *J. Morphol.* **225**, 51–60.
31. Tomilin AG. 1957 Mammals of the U.S.S.R. and adjacent countries. **9**: Cetacea. Moscow: Nauk S.S.S.R. (English Translation, 1967, Israel Program for Scientific Translations, Jerusalem)
32. Perkins J, Whitehead H. 1977 Observations on three species of baleen whales off northern Newfoundland and adjacent waters. *Fish. Res. Board Can.* **34**, 1436-1440.
33. Madsen CJ, Herman LM. 1980. Social and ecological correlates of cetacean vision and visual appearance. In: Herman LM, editor. Cetacean behavior: mechanisms & functions. Malabar, FL: R. E. Krieger Publications. p. 101–47.
34. Fish FE, Howle LE, Murray MM. 2008 Hydrodynamic flow control in marine mammals. *Integr. Comp. Biol.* **48**, 788–800.
35. Matthews LH. 1937 The humpback whale, *Megaptera nodosa*. Discovery Reports 17, 7-92.
36. Overholtz WJ, Nicolas JR. 1979 Apparent feeding by the fin whale, *Balaenoptera physalus*, and humpback whale, *Megaptera novaeangliae*, on the American sand lance, *Ammodytes americanus*, in the northwest Atlantic. *Fish. Bull.* **77**, 285–287.
37. Ichii T, Kato H. 1991 Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biol.* **11**, 479–487.

38. Brodie P. 1977 Form, function and energetics of Cetacea: a discussion. In: Harrison RJ (ed) Functional anatomy of marine mammals. New York: Academic Press.
39. Cooper LN, Sedano N, Johansson S, May B, Brown JD, Holliday CM, Kot BW, Fish FE. 2008) Hydrodynamic performance of the minke whale (*Balaenoptera acutorostrata*) flipper. *J. Exp. Biol.* **211**, 1859–1867. (doi: 10.1242/jeb.014134)
40. Segre PS, Seakamela SM, Meÿer MA, Findlay KP, Goldbogen JA. 2017 A hydrodynamically active flipper-stroke in humpback whales. *Curr. Biol.* **27**, R636–R637. (doi:10.1016/j.cub.2017.05.063)
41. Fish FE. 1994 Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Aust. J. Zool.* **42**, 1–16.
42. Miklosovic DS, Murray MM, Howle LE, Fish FE. 2004 Leading-edge tubercles delay stall on humpback whale (*Megaptera novaeangliae*) flippers. *Phys. Fluids* **16**, L39 (doi:10.1063/1.1688341).
43. Howell AB. 1930 Aquatic Mammals: their adaptations to life in the water. New York: Dover.
44. Chenoweth EM, Straley JM, McPhee MV, Atkinson S, Reifenstuhl S. 2017 Humpback whales feed on hatchery-released juvenile salmon. *R. Soc. open sci.* **4**, 170180. (doi: 10.1098/rsos.170180)
45. Pigliucci M. 2005 Evolution of phenotypic plasticity: Where are we going now? Trends Ecol. **20**, 481–486. (doi:10.1016/j.tree.2005.06.001)
46. Barlow JJ, Calambokidis E, Falcone A. 2011 Humpback whale abundance in the north pacific estimated by photographic capture-recapture with bias correction from simulation studies. *Mar. Mamm. Sci.* **27**, 793–818.
47. Katona S, Whitehead H. 1981 Identifying humpback whales using their natural markings. *Polar Record* **20**, 439-444. doi:10.1017/S003224740000365X

48. Straley JM, Gabriele CM. 2000 Humpback whales of southeast Alaska. Humpback whale fluke identification catalog. Third printing. National Park Service, Gustavus, Alaska.

49. Volk EC, Schroder SL, Grimm JJ. 1999 Otolith thermal marking. *Fish. Res.* **43**, 205–219. (doi:10.1016/S0165-7836(99)00073-9)

50. Millias JG. 1907 From Placentia Bay to Spitzbergen: a naturalist aboard a North Atlantic whaler. From "Newfoundland and Its Untrodden Ways". London. Extracts printed in Nature Canada, 2(4) 3-8 (1973)

51. Werth AJ, Kosma MM, Chenoweth EM, Straley JM. 2019 New views of humpback whale flow dynamics and oral morphology during prey engulfment. Mar. Mamm. Sci. **000**, 1-23. (doi.10.1111/mms.12614)

52. Pyenson ND, Goldbogen JA, Vogl AW, Szathmary G, Drake RL, Shadwick RE. 2012 Discovery of a sensory organ that coordinates lunge feeding in rorqual whales. *Nature* **485**, 498–501.

53. Allen WE. 1920 Behavior of loon and sardines. *Ecology* **1**, 309-310.

54. Breder CM. 1959 Studies on the social groups of fish. Bull. Am. Mus. Nat. Hist. **117**, 397-481.

55. Radakov DV. 1973 Schooling in the Ecology of Fish (Translated by H. Mills). New York: Halstead Press.

56. Pitcher TJ, Wyche CJ. 1983 Predator-avoidance behaviours of sand-eel schools: why schools seldom split. In: Predators and Prey in Fishes (Ed. by D. L. G. Noakes, D. G. Lindquist, G. S. Helfman & J. A. Ward), pp. 193-204. Boston: Dr W. Junk Publishers.

57. Pitcher TJ, Parrish JK. 1993 Functions of shoaling behaviour in teleosts. 363–439. In: TJ Pitcher, ed. Behaviour of teleost fishes, 2nd Ed. Chapman & Hall, New York.

58. Nemeth RS, Anderson JJ. 1992 Response of juvenile Coho and Chinook Salmon to strobe and mercury vapor lights. *North Am. J. Fish. Manag.* **12**, 684–692. (doi: 10.1577/1548-8675(1992)012<0684:ROJCAC>2.3.CO;2)
59. Chenoweth EM. 2018 Bioenergetic and economic impacts of humpback whale depredation at salmon hatchery release sites [dissertation]. Fairbanks (AK): University of Alaska Fairbanks.
60. Cade DE, Friedlaender AS, Calambokidis J, Goldbogen JA. 2016 Kinematic diversity in rorqual whale feeding mechanisms. *Curr. Biol.* **26**, 2617–2624. (doi:10.1016/j.cub.2016.07.037)
61. Johnson MP, Tyack PL. 2003 A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Ocean. Eng.* **28**, 3– 12. (doi:10.1109/JOE.2002.808212)

2.11 Figures

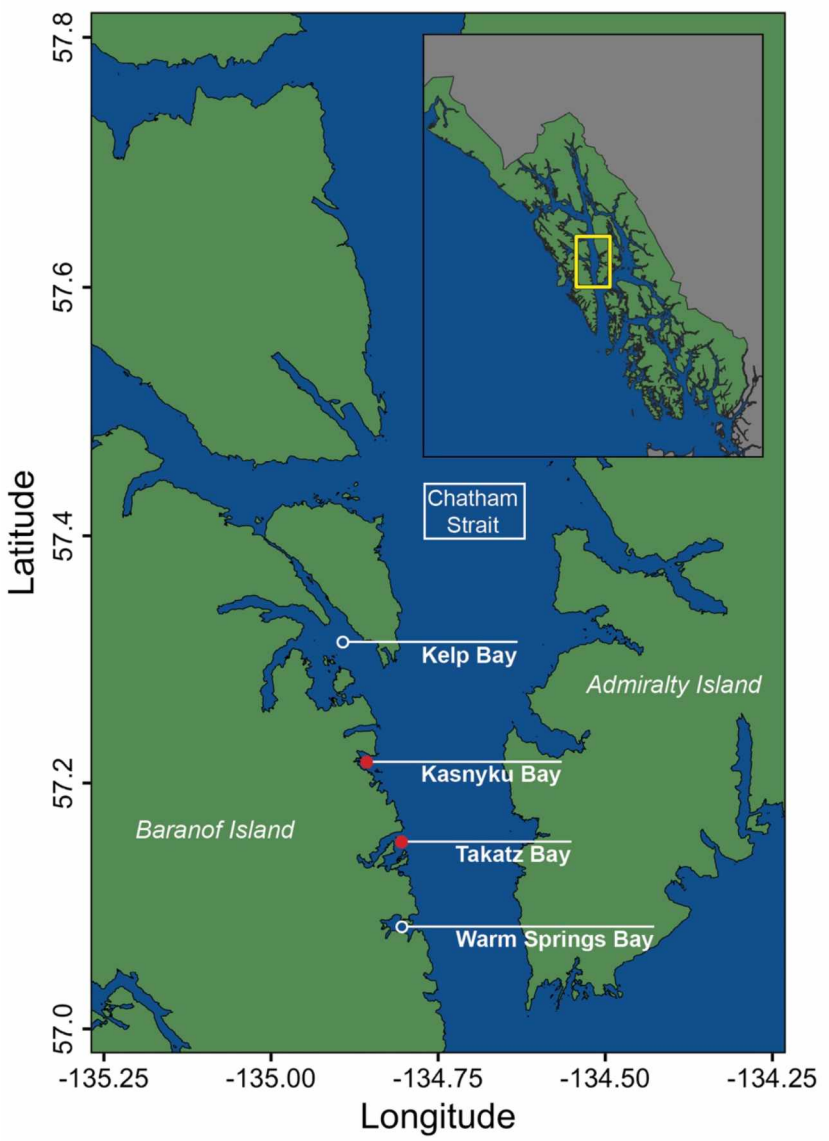

Figure 2.1. Study sites used to document foraging behaviours of humpback whales in Southeast Alaska (2016–2018). Red dots indicate release sites for juvenile hatchery-reared salmon.

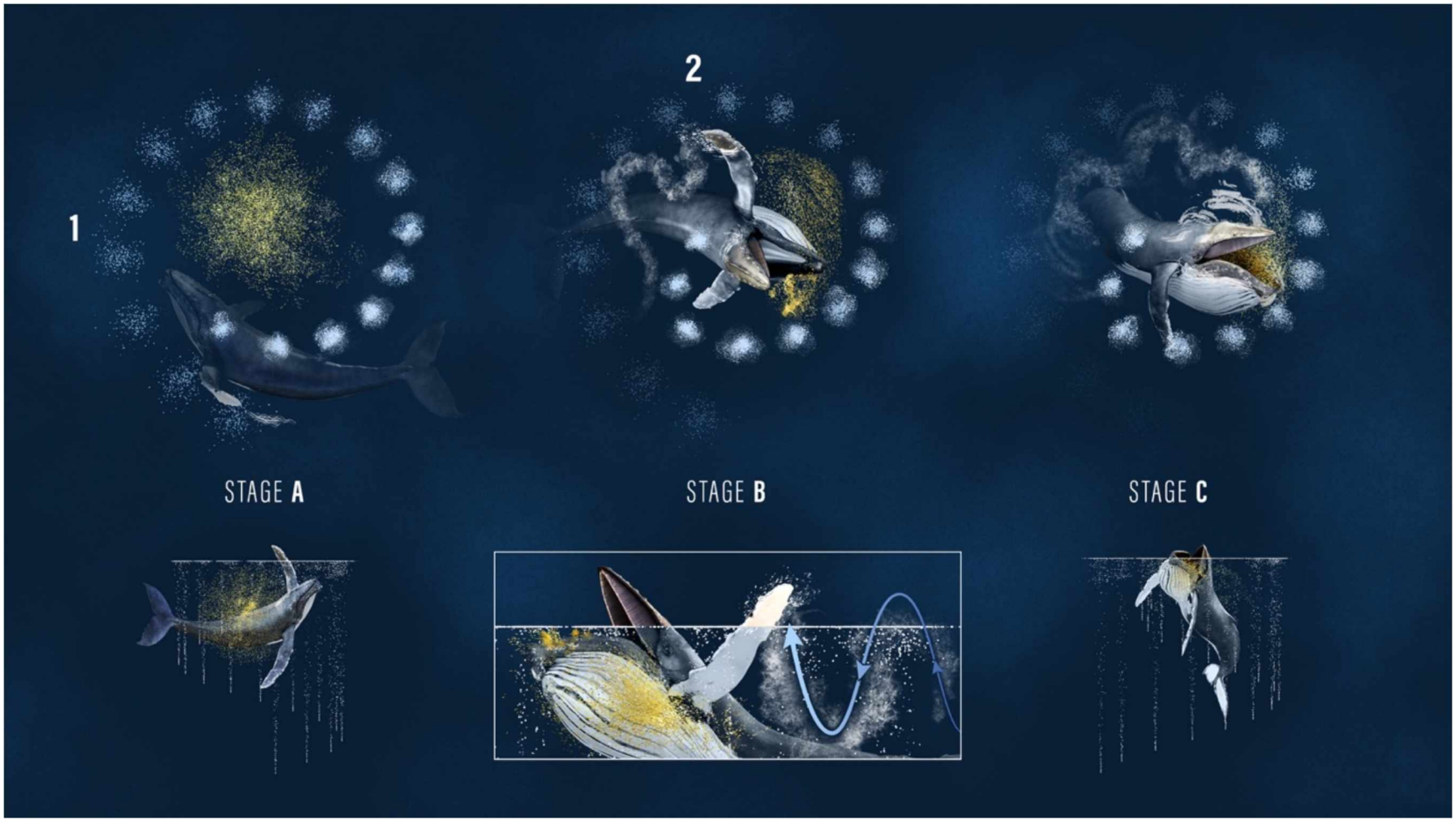

Figure 2.2. Graphical representations of horizontal pectoral herding by Whale A in Southeast Alaska. Prey are denoted in yellow. Stage A: Deployment of an upward-spiral bubble-net to corral the prey and establish the first barrier (1). Stage B: Movement of the left pectoral in and out of the water, along the edge of the bubble-net barrier, creating a secondary barrier (2). Stage C: Lunge to engulf the prey. Graphic by Kyle Kosma.

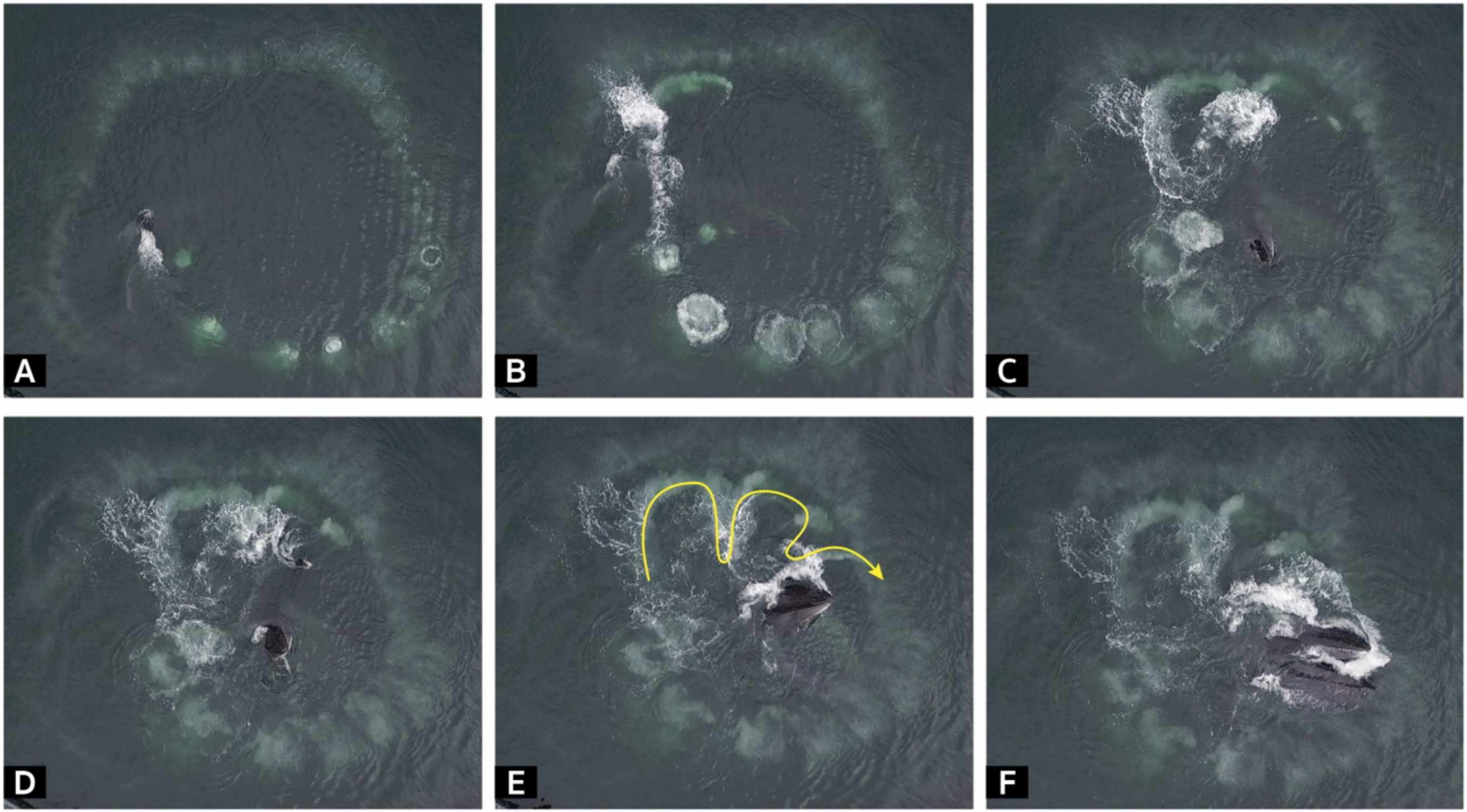

Figure 2.3. Photographic sequence involving horizontal pectoral herding by Whale A in Southeast Alaska. Movements progress from (A) beginning to (F) end. (A) Bubble-net formation; (B–E), horizontal pectoral herding; (F) terminal lunge. Yellow arrow represents the sinusoidal pectoral movement along the edge of the bubble-net barrier.

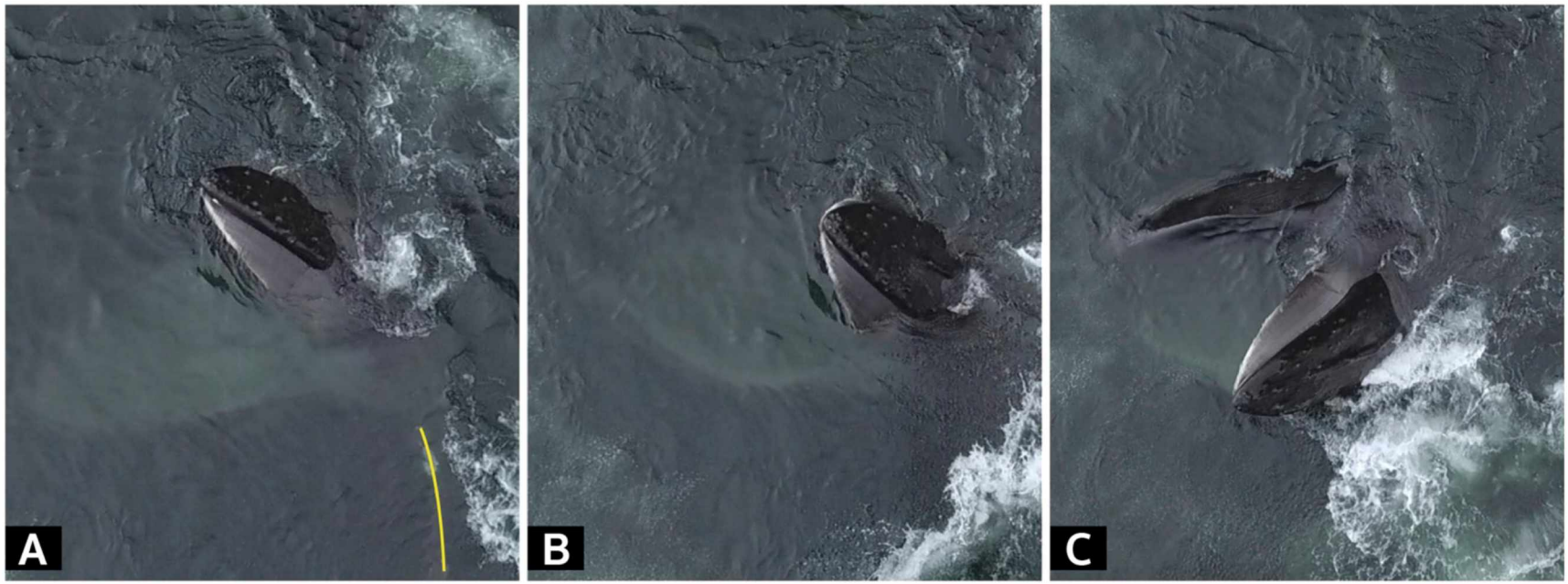

Figure 2.4. Photographic sequence of head tilt during the final portion of a lunge associated with horizontal pectoral herding by Whale A in Southeast Alaska. Movements progress from (a) earliest to (c) latest. Yellow line denotes the location of pectoral.

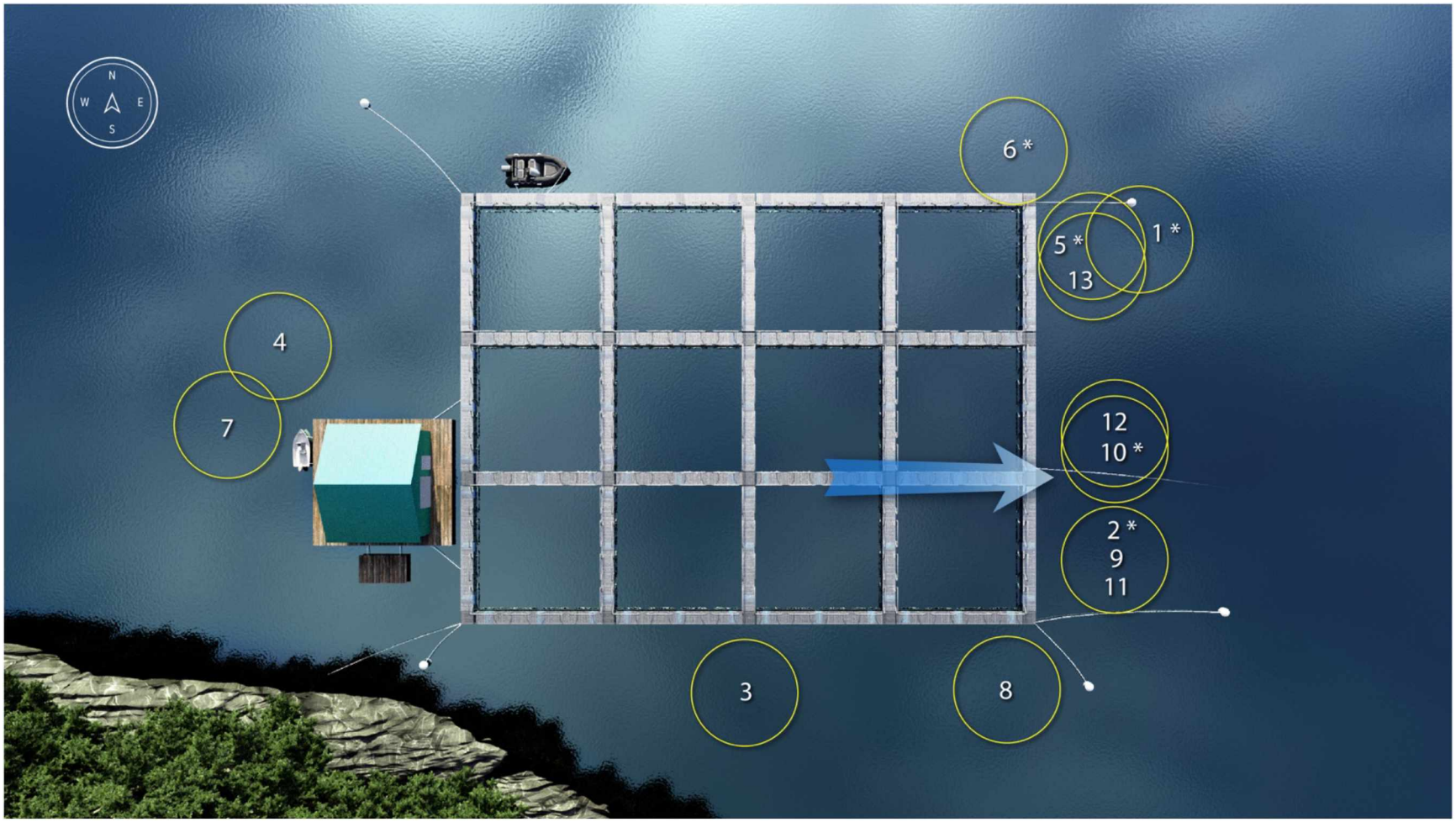

Figure 2.5. Graphical representation of the net pen structures at Hidden Falls Hatchery, in Kasnyku Bay (Southeast Alaska). Yellow circles represent bubble-nets created during feeding events for Whale B, numbered in chronological order. Blue arrow marks where juvenile coho salmon were being released into the marine environment. An asterisk denotes a feeding event conducted in sunlit waters. Events 1, 3, 4, 7, 11 and 12 involved a lateral lunge. Events 8, 9 and 13 involved a vertical lunge. Events 2, 5, 6 and 10 involved vertical pectoral herding. Graphic by Kyle Kosma.

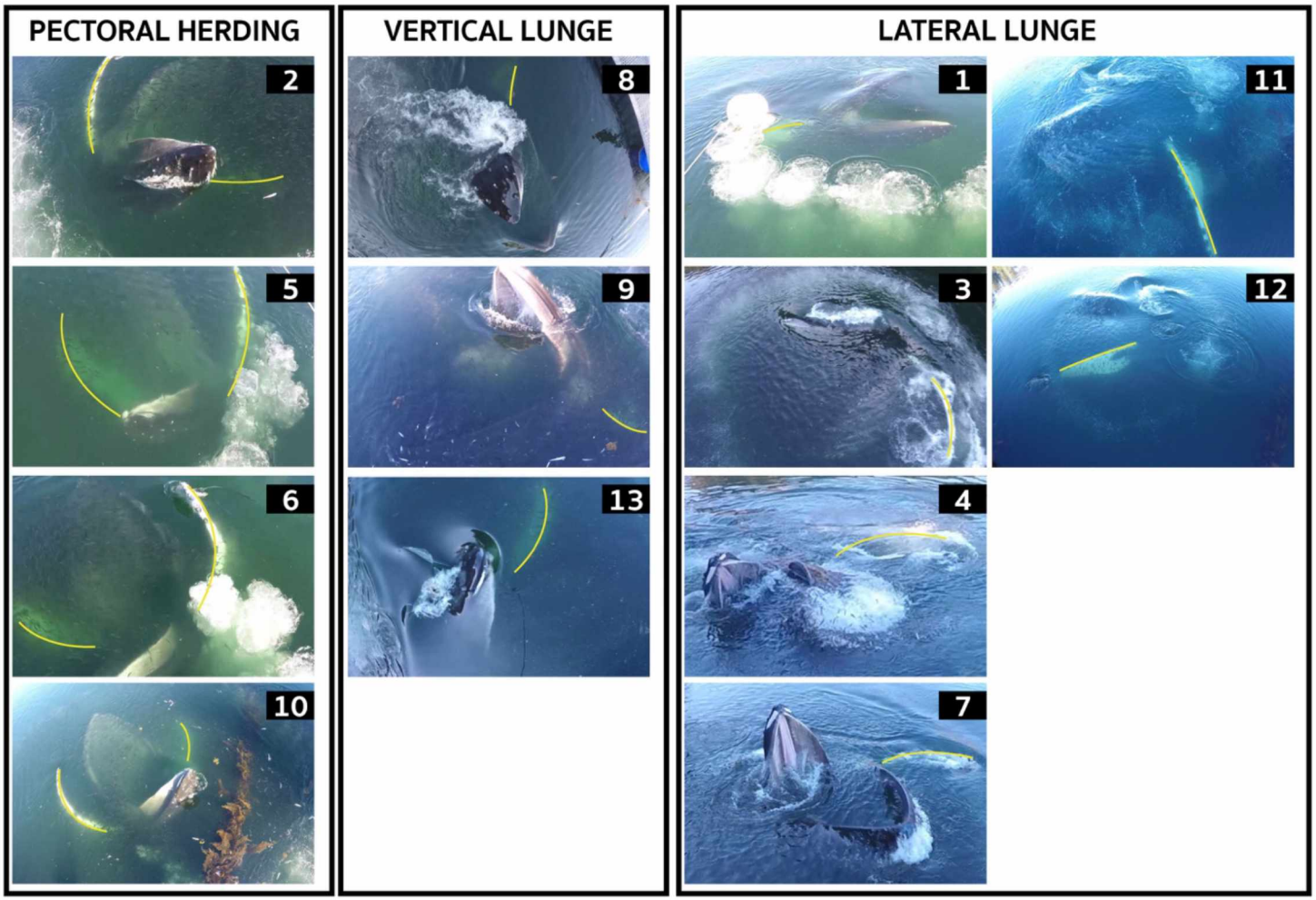

Figure 2.6. Snapshots from the footage of feeding events at Hidden Falls Hatchery, Kasnyku Bay (Southeast Alaska; 16 May 2017) by Whale B. Images are grouped according to three different kinematic feeding techniques at the conclusion of bubble-net formation: vertical pectoral herding, vertical lunge and lateral lunge. Events 2, 5, 6 and 10 involved vertical pectoral herding. Events 8, 9 and 13 involved a vertical lunge. Events 1, 3, 4, 7, 11 and 12 involved a lateral lunge. Yellow lines outline pectoral locations.

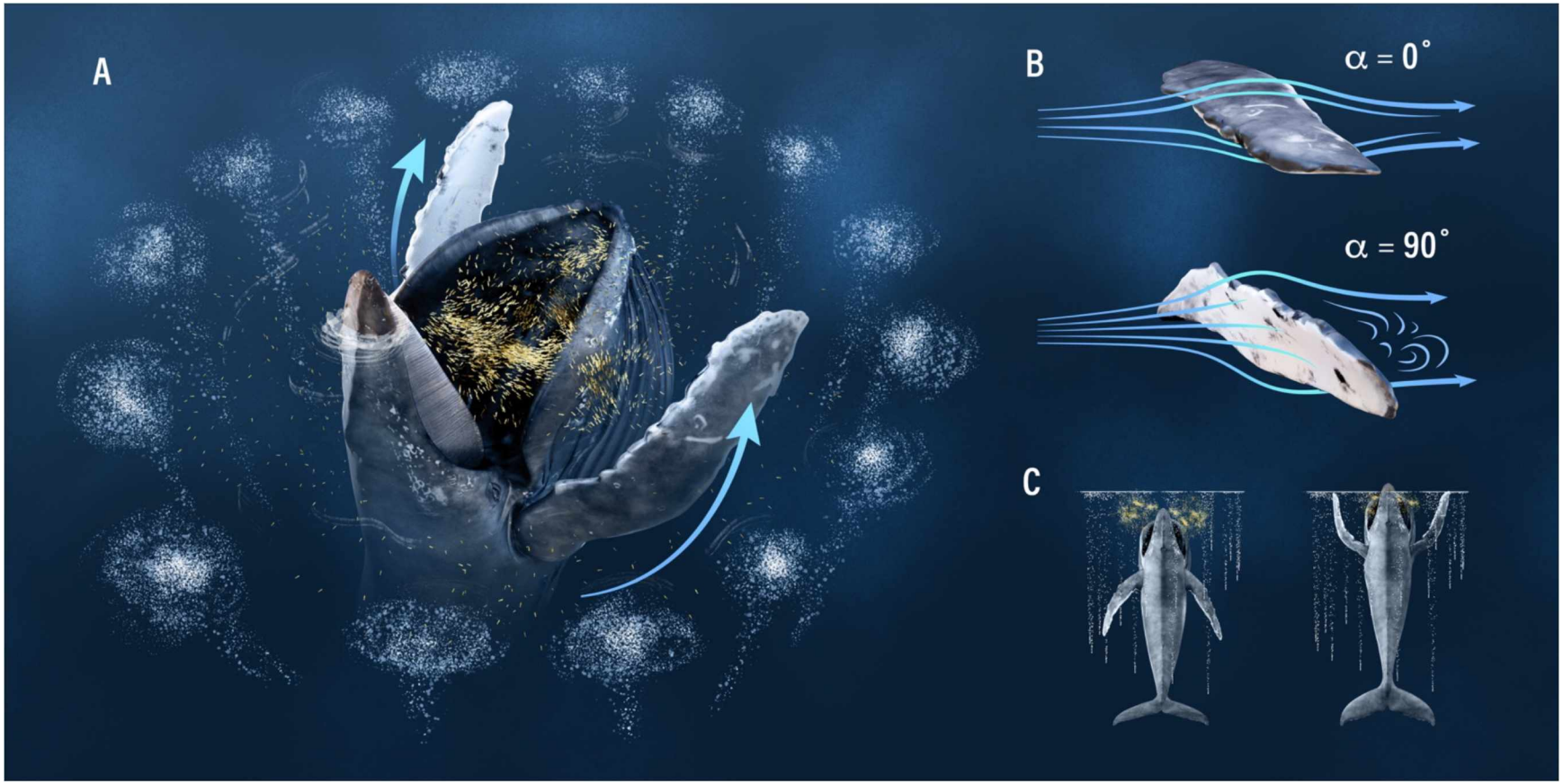

Figure 2.7. Graphical representation of vertical pectoral herding by Whale B in Southeast Alaska. Prey are denoted in yellow. (a) Whale deploys an upward-spiral bubble-net to corral prey and establish the first barrier; pectorals then protract to form a 'V' shape around the open mouth (depicted by blue arrows), creating a second physical barrier. (b) Change in the angle of attack (α) from pre- (0°) to peri- (90°) vertical pectoral herding. (c) Body position comparison between pre- (left) and peri- (right) vertical pectoral herding. Graphic by Kyle Kosma.

Figure 2.8. Before and after photographs of vertical pectoral herding by Whale B in Southeast Alaska (images relate to feeding events 5 and 10). Yellow lines denote pectorals. Red circles highlight the location of prey before pectoral movement and a gap in prey after pectoral movement.

2.12 Supplemental Tables

Table S2.1. Observations associated with Whale A (#2360 in Southeast Alaska Humpback Whale Catalog) in Southeast Alaska (2016 to 2018). Type of behaviour, type of bubble-net, number of feeding sessions, presence (P) or absence (A) of pectoral herding and head tilt, number of feeding events with pectoral herding (N/V means we observed pectoral herding but there were no photographs or videos from that day), and prey type(s) are shown for each date and location.

Date	Location	Behaviour	Bubble-net Type	Number Feeding Sessions	Pectoral Herding	Number Events with Pectoral Herding	Number of Head Tilts (P/A/UNK)	Prey Type
5/13/16	Takatz Bay	Feeding	Solo	1	P	4	1/2/1	juvenile salmon
5/14/16	Takatz Bay	Feeding	Group	1	A			juvenile salmon
5/20/16	Warm Springs Bay	Feeding	Solo	1	P	35	26/6/3	juvenile salmon
5/21/16	Warm Springs Bay	Milling	N/A	0	N/A			N/A
5/22/16	Warm Springs Bay	Feeding	Solo	1	P	N/V		juvenile salmon
5/23/16	Kelp Bay	Traveling	N/A	0	N/A			N/A
5/24/16	Warm Springs Bay	Feeding	Solo	1	P	4	1/2/1	juvenile salmon
5/25/16	Kelp Bay	Traveling	N/A	0	N/A			N/A
5/28/16	Kelp Bay	Traveling	N/A	0	N/A			N/A
5/30/16	Warm Springs Bay	Feeding	Solo	1	P	3	0/3/0	juvenile salmon
6/8/16	Kelp Bay	Feeding	Solo	1	P	5	1/0/4	juvenile salmon
6/16/16	Warm Springs Bay	Feeding	Solo	1	P	N/V		juvenile salmon
6/21/16	Warm Springs Bay	Feeding	Solo	1	P	2	0/0/2	juvenile salmon
5/17/17	Kelp Bay	Feeding	Solo	1	P	1	0/1/0	juvenile salmon
5/25/17	Kelp Bay	Traveling	N/A	0	N/A			N/A
5/28/17	Kelp Bay	Traveling	N/A	0	N/A			N/A
5/30/17	Kasnyku Bay	Traveling	N/A	0	N/A			N/A
5/31/17	Kasnyku Bay	Feeding	Solo	1	P	3	0/1/2	juvenile salmon
6/1/17	Kasnyku Bay	Feeding	Solo	1	P	45	26/17/2	juvenile salmon
6/6/17	Kasnyku Bay	Feeding	Solo	1	P	5	1/3/1	juvenile salmon
6/9/17	Kasnyku Bay	Feeding	Solo	1	P	5	1/4/0	juvenile salmon

Table S2.1 (cont'd). Type of behaviour, type of bubble-net, number of feeding sessions, presence (P) or absence (A) of pectoral herding and head tilt, number of feeding events with pectoral herding (NV means we observed pectoral herding but there were no photographs or videos from that day), and prey type(s) are shown for each date and location.

Date	Location	Behaviour	Bubble-net Type	Number Feeding Sessions	Pectoral Herding	Number Events with Pectoral Herding	Number of Head Tilts (P/A/UNK)	Prey Type
6/10/17	Kelp Bay	Feeding	Group	1	A			Pacific herring
6/12/17	Kelp Bay	Feeding	Group	1	A			Pacific herring
6/28/17	Kelp Bay	Feeding	Solo	1	P	9	5/2/2	Pacific herring or juvenile salmon
7/8/17	Kelp Bay	Milling	N/A		N/A			N/A
7/15/17	Point Wilson	Feeding	Group	1	A			Pacific herring
5/22/18	Kasnyku Bay	Feeding	Solo	1	P	14	8/6/0	juvenile salmon

Table S2.2. Observations associated with Whale B (#2227 in Southeast Alaska Humpback Whale Catalog) in Southeast Alaska (16 May 2017). Time, location, light condition, number of feeding event, feeding behaviour, prey response, and details surrounding surface break are shown for each video. All feeding events involved a solo bubble-net.

Video Title	Time	Location	Light Condition	Number of Feeding Event	Feeding Behaviour	Prey Response	Surface Break
05162017_01_lateral	16:22	NE	Sun	1	Lateral Lunge	N/A	head first
05162017_02_herd	16:35	SE	Sun	2	Pectoral Herding	N/A	left pectoral and head in same second
05162017_03_lateral	16:38	S	Shade	3	Lateral Lunge	N/A	left pectoral first
05162017_04_lateral	16:46	W	Shade	4	Lateral Lunge	N/A	left pectoral first
05162017_05_herd	16:59	NE	Sun	5	Pectoral Herding	P	unknown
05162017_06_herd	17:02	NE	Sun	6	Pectoral Herding	P	left pectoral and head in same second
05162017_07_lateral	17:12	SW	Shade	7	Lateral Lunge	A	left pectoral and head in same second
05162017_08_vertical	17:14	SE	Shade	8	Vertical Lunge	A	head first
05162017_09_vertical	17:29	SE	Shade	9	Vertical Lunge	P	head first
05162017_10_herd	17:37	E	Sun	10	Pectoral Herding	P	left pectoral and head in same second
05162017_11_lateral	17:57	SE	Shade	11	Lateral Lunge	N/A	head first
05162017_12_lateral	18:19	E	Shade	12	Lateral Lunge	N/A	head first
05162017_13_vertical	18:33	NE	Shade	13	Vertical Lunge	N/A	head first

General Conclusions

In trophic ecology, individuals of the same species are often treated as ecologically equivalent (DeAngelis and Gross 1992; Łomnicki and Lomnicki 1980). However, generalist predator populations can be made up of many individual specialists that target different prey (Bolnick *et al.* 2003). The successful adoption of new prey items within a generalist predator population will differ in terms of how variable individual diets are within that population (Pintor and Byers 2015). In Chatham Strait, at least three humpback whales have consistently incorporated hatchery-released juvenile salmon into their diets. Though all three whales successfully adopted this new prey source, each varied in their degree of consumption. Foraging tactics for aggregating juvenile salmon during a solo bubble-net also varied among individuals. This thesis contributes to our understanding of humpback whale predation on hatchery-reared juvenile salmon, provides insight into isotopic incorporation rates in the skin of humpback whales, and deepens our knowledge on foraging tactics used by a large marine predator.

Individual Specialization

Humpback whale predation at release sites is geographically widespread in Southeast Alaska (Chenoweth 2018); however, only a few individuals with specialized behaviors have incorporated this anthropogenically sourced prey into their annual diets. Our findings indicated different diet compositions of humpback whales foraging on hatchery-reared juvenile salmon in comparison to the local population. Stable isotope analysis showed minimal temporal variability in the diets of all whales sampled throughout the study area but suggested some degree of foraging specialization among hatchery-associated whales. The three hatchery-associated whales fed at significantly higher trophic levels than other humpback whales foraging on marine-origin prey. Differences in trophic levels, which

persisted throughout the various layers of skin and over our two-year study, likely reflect differences in prey selectivity between the two groups of foraging whales. Isotopically, hatchery-associated whales reflected a piscivorous diet, whereas other whales consumed more planktivorous prey. We believe that either a) the three hatchery-associated whales were forage fish specialists, which led to their discovery of hatchery-released juvenile salmon or b) the incorporation of this new prey item led to the development of a more forage fish specialization. Repeat sampling and stable isotope analysis across a relatively broad time scale reveals differences in foraging habits beyond the incorporation of hatchery-released salmon as a new prey source.

Specialized foraging strategies are dependent on a stable predictable resource (West-Eberhard 1989). Juvenile salmon have been released from Hidden Falls Hatchery every spring since the late 1970s (Northern Southeast Regional Aquaculture Associaion 2019), generating up to ~50 years of predictable availability for predators in the area. This predictability, along with known release dates, provided a semi-controlled feeding experiment to test the incorporation and contribution of hatchery-released salmon into humpback whale diets. These conditions allowed us to examine stable nitrogen and carbon isotope incorporation and turnover rate in a way not previously possible for free-ranging large cetaceans. Though our stable isotope results were variable, we measured a significant isotopic shift in one of our hatchery-associated whales that suggests isotopic incorporation rates between 74 and 85 days. This time period for prey incorporation into humpback whale skin is slightly larger than the incorporation rates of bottlenose dolphins (Hicks *et al.* 1985) and beluga whales (70 to 75 d; St. Aubin *et al.* 1990). An accurate estimate of incorporation rate is imperative for interpreting isotopic mixing model results. Though we see our estimate as preliminary, we believe that it provides valuable information

for the temporal movement of stable isotopes through the tissue of large, baleen whales. Future studies could continue to use salmon hatchery releases as controlled feeding experiments, but would need to follow and sample hatchery-associated whales for longer (ideally > 100 d) to better resolve turnover rates.

Innovative Foraging Tactics

Foraging specialization within a generalist predator population is only possible if there are adaptive foraging behaviors at the individual level. Our observations of horizontal and vertical pectoral herding provided evidence of behavioral plasticity in foraging and suggested considerable variation among individual humpback whales, including those who have incorporated hatchery-released juvenile salmon into their diets. We documented two of the three hatchery-associated whales using 'pectoral herding' to further condense prey within a solo bubble-net. This study provided the first empirical evidence of this innovative foraging tactic and is the first to document pectoral herding within a solo bubble-net. Though we believe that this behavior is likely employed by other whales foraging on non-salmonid prey, further documentation of solo bubble-net feeding would further our understanding about the conditions that promote the use of pectoral herding by humpback whales.

Summary and Implications for Future Study

The whales we observed appear to be highly flexible individuals that successfully use different tactics to approach the same prey and in the same situation (Wiley *et al.* 2011). Hatchery-associated whales exhibited higher trophic level diets than other whales in the area, suggesting some degree of specialization in foraging behavior. However, all three hatchery-associated whales employed a different tactic for foraging on juvenile hatchery-

released salmon: horizontal pectoral herding, vertical pectoral herding, and streamline lunge. This flexibility may enable individual humpback whales to effectively acclimate to variable environments while gaining potential survivorship and fitness benefits (Hadfield and Strathmann 1996). Diversity in foraging behaviors could be advantageous to the humpback whale population as they experience changes in their local environment due to climate change. Humpback whales have been labeled as a promising indicator species because they fed on a diverse array of prey and are distributed throughout the world's oceans (Fleming *et al.* 2016). Tracking the variations in humpback whale behavior will provide crucial insight into the broader changes our oceans will experience, but they may not be prescient indicators for the fates of more specialized marine species.

Though we were unable to effectively estimate the contribution of hatchery salmon to the diets of humpback whales, this work provides baseline information with which to build upon in future study. We provided a preliminary estimate of isotopic incorporation rate and have identified the need for more extensive prey sampling in nearshore waters. Our study also deepened our knowledge about how these animals are able to exploit a non-schooling prey species of considerable commercial value. Each of these components bring us a few steps closer to understanding the predation impact of humpback whales on the survival of juvenile salmon and the benefits of hatchery production. We illustrated that multiple whales have similar foraging preferences but employ disparate foraging tactics to consume the same prey. Future study should focus on describing the behavior of these individual whales on a large temporal scale to better understand their overall foraging behaviors. Understanding the behaviors that drive humpback whale predation will help hatchery management in Southeast Alaska and therefore the promotion of a sustainable salmon fishery. The knowledge we gain about the predation of humpback whales incorporating hatchery-

released salmon into their diet can be used to address the impact this predator might have on other commercially important fish species.

References: General Introduction and General Conclusions

Araki, H. and Schmid, C. 2010. Is hatchery stocking a help or harm? Evidence, limitations and future directions in ecological and genetic surveys. Aquaculture, 308(SUPPL.1), S2–S11. https://doi.org/10.1016/j.aquaculture.2010.05.036

Baker, C. S. 1985. The population structure and social organization of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. University of Hawaii. Retrieved from: http://search.ebscohost.com/login.aspx?direct=true&db=cat07106a&AN=uaf.3528999&site=eds-live.

Beamish, R. J. and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography. 49(1–4):423–437.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., and Forister, M. L. 2003. The ecology of individuals: Incidence and implications of individual specialization. American Naturalist. 161(1):1–28.

Chenoweth, E. M., Straley, J. M., McPhee, M. V., Atkinson, S., and Reifenstuhl, S. 2017. Humpback whales feed on hatchery-released juvenile salmon. Royal Society Open Science. 4(7):170180.

Chenoweth, E. 2018. Bioenergetic and economic impacts of humpback whale depredation at salmon hatchery release sites. PhD Dissertation, University of Alaska Fairbanks. 147 pp.

Chenoweth, E. M. and Criddle, K. R. 2019. The economic impacts of humpback whale depredation on hatchery-released juvenile Pacific salmon in Southeast Alaska. Marine and Coastal Fisheries. 11(1):62–75.

D'Vincent, C. G., Nilson, R. M., and Hanna, R. E. 1985. Vocalization and coordinated feeding behavior of the humpback whale in Southeastern Alaska. Scientific Reports of the Whale Research Institute. 36(36):41–47.

DeAngelis, D. and Gross, L. 1992. Individual-based models and approaches in ecology: populations, communities, and ecosystems. Boca Raton, FL. Chapman and Hall. 545 pp.

Fleming, A. H., Clark, C. T., Calambokidis, J., and Barlow, J. 2016. Humpback whale diets respond to variance in ocean climate and ecosystem conditions in the California Current. Global Change Biology. 22(3):1214–1224.

Goldbogen, J. A., Cade, D. E., Calambokidis, J., Friedlaender, A. S., Potvin, J., Segre, P. S., and Werth, A. J. 2017. How baleen whales feed: the biomechanics of engulfment and filtration. Annual Review of Marine Science. 9(1):367–386.

Hadfield, M. G. and Strathmann, M. F. 1996. Variability, flexibility and plasticity in life histories of marine invertebrates. Oceanologica Acta. 19:323–334.

Hain, J. H. W., Carter, G. R., Krauss, S. D., Mayo, C. A., and Winn, H. E. 1982. Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. Fisheries Bulleti. 80:259–268.

Hartt, A. 1980. Juvenile salmonids in the oceanic ecosystem: the critical first summer. *In* W. J. McNeil and D. C. Himsworth (eds.). Salmonid Ecosystems of the North Pacific. Corvallis, OR. Oregon State University Press. 25–57.

Hendrix, a N., Straley, J., Gabriele, C. M., and Gende, S. M. 2012. Bayesian estimation of humpback whale (*Megaptera novaeangliae*) population abundance and movement patterns in southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences. 69:1783–1797.

Hicks, B. D., St Aubin, D. J., Geraci, J. R., and Brown, W. R. 1985. epidermal growth in the bottlenose dolphin, *Tursiops truncatus*. The Journal of Investigative Dermatology. 85(1):60–63.

Ingebrigtsen, A. 1929. Whales caught in the North Atlantic and other seas. Rapports et Process-Verbaux Des Réunion Conseil International Exploration de La Mer. 56:1–26.

Jurasz, C. M. and Jurasz, V. P. 1979. Feeding modes of the humpback whale, *Megaptera novaeangliae*, in Southeast Alaska. The Scientific Reports of the Whales Research Institute. 31:69–83.

Kosma, M. M., Werth, A. J., Szabo, A. R., and Straley, J. M. 2019. Pectoral herding: an innovative tactic for humpback whale foraging. Royal Society Open Science. 6:191104. doi:10.1098/rsos.191104.

Łomnicki, A. and Lomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos. 35(2):185.

McMillan, C. J., Towers, J. R., and Hildering, J. 2018. The innovation and diffusion of "trap-feeding", a novel humpback whale foraging strategy. Marine Mammal Science. 35(3):779–796.

Moran, J. R., Heintz, R. A., Straley, J. M., and Vollenweider, J. J. 2018. Regional variation in the intensity of humpback whale predation on Pacific herring in the Gulf of Alaska. Deep-Sea Research Part II: Topical Studies in Oceanography. 147(2017):187–195.

Northern Southeast Regional Aquaculture Association. 2019. Hidden Falls. Retrieved from: https://www.nsraa.org/?page_id=391.

Parks, S. E., Cusano, D. A., Stimpert, A. K., Weinrich, M. T., Friedlaender, A. S., and Wiley, D. N. 2014. Evidence for acoustic communication among bottom foraging humpback whales. Scientific Reports. 4:1–7.

Pintor, L. M. and Byers, J. E. 2015. Individual variation in predator behavior and demographics affects consumption of non-native prey. Behavioral Ecology. 26(3):797–804.

Sharpe, F. A. 2001. Social foraging of the southeast Alaskan humpback whale, *Megaptera novaeangliae*. PhD Dissertation, Simon Fraser University. 129 pp.

Sharpe, F. A and Dill, L. M. 1997. The behavior of Pacific herring schools in response to artificial humpback whale bubbles. Canadian Journal of Zoology. 75(1982):725–730.

St Aubin, D. J., Smith, T. G., and Geraci, J. R. 1990. Seasonal epidermal molt in beluga whales, *Delphinapterus leucas*. Canadian Journal of Zoology. 68(2):359–367.

Straley, J. M., Moran, J. R., Boswell, K. M., Vollenweider, J. J., Heintz, R. A., Quinn, T. J., *et al.* Rice, S. D. 2017. Seasonal presence and potential influence of humpback whales on wintering Pacific herring populations in the Gulf of Alaska. Deep-Sea Research Part II: Topical Studies in Oceanography. 147(2017):173–186.

U.S. Department of Commerce. 2016. Technical Amendments and Recodification of Alaska Humpback Whale Approach Regulations. 81 RF 62018. 4 pp.

Vercessi, L. 2015. Alaska salmon fisheries enhancement program: 2014 Annual Report. Fishery Management Report. 15-15. 99 pp.

Ware, C., Wiley, D. N., Friedlaender, A. S., Weinrich, M., Hazen, E. L., Bocconcelli, A., *et al.* Abernathy, K. 2014. Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, U.S.A. Marine Mammal Science. 30(2):494–511.

Watkins, W. A. and Schevill, W. E. 1979. Aerial observation of feeding behavior in four baleen whales: *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. Journal of Mammalogy. 60(1):155–163.

Weinrich, M.T., Lambertsen, R. H., Baker, C. S., Schilling, M. R., and Belt, C. R. 1991. Behavioural responses of humpback whales (*Megaptera novaeangliae*) in the Southern Gulf of Maine to biopsy sampling. Report to the International Whaling Commission, Special Issue. 13:91–97.

Weinrich, Mason T., Schilling, M. R., and Belt, C. R. 1992. Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. Animal Behaviour. 44(6):1059–1072.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics. 20(1989):249–278.

Wiley, D. N., Ware, C. R., Bocconcelli, A., Cholewiak, D. M., Friedlaender, A. S., Thompson, M. A., and Weinrich, M. T. 2011. Underwater components of humpback whale bubble-net feeding behaviour. Behaviour. 148(5):575–602.

Witteveen, B. H. 2008. Using stable isotopes to assess population structure and feeding ecology of North Pacific humpback whales (*Megaptera novaeangliae*). PhD Disseration, University of Central Florida. 144 pp.

Appendix: Research Approval

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 17, 2016

To: Janice Straley
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [907314-2] Can Stable Isotopes be Used to Estimate the Contribution of Hatchery Salmon to the Diet of Humpback Whales?

The IACUC reviewed and approved the Response/Follow-Up referenced above by Designated Member Review.

Received:	May 15, 2016
Approval Date:	May 17, 2016
Initial Approval Date:	May 17, 2016
Expiration Date:	May 17, 2017

This action is included on the June 9, 2016 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix: Research Approval (cont'd)

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 11, 2017

To:	Janice Straley Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[907314-4] Can Stable Isotopes be Used to Estimate the Contribution of Hatchery Salmon to the Diet of Humpback Whales?

The IACUC reviewed and approved the modification to the Personnel List referenced above by Administrative Review.

Received:	March 21, 2017
Approval Date:	April 11, 2017
Initial Approval Date:	May 17, 2016
Expiration Date:	May 17, 2018

This action is included on the May 11, 2017 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

Appendix: Research Approval (cont'd)

STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 115526
JUNEAU, ALASKA 99811-5526

Permit No. **CF-16-049**

Expires: **12/31/2016**

FISH RESOURCE PERMIT
(For Scientific/Collection Purposes)

This permit authorizes: **Jan Straley**
(whose signature is required on page 3 for permit validation)
of
University of Alaska Southeast
1332 Seward Ave., Sitka, AK 99835
(907)747-7779 **jmstraley@uas.alaska.edu**

to conduct the following activities from **February 16, 2016** to **December 31, 2016** in accordance with AS 16.05.930 and AS 16.05.340(b).

Purpose: To identify prey of humpback whales, or other large cetaceans.

Location: Southeast Alaska, including offshore (54˚-60˚N, 132˚-142˚W), and Prince William Sound (60°-61°N, 144°-148°W)

Species: See **Species List** on pages 3-4.

Method of Collection: Dip nets, trawls, hook-and-line, minnow traps, gill nets, zooplankton nets, cast nets and light traps. See **Stipulations** section.

Disposition: Collected specimens will be sacrificed and frozen or preserved for analysis. See **Stipulations** section.

A COLLECTION REPORT IS DUE January 30, 2017 and a **COMPLETION REPORT IS DUE June 30, 2017**. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfg.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 2/16/16
Permit Coordinator
Division of Commercial Fisheries
Alaska Department of Fish and Game

Appendix: Research Approval (cont'd)

STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 115526
JUNEAU, ALASKA 99811-5526

Permit No. **CF-17-056**

Expires: **12/31/2017**

FISH RESOURCE PERMIT
(For Scientific/Collection Purposes)

This permit authorizes: **Jan Straley**
(whose signature is required on page 3 for permit validation)
of
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(907)747-7779 **jmstraley@uas.alaska.edu**

to conduct the following activities from **March 1, 2017** to **December 31, 2017** in accordance with AS 16.05.930 and AS 16.05.340(b).

Purpose: To identify prey of humpback whales, or other large cetaceans.

Location: Southeast Alaska, including offshore (54°-60°N, 132°-142°W)

Species: See **Species List** on pages 3-4.

Method of Collection: Dip nets, trawls, hook-and-line, minnow traps, gill nets, zooplankton nets, cast nets and light traps. See **Stipulations** section.

Disposition: Collected specimens will be sacrificed and frozen or preserved for analysis. See **Stipulations** section.

A COLLECTION REPORT IS DUE January 30, 2018 and a **COMPLETION REPORT IS DUE June 30, 2018**. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfg.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
3. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
4. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
5. UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 3/15/17
Deputy or Assistant Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE
Silver Spring, MD 20910

JUL 31 2015

Ms. Janice Straley
University of Alaska Southeast
1332 Seward Avenue
Sitka, Alaska 99835

Dear Ms. Straley:

The National Marine Fisheries Service has issued Permit No. 14122-01, which amends and replaces Permit No. 14122, for research activities on marine mammals. This minor amendment extends the duration of your permit one year. The changes to specific Terms and Conditions are reflected in bold font.

You may continue the research activities authorized in Permit No. 14122-01 until (1) our agency has made a decision on your new application, or (2) you have exhausted the total number of takes authorized for the fifth year of the permit, whichever occurs first.

In addition to extending your permit, we have added Dr. Andrew Szabo as a Co-investigator (CI) per your request and pursuant to Condition C.6. Please note that as Permit Holder, you are ultimately responsible for the activities of individuals operating under the authority of this permit and the taking, import, export and any related activities conducted under the permit. You must be on site during activities conducted under this permit unless a CI is present to act in place of the PI. Please ensure the CIs receive a copy of this letter and the permit. Personnel listed in the permit may only use the permit with your permission as Permit Holder.

This letter also confirms that you may use dart tags with either two or three barbs. You requested authority to use three-barb tags to increase tag retention in cases where two-barb tags have failed. The anticipated effects from using three-barbed dart tags will be less than that of the fully implantable tags, which you are already authorized to use. As your take table already lists dart tags, no change to your permit is required.

Please note that some of your research may require a special use permit from the Alaska Maritime National Wildlife Refuge. Please contact the Refuge office at 2355 Kachemak Bay Drive, Suite 101, Homer, Alaska 99603 (phone: 907-235-6546; FAX: 907-235-7783).

As a reminder, import and export of species, or parts of species, listed on the Appendices to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) requires a CITES Permit. For further information please contact Ms. Lisa Lierheimer, U.S. Fish and Wildlife Service (USFWS), Division of Management Authority (DMA), Branch of Permits, MS: IA, 5275 Leesburg Pike, Falls Church, VA 22041-3803 (1-800-358-2104).

UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE
Silver Spring, MD 20910

Ms. Janice Straley
University of Alaska Southeast
1332 Seward Avenue
Sitka, Alaska 99835

MAY 17 2016

Dear Ms. Straley:

Thank you for your request to add Madison Kosma as a Co-investigator (CI) to Permit No. 14122-01 to conduct cetacean research in Alaskan waters. Following General Condition C.6 of your permit, Ms. Kosma has been included as a CI and is authorized to conduct all research activities specified in the permit.

Please note that as Permit Holder and Principal Investigator, you are ultimately responsible for the activities of individuals operating under the authority of this permit, including the taking, import, export and any related activities. You must be on site during activities conducted under this permit unless a CI is present to act in your place. Please attach this letter to Permit No. 14122-01 and ensure the CIs receive a copy of this letter and the permit. Personnel listed in the permit may only use the permit with your permission as Permit Holder.

It is your responsibility to notify the NMFS Assistant Regional Administrator for Protected Resources at least two weeks before planned fieldwork begins, as specified in your permit. Notification must include:

- locations and/or survey routes,
- estimated dates, and
- number and roles of participants.

Please contact Carrie Hubard or Amy Sloan at (301) 427-8401 or via email at carrie.w.hubard@noaa.gov or amy.sloan@noaa.gov if you have questions.

Sincerely,

Jolie Harrison
Chief, Permits and Conservation Division
Office of Protected Resources

UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE
Silver Spring, MD 20910

JUL 2 0 2017

Janice Straley
University of Alaska Southeast
1332 Seward Ave
Sitka, Alaska 99835

Dear Ms. Straley:

The National Marine Fisheries Service (NMFS) has issued Permit No. 18529-01 to you, for research activities on marine mammals. We have removed the condition that limited you to three approaches per day, added unmanned aircraft system activities, and added two Co-investigators. The changes to specific Terms and Conditions are reflected in bold font.

This permit is effective upon your signature and valid through August 31, 2021. To use your permit:

1. Read the permit, including attachments. If you have questions, call your permit analyst – Carrie Hubard or Amy Hapeman – at 301-427-8401 before signing the permit.
2. Sign and date both the original and "File Copy" signature pages.
3. Keep the original signature page with your permit.
4. Return the "File Copy" signature page to our office by:
   a. Email to your permit analyst;
   b. Fax (301-713-0376); or
   c. Mail (NMFS Permits and Conservation Division (F/PR1), 1315 East-West Hwy, Silver Spring, MD 20910).

Some of your research may require a special use permit from the Alaska Maritime National Wildlife Refuge. Please contact the Refuge office at 2355 Kachemak Bay Drive, Suite 101, Homer, Alaska 99603; phone (907)235-6546; fax (907)235-7783.

The import and export of species, or parts of species, listed on the Appendices to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) requires a CITES Permit. For further information please contact Ms. Mary Cogliano, U.S. Fish and Wildlife Service (USFWS), Division of Management Authority (DMA), Branch of Permits, MS: IA, 5275 Leesburg Pike, Falls Church, VA 22041-3803 (1-800-358-2104).

Unmanned aircraft systems (UAS) fall under the jurisdiction of the Federal Aviation Administration (FAA; http://www.faa.gov/). You must be compliant with FAA requirements when operating UAS under this permit. The FAA considers scientific research as either public

UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE
Silver Spring, MD 20910

JUL 11 2018

Janice Straley
University of Alaska Southeast
1332 Seward Ave
Sitka, Alaska 99835

Dear Ms. Straley:

Thank you for your request to remove Simon Niblett as a Co-investigator (CI) from Permit No. 18529-01 and to authorize Kelly Cates and Madison Kosma as unmanned aircraft system (UAS) pilots. Following General Condition C.7 of your permit, we've removed Mr. Niblett and changed Ms. Cates' and Ms. Kosma's permitted roles to show that they are now authorized as UAS pilots. An updated Appendix 2 is attached.

Please note that as Permit Holder and Principal Investigator, you are ultimately responsible for the activities of individuals operating under the authority of this permit, including the taking and any related activities. You must be on site during activities conducted under this permit unless a CI is present to act in your place. Please attach this letter to Permit No. 18529-01 and ensure the CIs receive a copy of this letter and the permit. Personnel listed in the permit may only use the permit with your permission as Permit Holder.

It is your responsibility to notify the NMFS Assistant Regional Administrator for Protected Resources at least two weeks before planned fieldwork begins, as specified in your permit. Notification must include:

- locations and/or survey routes,
- estimated dates, and
- number and roles of participants.

Please contact Carrie Hubard or Sara Young at (301) 427-8401 or via email at carrie.w.hubard@noaa.gov or sara.young@noaa.gov if you have questions.

Sincerely,

for Jolie Harrison
Chief, Permits and Conservation Division
Office of Protected Resources

Enclosure

Printed on Recycled Paper