

BIOENERGETIC AND ECONOMIC IMPACTS OF HUMPBACK WHALE  
DEPREDATION AT SALMON HATCHERY RELEASE SITES

By

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## Abstract

Since 2008, humpback whales have been documented depredating hatchery-produced juvenile salmon, a novel prey, at points of their release in Southeast Alaska. The objectives of this dissertation are to determine the spatial distribution, seasonal distribution, and frequency of humpback whale foraging at release sites, determine whether whale presence is affecting the economic productivity of hatchery operations, and compare the bioenergetic benefits for whales feeding on juvenile salmon at hatchery release sites relative to typical prey. Five hatchery release sites were monitored over six years during the spring release season for whale presence/absence, numbers, and behaviors. Linear models were used to determine that for coho salmon, cohorts with frequent humpback whale presence had lower marine survival than cohorts with less or no humpback whale presence, but this was not seen for chum or Chinook salmon. Over six years, these sites lost an estimated 23% of revenue from coho salmon totaling almost a million dollars per year in addition to increased rearing costs to mitigate whale predation. A process model was developed to compare the net energy gain for humpback whales foraging on krill, herring and juvenile salmon. Whales were found to feed profitably on krill and chum salmon where they occurred in dense enough distributions and on herring when large coordinated groups impeded the escape of prey. Coho salmon typically distributed too diffusely for humpback whales to recuperate the full energetic costs of engulfment, indicating that behaviors such as bubble net feeding may be essential for increasing prey aggregation to an energetically profitable level, or humpback whales may be feeding to mitigate energetic losses. As intraspecific competition increases due to recovery and or changes to prey resources, generalist humpback whales may expand feeding to exploit new and less profitable prey resources.



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## General Introduction

Rorqual whales are the largest predators to have ever existed on earth. Among this group, humpback whales are superlative as diverse and innovative foragers (Jurasz and Jurasz 1979; Weinrich et al. 1992) and for the rate at which the population has increased in recent decades following the cessation of industrial whaling (Calambokidis et al. 2008; Fleming and Jackson 2011). Humpback whales feed on a wide variety of prey including commercially valuable species and depleted populations (Straley et al. 2017; Moran et al. 2018). Within the last decade, humpback whales have been observed feeding on juvenile salmon at hatchery release sites. Juvenile salmon are a previously undocumented prey species for humpback whales. To better understand the broad economic and ecological impacts of humpback whales, we need to better understand their modes of prey selection.

Humpback whales are generalist predators that typically capture krill and schooling fish using energetically demanding lunge feeding to engulf prey (Goldbogen et al. 2008). Their expandable throat pleats allow them to engulf a volume of water approximately equal to their body weight (Goldbogen et al. 2012) and filter it through their baleen, retaining small prey items. Goldbogen et al. (2012) estimated the metabolic energetic cost of a single lunge by an average-length humpback whale (14 m) to be about 1,023 kJ, highlighting the need for whales to feed on dense aggregations of prey to recuperate these energetic costs. It is unknown how this population will respond to resource limitation resulting from their own population growth or changes in the populations of their typical prey.

Whales feeding at hatchery release sites exhibit a novel foraging strategy by targeting anthropogenically-sourced prey. In Alaska, salmon hatcheries typically release large quantities of captively-reared juvenile salmon into the ocean at the same locations each spring (Heard

2012). Hatchery management has directly implicated humpback whale predation for poor marine survival of their released salmon in some years (Reifenstuhl 2012, 2015). Hatchery managers have experimented with different strategies for releasing their fish in order to minimize losses due to humpback whales. However, there had been no rigorous effort to disentangle the effect of humpback whale predation on marine survival from other possible factors including other predators and environmental conditions or to quantify the value of losses to whales.

The goal of this dissertation is to quantitatively describe this behavior and estimate its practical economic impacts on fishermen supported by hatcheries and its energetic impacts on humpback whales that feed there. In Chapter 1, I describe the frequency, distribution and temporal scale of humpback whale feeding at hatchery release sites. In Chapter 2, I isolate and quantify the economic impacts of humpback whale foraging in terms of lost revenue from hatchery production. Finally, in Chapter 3, I place this prey source in the context of other prey that the whales can and do feed on near release sites and throughout the summer feeding season in Southeast Alaska. I accomplish this using a process model that incorporates the effects of prey patch characteristics and whale behaviors on the net energy gain whales obtain through foraging. This information is essential to interpret the energetic incentives for humpback whales to feed at release sites and more broadly to assess factors that influence foraging behaviors in humpback whales and related species.

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## Chapter 1: Humpback Whales Feed on Hatchery-Released Juvenile Salmon.<sup>1</sup>

### 1.1. Abstract

Humpback whales are remarkable for the behavioural plasticity of their feeding tactics and the diversity of their diets. Within the last decade at hatchery release sites in Southeast Alaska, humpback whales have begun exploiting juvenile salmon, a previously undocumented prey. The anthropogenic source of these salmon and their important contribution to local fisheries makes the emergence of humpback whale predation a concern for the Southeast Alaska economy. Here, we describe the frequency of observing humpback whales, examine the role of temporal and spatial variables affecting the probability of sighting humpback whales and describe prey capture behaviours at five hatchery release sites. We coordinated twice-daily 15min observations during the spring release seasons 2010–2015. Using logistic regression, we determined that the probability of occurrence of humpback whales increased after releases began and decreased after releases concluded. The probability of whale occurrence varied among release sites but did not increase significantly over the six-year study period. Whales were reported to be feeding on juvenile chum, Chinook and coho salmon, with photographic and video records of whales feeding on coho salmon. The ability to adapt to new prey sources may be key to sustaining their population in a changing ocean.

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<sup>1</sup> Chenoweth, E. M., Straley, J. M., McPhee, M. V., Atkinson, S., & Reifenhohl, S. (2017). Humpback whales feed on hatchery-released juvenile salmon. *Royal Society Open Science*, 4(170180).

## 1.2. Background

Humpback whales (*Megaptera novaeangliae*) are notable among baleen whales for their diet diversity. Their large flukes and long pectoral fins allow for quick acceleration and manoeuvring enabling humpback whales to capture highly mobile prey [1]. This energetically-demanding filter feeding requires prey to be aggregated for capture by humpback whales [2,3]. Humpback whales demonstrate particularly complex and sometimes innovative foraging tactics [4–7]. Behavioural plasticity may be an important aspect of their persistence by allowing them to adapt to changing environments and avoid competition [8,9].

Humpback whales feed primarily on euphausiids and small schooling fish [10–12]. In Southeast Alaska, the humpback whale population has been increasing since the end of commercial whaling in the early 1970s [13–15]. Increased intraspecific competition can lead to an increase in a population's diet diversity with the inclusion of less-preferred prey items [9]. Humpback whales have not been documented feeding on wild juvenile salmon (Salmonidae) in the scientific literature despite the fact that juvenile salmon numerically dominate the inshore and coastal waters of Southeast Alaska [16] and some species of juvenile salmon have been found in schools or aggregations [17]. A review of the scientific literature revealed a single reference for salmon as prey for humpback whales [18]. The author [18] found adult pink salmon (*Oncorhynchus gorbuscha*) in the stomachs of humpback whales feeding near a run in the Kurile Islands of Russia.

Despite the lack of scientific record, hatchery personnel observed humpback whales feeding on juvenile salmon along shore near a release site as early as 1999. In 2008, a humpback whale was video recorded at Hidden Falls hatchery (<http://rsos.royalsocietypublishing.org/content/4/7/170180.figures-only>). In recent years (2011,

2015, 2016) of historically poor returns of chum salmon, hatchery managers have implicated humpback whale predation. Modified rearing and release protocols have been implemented to minimize humpback whale predation [19–21] but the success of these strategies is difficult to measure.

The objectives of this present study were to document juvenile salmon as prey for humpback whales in Southeast Alaska, model the main factors affecting the probability of sighting humpback whales at release sites and describe humpback whale foraging behaviors at these sites.

### 1.3. Materials and methods

#### 1.3.1. Study area

This study was located at five hatchery release sites in protected coves on the eastern side of Baranof Island in Southeast Alaska, adjacent to Chatham Strait, a deep (up to 600 m), 240-km long, 15-km wide channel within the Alexander Archipelago (Figure 1.1). Three different organizations participated in data collection at five release sites: Hidden Falls, managed by the Northern Southeast Regional Aquaculture Association (NSRAA); Takatz (NSRAA); Mist Cove (NSRAA); Little Port Walter (NOAA); and Port Armstrong (Armstrong Keta Inc.).

#### 1.3.2. Hatchery processes

Salmon hatcheries have operated sporadically in Southeast Alaska since the late 19th century [22]. In the 1970s, production increased to augment low wild stock catches and abundance. Releases increased until the mid-1990s with over 400 million juvenile salmon released annually in Southeast Alaska [23,24]. In Alaska, salmon hatcheries fertilize eggs and rear hatchlings in captivity. After 6-18 months, salmon are transferred to floating salt water net



pens for acclimatization prior to ocean release [23]. Specific rearing practices vary by site and species, with longer rearing times generally leading to fewer, larger fish at the time of release. Chinook (*O. tshawytscha*) and coho salmon (*O. kisutch*) are typically released at larger sizes than pink and chum salmon (*O. keta*). After release, salmon are not restrained or fed and must eventually make their way to the open ocean, comingling with wild salmon. The salmon that survive to adulthood are then caught by commercial, sport, and personal-use fisheries as they make their way back to the release sites to spawn [25]. The five sites included in our study release Chinook, coho, chum and pink salmon. The numbers and species released vary substantially by site and, to a lesser extent, by year. Hidden Falls releases Chinook, coho and chum salmon; Takatz releases chum salmon only; Mist Cove releases coho salmon only; Little Port Walter releases Chinook salmon only; and Port Armstrong releases all four species. Hidden Falls and Port Armstrong released the largest biomasses annually (mean 180,000 kg each) followed by Takatz (110,000 kg), Mist Cove (47,000 kg), and Little Port Walter (3,500 kg) (Appendix 1A). Chum salmon are the species released in greatest abundance and with the greatest economic importance in this region [26].

### 1.3.3. Behavioural observations at release sites

A standardized data collection protocol was developed in collaboration with hatchery managers. Each organization designated observers from among their on-site staff to participate in behavioural data collection. Behavioural observations were conducted at each of the five release sites over six years (2010-2015). Each site was systematically sampled twice a day, once in the morning and once in the afternoon. Observation times were selected by observers at the beginning of each season and remained consistent throughout the season to prevent biasing observations toward low-probability events. Whale observations outside of the pre-determined

sampling times were designated separately as opportunistic sightings. Observations were to begin about a week prior to releases and then 1-2 weeks after releases, when possible. Observations were recorded on standardized forms, with information on humpback whale presence, abundance, and behaviours (sleeping/logging, breaching, surface feeding), as well as the presence of other possible salmon predators. Forms included a list of physical barriers whales may have used to aid in prey capture. This list was modified from a list of barriers compiled by the Glacier Bay Humpback Whale Monitoring Program (Christine Gabriele, pers. comm.) to include net pens and docks in addition to surface, shoreline, tide-rip, and kelp. Observers also noted the timing, location, species, abundance, age and mass of juvenile salmon released. During the coho salmon release at Hidden Falls in 2014, photography and videography were used to document feeding events (Go Pro Hero 4).

To determine which factors affected the presence of humpback whales at release sites, we modelled the probability of sighting a whale at a hatchery release site using a logistic generalized linear model (GLM) and Akaike Information Criteria (AICc)-based model selection [27,28]. Tested covariates included release site, year, and a categorical variable for timing of the observation period relative to releases. Staff occasionally extended their observations beyond 15 minutes, which could increase the probability of sighting a whale. We therefore included observation duration as a covariate, and all model results were presented based on model predictions for a 15-minute observation period (Equation 1.1):

$$\ln\left(\frac{\pi_{ijk}}{1-\pi_{ijk}}\right) = \beta_0 + \beta_1(\text{year}_i) + \text{site}_j * \text{timing}_k + \beta_2(\text{duration}_i) + e_i \quad [\text{Equation 1.1}]$$

where  $\pi_{ijk}$  is the probability of observing a whale in year  $i$  at site  $j$  with timing  $k$ ; year is an ordinal variable from 2010 to 2015; site is a categorical variable with five factor levels ( $j$ ) for the five release sites (Hidden Falls, Takatz, Mist Cove, Little Port Walter and Port Armstrong);

timing is a categorical variable referring to the timing of the observation with reference to the release season defined by the first release of the year and the last release of the year from that site with three factor levels (k): before, during, and after; and duration is a continuous variable describing the total duration of observation effort expressed as a fraction of 24 hours. For observations conducted after the final release, an additional covariate (f.release) for the number of elapsed days since the last release was included (Equation 1.2).

For k = after [Equation 1.2]

$$\ln\left(\frac{\pi_{j(k=\text{after})}}{1-\pi_{j(k=\text{after})}}\right) = \beta_0 + \beta_1(\text{year}) + \text{site}_j + \beta_2(\text{duration}) + \beta_3(\text{f.release}) + e_i$$

where  $\pi_{j(k=\text{after})}$  is the probability of observing a whale in year i at site j after the final release at that site has occurred (i.e., k = after) where other variables are defined identically to the above and, f.release is an ordinal variable that expresses the number of days that have elapsed since the final release at a particular site in a particular year.

## 1.4. Results

### 1.4.1. Humpback whale feeding behaviour at release sites

Observers recorded data on the presence or absence of humpback whales during 2,252 observation periods at five hatchery release sites over six years. Humpback whales were reported to be targeting releases of chinook, chum and coho salmon. For each of these three species, whales were observed feeding when no other species had been released from that site. Underwater video and photographs showed humpback whales targeting coho salmon at Hidden Falls hatchery in 2014 (Figure 1.2; <http://rsos.royalsocietypublishing.org/content/4/7/170180.figures-only>). When humpback whales were noted near the release sites (n = 124 sightings), 81% of those sightings were of

single individuals (n= 100); 10% of whale observations had a group size of 2 (n = 13); and 9% were 3 or more whales (n = 11) with a single observation of 10 animals, although this group was specifically noted as feeding on herring (*Chupea pallasii*). For 60% of observations when whales were sighted (n = 75), at least one barrier was noted. For the remaining 40% of whale sightings (n = 49), observers either did not note feeding in the presence of a feeding barrier, noted that no feeding barrier was present, or were uncertain. The most common barriers noted other than the surface (presumed for any observed feeding events) were shoreline (42%), bubbles (27%), dock or net pen (16%), tide (5%) and kelp (2%). Multiple feeding barriers were recorded in 26% of observations. In addition to these feeding behaviours, whales were noted as sleeping/logging (i.e., holding stationary at the surface; 2%) and breaching (5%).

#### 1.4.2. Probability of sighting a whale

When modelling the probability of whale sightings over all time periods, the best models included *site*, *timing* and observation *duration* as explanatory variables (Table 1.1). The probability of whale sightings increased notably once salmon were released (Figure 1.3). Probability of whale sightings was highest at the Takatz and Hidden Falls sites, and lowest at Port Armstrong. As expected, the probability of a whale sighting increased with observation duration. Overall, the probability of whale sightings decreased with year, but year was not included in the top model (including year resulted in  $\Delta AICc = 0.6$  from the top model).

At several hatcheries, there was considerable variability in the frequency of whale observations among years (Figure 1.3). For example, Hidden Falls recorded no whales observed during scheduled observation periods in 2012 despite frequent observations in 2010 and 2013, however whales were not entirely absent, as they were noted opportunistically. The following predicted probabilities for fifteen-minute observation periods during the release season at each

site were generated from the top-ranked model: Takatz (0.08) and Hidden Falls (0.05) compared to Mist Cove (0.03) Little Port Walter (0.02) and Port Armstrong (0.01).

For the final-release model (Table 1.2), we found again that site and observation duration (coefficient again positive) were important predictors. Also important was elapsed time since the final release (f.release). These variables were included in the top two models and its coefficient was negative in all tested models, causing predicted probabilities decreased with time after the final release. As in the overall model, year was less important, and again excluded from the top model ( $\Delta AICc = 1$ ).

## 1.5. Discussion

Here we document humpback whales feeding on a novel prey. These feeding events were documented with direct observations as well as photographic and videographic evidence from the hatchery release sites. Using standardized observation methodology, we determined that humpback whale presence was closely associated with the release of juvenile salmon. Hatchery-released salmon were abundant in the region for only a few decades [23] before whales began to exploit them annually at multiple sites. The rapid release of large numbers of juvenile hatchery salmon, which differs from the protracted marine migration of their wild conspecifics, likely increased their profitability as prey for humpback whales, which rely on dense aggregations of prey. Wild Chinook and coho salmon in particular are known for agonistic behaviours and diffuse distributions [29,30], which may make them atypical prey for filter-feeding whales in a natural system. The extent to which humpback whales may target wild salmon or hatchery-released salmon after their outmigration from the release sites is unknown.

As expected, humpback whales were most common while releases were in progress; however, whales were also seen prior to and following releases. It is possible that pre-release humpback whale observations reflect whales assessing the prey field periodically in anticipation of a release but only spending time there when sufficient prey are encountered. Prey anticipation by Dolly Varden (*Salvelinus malma*) has been noted at release sites in Southeast Alaska (pers comm. Eric Prestegard) and by sculpin (*Cottus* spp.) anticipating spawning sockeye salmon (*O. nerka*) [31]. The decline in whale sightings after releases have concluded is best explained by a decrease in prey availability due to the dispersal and mortality of juvenile salmon from the release area. These local declines in humpback whale sightings were notable because they occur despite a concomitant seasonal increase in humpback whale populations in the region [15].

Hidden Falls and Takatz had the highest rates of whale sightings. Hidden Falls and Port Armstrong release the greatest biomass of salmon each year, but Takatz and Hidden Falls are located near each other and are not truly independent, with whales and potentially also salmon moving between these areas. Hidden Falls, Takatz and Mist Cove also tend to release salmon later than more southerly sites. The later timing of these releases (May and June) compared to Port Armstrong (April) may correspond with more whales present on the feeding grounds following their spring migration [15].

While at release sites, humpback whales often fed near physical barriers. Whales feeding near barriers may simply be a result of salmon distribution near these structures, or conversely feeding near barriers could be a tactic used by whales for aggregating prey or impeding prey escape. The frequent use of bubbles offered stronger evidence of forced prey aggregation. Feeding near barriers has been observed and noted by researchers Glacier Bay National Park for decades (Glacier Bay unpublished data). It has also been offered as an explanation for the use of

bubbles to corral prey as well as nearshore, tidally mediated, and surface-feeding behaviours [32–34]. These behaviours may be necessary to aggregate Chinook and coho salmon into a sufficient density for profitable feeding, as these species do not school as densely as pink, chum, or sockeye salmon juveniles [17,35]. Species preference could not be directly tested because at Hidden Falls and Port Armstrong, multiple species were released in succession, with overlapping presence at the release site. In addition, species releases at single-species sites were confounded by differences in biomass, release timing and location.

Despite the increase in humpback whales regionally and the relatively recent introduction of hatchery salmon as a prey source, we found no evidence of an increasing trend in humpback whale predation at release sites across years. One explanation is that the resource is currently being fully exploited at these release sites and the prey or habitat characteristics cannot support more frequent feeding. It is also possible that hatcheries are not particularly favourable places to feed compared to other foraging opportunities available to humpback whales. This is supported by the observation of whales feeding predominantly as individuals rather than feeding aggregations. Finally, it may be too soon to detect an increase over the substantial interannual variability. Even if these sites are fully exploited, hatchery predation could still be spreading to other releases sites in the region. If recent increases in the humpback whale population both locally and throughout the North Pacific [13,14] result in increased intraspecific competition, one possible outcome is increased dietary diversity of the population via individual specialization on less-preferred prey [9].

The interaction between humpback whales and an anthropogenically derived food source bears further investigation as both a novel predator-prey interaction and for the potential economic impact. Future studies will directly test whether high humpback whale predation on a

salmon cohort at the point of release is related to poor marine survival of released salmon and the economic impacts of that predation to local fisheries. During this study, hatchery staff noted many strategies for mitigation predation, primarily aimed at reducing the density of salmon aggregations at the releases site. One of the most wide-spread methods was to release fish slowly over time, a strategy known as a “trickle” release as opposed to a more traditional “mass” release. Staff also tried releasing fish at night, on an outgoing tide, or in a less sheltered location. The most intensive strategy employed by NSRAA was to release salmon at a larger size so that they will move from the littoral habitat more quickly [21]. A longitudinal study in space and time will be necessary to isolate the effects of these strategies on marine survival. Future studies will also characterize the prey field at release sites to determine the prey quality associated with foraging at hatchery release sites.

Phenotypic plasticity in foraging behaviour offers advantages over strict specialization under certain conditions [8]. Phenotypic plasticity that leads to dietary diversity across time, space, or among individuals and can be an important evolutionary strategy to persist or thrive in changing environmental conditions [36] or high intraspecific competition [9]. The resulting behavioural innovations may be a key reason why humpback whale populations have recovered so successfully in much of the world [37] and Southeast Alaska in particular [14].



1.6. Figures

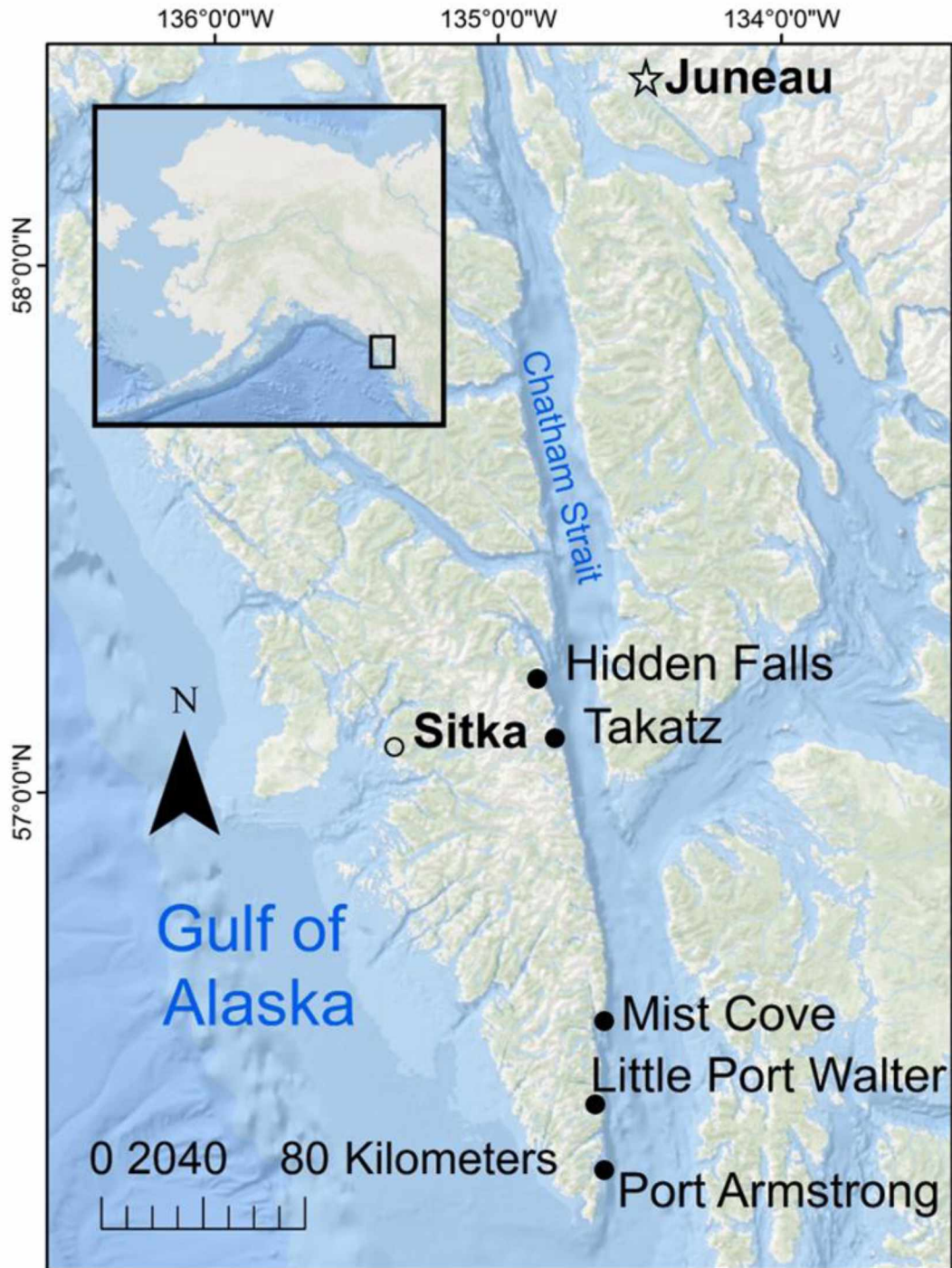


Figure 1.1 Five participating release sites are shown with dark dots. Cities Juneau and Sitka are shown for reference.



Figure 1.2 Humpback whales feeding in front of saltwater holding pens for salmon after a release in May 2014 (Monique Anderson).

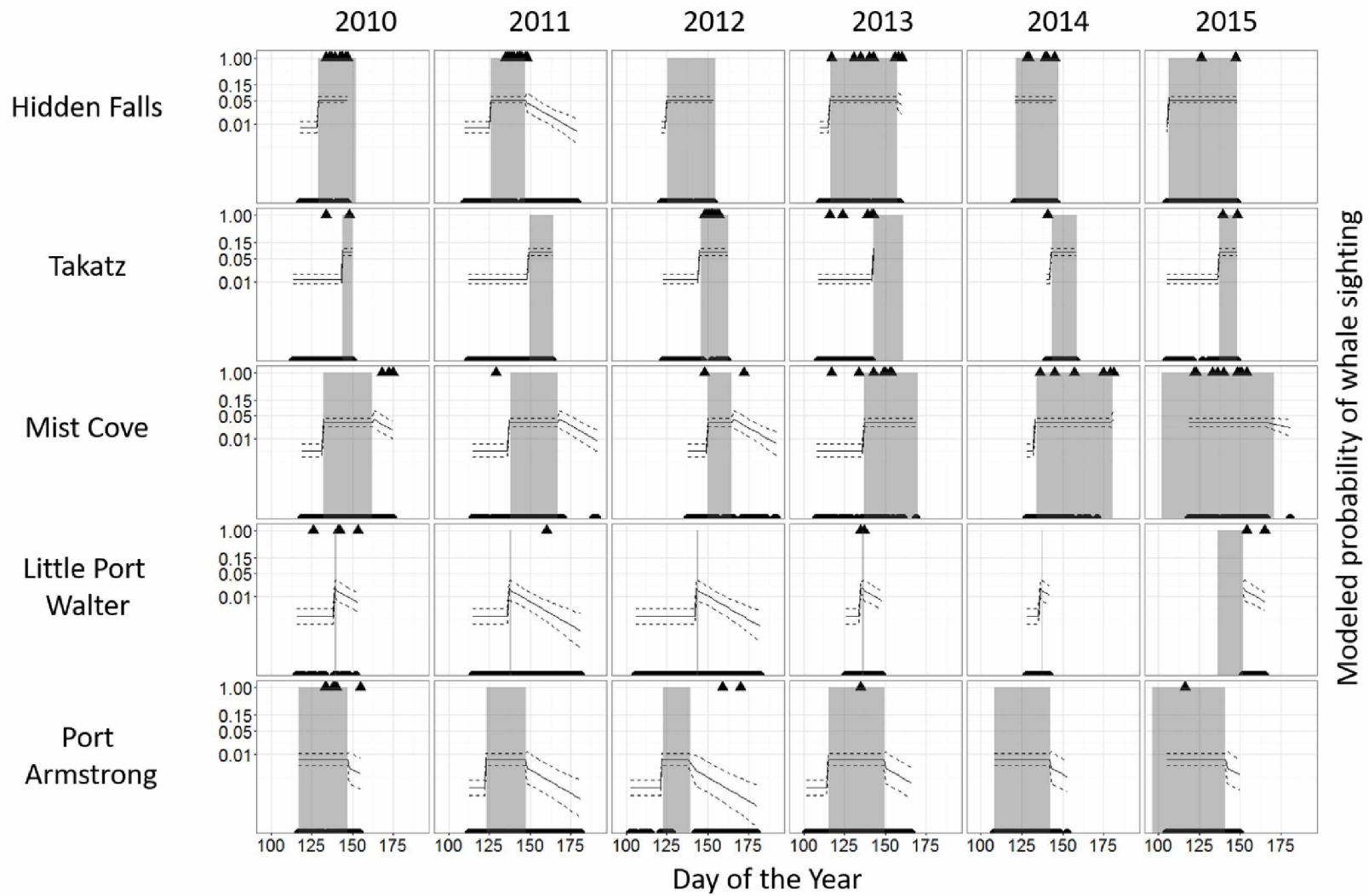


Figure 1.3 Probability (solid line) of sighting a whale before, during (grey shading) or after the release period at five hatcheries. The triangles on the top of each panel represent whale sightings, on the bottom represent observations where no whales were observed. Probabilities were generated from the top-ranked binomial models from tables 1 and 2. Dashed lines represent standard error.

## 1.7. Tables

Table 1.1 Top candidate logistic models for describing the probability of sighting a humpback whale at a release site (response) based on temporal and spatial predictors.

Rank	Model Parameters	K	Residual dev.	AICc	$\Delta$ AICc
1	site + timing + duration	9	844.8	860.9	0.0
2	site + timing + duration + year	10	843.4	861.5	0.6
3	site + timing + duration + site:timing	16	834.5	864.7	3.8
4	site + timing + duration + year + site:timing	17	833.0	865.3	4.4
5	site + timing + year	9	870.9	887.0	26.1
6	site + timing	8	874.4	888.4	27.6

All models include an intercept term. The full model (EQ1) is shown here as the third-ranked model. K is the total number of parameters, AICc is the Akaike Information Criterion adjusted for sample size.  $\Delta$  AICc is the difference between the AICc each model and the AICc for the top ranked model.

Table 1.2 Top candidate logistic models for describing the probability of sighting a humpback whale at a release site (response) after releases have concluded.

Rank	Model Parameters	K	Residual dev.	AICc	$\Delta$ AICc
1	duration + site + f.release	7	138.1	150.3	0.0
2	duration + site + f.release + year	8	137.1	151.3	1.0
3	duration + site	6	143.5	153.6	3.3
4	duration + site + year	7	141.6	153.8	3.5
5	duration + f.release	4	148.7	154.8	4.5
6	duration + f.release + year	5	148.7	156.8	6.5

All models include an intercept term. The full model (EQ2) is shown here as the second-ranked model. K is the total number of parameters, AICc is the Akaike Information Criterion adjusted for sample size.  $\Delta$  AICc is the difference between the AICc each model and the AICc for the top ranked model.

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Appendix A1: Release data for five hatchery release sites over six years.

Hatchery	Year	Species	N Released	Mean mass (g)	Start of Releases	End Releases
Hidden Falls	2010	Chinook	940,000	69.8	5/28/2010	6/1/2010
		chum	40,268,000	2.1	5/13/2010	5/22/2010
		coho	2,060,000	21.3	5/9/2010	5/26/2010
	2011	Chinook	535,000	53.1	5/13/2011	5/18/2011
		chum	37,601,000	2.2	5/20/2011	5/27/2011
		coho	3,048,000	21.7	5/6/2011	5/27/2011
	2012	Chinook	523,000	55.1	5/7/2012	5/10/2012
		chum	46,246,000	2.3	5/18/2012	6/2/2012
		coho	2,209,000	21.9	5/4/2012	5/26/2012
	2013	Chinook	518,000	61.8	4/26/2013	5/8/2013
		chum	34,867,000	2.6	5/3/2013	6/2/2013
		coho	3,137,000	23.5	5/1/2013	6/6/2013
Chinook		558,000	66.8	5/1/2014	5/4/2014	
chum		26,035,000	2.2	5/21/2014	5/27/2014	
coho		2,685,000	24.2	5/5/2014	5/27/2014	
2015	Chinook	558,000	66.8	4/16/2015	5/14/2015	
	chum	28,416,000	2.6	5/12/2015	5/28/2015	
	coho	2,685,000	24.2	5/3/2015	5/19/2015	
Takatza	2010	chum	39,039,000	2.1	5/24/2010	5/30/2010
	2011		38,901,000	2.5	5/29/2011	6/13/2011
	2012		40,447,000	2.5	5/24/2012	6/30/2012
	2013		39,654,000	2.8	5/23/2013	6/10/2013
	2014		42,433,000	2.8	5/23/2014	6/7/2014
	2015		43,224,000	2.8	5/17/2015	5/28/2015
Mist Cove	2010	coho	1,193,000	16.4	5/12/2010	6/11/2010
	2011		647,000	22.3	5/17/2011	5/25/2011
	2012		2,015,000	19.3	5/29/2012	6/13/2012
	2013		2,567,000	20.8	5/17/2013	6/19/2013
	2014		2,417,000	23.8	5/13/2014	6/29/2014
	2015		2,498,000	39.7	4/12/2015	6/20/2015
Little Port Walter	2010	Chinook	238,000	18.1	5/19/2010	5/19/2010
	2011		180,000	22.0	5/17/2011	5/17/2011
	2012		150,000	16.2	5/22/2012	5/22/2012
	2013		139,000	16.9	5/15/2013	5/16/2013
	2014		211,000	28.5	5/16/2014	5/16/2014
	2015		149,000	14.7	5/16/2015	6/1/2015
Port Armstrong	2010	Chinook	276,000	31.7	5/8/2010	5/17/2010
		chum	27,296,000	1.2	4/27/2010	4/27/2010
		coho	3,224,000	17.1	5/8/2010	5/27/2010
		pink	53,677,000	0.5	4/29/2010	4/29/2010
	2011	Chinook	250,000	30.0	5/15/2011	5/15/2011
		chum	28,445,000	1.3	5/7/2011	5/7/2011
		coho	1,757,000	18.5	5/15/2011	5/27/2011
		pink	75,506,000	0.5	5/3/2011	5/7/2011
	2012	Chinook	402,000	41.9	5/12/2012	5/18/2012
		chum	52,919,000	1.9	5/1/2012	5/1/2012
		coho	4,761,000	19.7	5/18/2012	5/18/2012
		pink	82,734,000	0.5	5/1/2012	5/1/2012
	2013	Chinook	239,000	13.6	5/14/2013	5/14/2013
		chum	31,525,000	1.8	4/25/2013	5/4/2013
		coho	2,462,000	25.7	5/18/2013	5/29/2013
		pink	52,090,000	0.7	4/25/2013	5/4/2013
	2014	Chinook	161,000	14.7	5/14/2014	5/14/2014
		chum	25,029,000	2.4	4/25/2014	4/30/2014
coho		1,748,000	24.3	5/17/2014	5/22/2014	
pink		79,659,000	0.4	4/18/2014	5/7/2014	
2015	Chinook	508,000	21.0	5/8/2015	5/17/2015	
	chum	22,817,000	3.0	4/6/2015	4/11/2015	
	coho	1,945,000	69.8	5/15/2015	5/21/2015	
	pink	87,665,000	0.7	4/20/2015	5/6/2015	

## Chapter 2: The Economic Impacts of Humpback Whale Depredation on Hatchery-Released Juvenile Salmon in Southeast Alaska<sup>1</sup>

### 2.1. Abstract

The goal of this study was to determine whether humpback whale depredation on hatchery-released juvenile Coho and Chum Salmon is affecting the economic productivity of hatcheries in Southeast Alaska. From 2010-2015, observers monitored five release sites in Chatham Strait, Alaska. Observers indicated that humpback whales were present at the release of 23 of 54 salmon cohorts (defined by release year, species, site, and release strategy). A linear model was used to determine whether humpback whale presence at a cohort release affected the proportion of that cohort that survived to harvest and to estimate the effect in terms of lost fish. The lost value was then calculated based on the average return weight and price of individual fish of that species across return years. Marine survival of Coho Salmon was significantly lower for cohorts with high humpback whale depredation, but not for other species. Return rates for Chum Salmon were historically low even for cohorts from years when whales were not observed near hatchery releases. This finding suggests that for Chum Salmon and Chinook Salmon, whale depredation may result in losses to other predators along a predator gauntlet, without a measurable effect on the number of adult salmon ultimately available to fishermen. Driven primarily by losses of Coho Salmon, an estimated US \$1 million per year (95% CI \$665,000 – \$1,325,000) in revenue (12% of total revenue) was lost to these five sites due to whale depredation. Costs of rearing have also increased as hatchery managers have modified

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<sup>1</sup> Formatted and in review with Marine and Coastal Fisheries with authors Chenoweth, E.M. and Criddle, K.

production and release strategies to reduce whale depredation at release sites. Hatchery managers are currently experimenting with alternative release sites to improve the marine survival of their salmon and continue providing economic benefits for Southeast Alaska.

## 2.2. Introduction

Humpback whales (*Megaptera novaeangliae*) have recently been documented depredating juvenile salmon at hatchery release sites with potential adverse economic consequences for the fisheries those hatcheries support (Chenoweth et al. 2017). While some researchers are skeptical that marine mammals exert large-scale impacts on fisheries yield (Gerber et al. 2009; Morissette et al. 2012) and others point to positive ecosystem impacts of increased marine mammal populations (Lavery et al. 2014; Roman et al. 2014) there are ample accounts of specific commercial fisheries experiencing conflicts with marine mammals (Jeffries and Scordino 1997; Nash et al. 2000; Wright et al. 2007; Sigler et al. 2008; Larson et al. 2013; Peterson et al. 2013; Werner et al. 2015; Straley et al. 2017). Recent increases in the number of humpback whales in Southeast Alaska (Barlow et al. 2011; Hendrix et al. 2012) as well as increases or range shifts in many populations of marine mammals worldwide (MacLeod 2009; Simmonds and Elliott 2009; Magera et al. 2013; Roman et al. 2013) intensify these concerns.

Private non-profit organizations operate large-production salmon hatcheries in Southeast Alaska. The hatchery organizations' stakeholders are the licensed commercial fishermen that own limited-entry salmon permits for the region. Hatchery operations are funded primarily through the harvest and sale of a portion of the adult salmon that return to the hatchery and a self-imposed 3% tax on fishermen's commercial landings. They operate alongside wild runs to augment the number of salmon available for harvest (Heard 2001, 2012). Understanding and

minimizing interactions between wild and hatchery stocks remains an active area of research and policy (Quinn 1993; Hilborn and Eggers 2001; Ruggerone et al. 2010; Sturdevant et al. 2011; Debertain et al. 2016). Consequently, the State of Alaska regulates salmon hatchery releases with respect to numbers, species, location, and timing. Hatcheries in Southeast Alaska had an estimated direct (jobs and value created by the hatcheries themselves), indirect (jobs and value in related sectors), and induced (jobs and value created by local owners of input factors) economic output of US \$171 million dollars and 971 jobs in 2008 (McDowell Group 2010).

Recent observations of humpback whales feeding near juvenile salmon release sites have coincided with declines in hatchery salmon marine survival. Historically, Chum Salmon (*Oncorhynchus keta*) have been the most lucrative hatchery species in the region, accounting for 90% of ex-vessel value (McDowell Group 2010). For the Northern Southeast Regional Aquaculture Association (NSRAA), the rate of return for Chum Salmon has averaged about 3% (NSRAA 2016a). These hatchery-reared Chum Salmon are estimated to account for about 75% of the value of NSRAA-produced salmon (McDowell Group 2009). A highly variable but downward trend in marine survival is apparent from historical Chum Salmon returns to Hidden Falls hatchery and the adjacent Kasnyku Bay release site since the late 1980s (Figure 2.1). Because juvenile salmon reared at Hidden Falls but released elsewhere have had more typical marine survivals, it seems likely that the decline in marine survival of Chum Salmon released at Kasnyku Bay and nearby Takatz Bay is related to conditions at the release sites themselves (NSRAA 2017). In 2016, returns declined across species and NSRAA sites, and NSRAA revenues declined to \$6 million, the lowest since 2007. This change in fortune is particularly stark because Hidden Falls hatchery and Kasnyku Bay release site had been upheld as a model hatchery program due to the consistently high marine survivals (Bachen 1993).

Understanding the role of humpback whale depredation in years of low marine survival is essential to identifying a financially optimal release strategy. Because juvenile salmon face a gauntlet of predators and experience high mortality in their first year at sea (Parker 1968; Farley et al. 2007), it is unclear whether humpback whale depredation is limiting marine survival of released cohorts. Some options for mitigating depredation from whales increase operational costs and others likely increase the exposure of juvenile salmon to other predators that may exert greater levels of mortality. For example, hatcheries traditionally release their fish en masse to overwhelm common local predators such as Dolly Varden (*Salvelinus malma*) and other piscivorous fishes, river otters, mink, harbor seals, and gulls. That strategy is supported by studies in fresh water, where juvenile salmon have been shown to survive better when migrating in large numbers, satiating place-based predators (Furey et al. 2016). However hatchery staff have started implementing a more gradual release (known colloquially as a “trickle release”) to deter whale depredation by minimizing the biomass of salmon entering the release area at a single time (NSRAA 2011; Reifentstahl 2012). Hatchery operators have also started rearing Chum Salmon to a larger size (Reifentstahl 2012), hoping that they will spend less time in nearshore habitat (Orsi et al. 2004) where they seem particularly susceptible to whale depredation. However, hatcheries incur additional feed and labor costs in rearing salmon to larger sizes, costs that could offset reductions in whale depredation.

The primary objectives of this study are 1) to determine whether humpback whale depredation is affecting the marine survival of hatchery-released juvenile salmon and 2) to quantify any associated economic losses to hatcheries and commercial fishermen. Understanding the extent to which humpback whale depredation reduces marine survival will help managers

choose among production and release strategies that involve substantial differences in cost, risk, or exposure to other predators.

### 2.3. Methods and Model Specification

Our approach was conceptually simple: we partnered with aquaculture associations to monitor whale presence at the release of salmon cohorts and analyzed the fate of those cohorts for evidence of a decrease in the marine survival due to whale depredation. We then calculated the value of those lost fish. We used multiple linear regression to estimate the effect of humpback whale depredation on the marine survival of juvenile salmon cohorts and the value to the fisheries they support. Humpback whale depredation information for this analysis came from whale observations by hatchery staff at five sites across six years and for four species of salmon: Chum Salmon, Coho Salmon (*O. kisutch*), Pink Salmon (*O. gorbuscha*), and Chinook Salmon (*O. tshawytscha*). Cohorts were defined as unique by year, site, species, and release strategy. Fifty-four salmon cohorts were included as observations in a linear model with marine survival as the response variable (Table 2.1). We accounted for a series of management and environmental covariates by including them in the model.

To quantify the degree of humpback whale depredation pressure on a specific cohort, hatchery staff observed release sites at five remote facilities on eastern Baranof Island during spring and early summer from 2010 through 2015. The sites are located in small bays that open into Chatham Strait. NSRAA operates release sites in Kasnyku Bay, Takatz Bay and Mist Cove; NOAA operates releases at Little Port Walter, and Armstrong Keta Inc. operates releases at Port Armstrong. Staff at each site observed the release area for 15 minutes twice a day during the release season and noted when humpback whales were present (Chenoweth et al. 2017). Staff

also noted at the time of release whether a whale had been observed in the area at any time that day (including outside of standardized observation times). To calculate a humpback whale depredation pressure index (*WDPI*) by cohort, we summed all whales observed during standardized observation periods on any day when salmon were released or the two days following. If whales were not noted during observation periods but were noted at the time of the release to have been in the area that day, these additional sightings were included. The total number of sightings was divided by the total number of effort days. While depredation after the first 2 days following a release could also be important—including depredation along the shoreline and out of sight of hatchery observers—we expected *WDPI* to be a useful metric because: 1) it indicates whether interested whales were in the area cued into the release in its early stages, 2) predation is expected to be most efficient immediately following a release when juvenile salmon are most densely aggregated, and 3) previous analysis showed that probability of depredation declines with elapsed time after a release (Chenoweth et al. 2017). One unusual observation, where 10 whales observed near a release site were noted by the observer to be feeding on herring, was omitted because salmon were not the target prey.

Marine survival for each cohort was reported by the participating aquaculture associations and included the proportion of all released juvenile fish that returned as adults and were caught by the common property fisheries, retained for broodstock at the hatcheries, or were captured and sold to recover operational costs (Armstrong-Keta Inc. 2016; NSRAA 2016b; NOAA unpublished data). In two cases, species were subdivided by distinctive rearing strategies that were expected to affect marine survival. Chinook Salmon were released in their first spring (0-year-old) at a mean mass of 16 g (SD = 2.5) or in their second spring (1-year-old) at a mean mass of 43 g (20). By releasing 0-year-old Chinook Salmon, operators aimed to reduce rearing

costs. Chum Salmon were subdivided into “regular” 2 g (0.4) or “late” 6 g (4) categories, with late Chum Salmon being held longer and released later in the same season. The policy of retaining Chum Salmon longer was adopted specifically to reduce depredation by humpback whales (NSRAA 2011). Figure 2.1 shows returns of regular Chum Salmon only for continuity.

For cohorts of Chinook Salmon and Chum Salmon that had not yet completed their return, we estimated the eventual marine survival. Juvenile Pink Salmon and Coho Salmon mature and return to hatcheries as adults after only one year at sea. However, Chinook Salmon can remain at sea for two to four years, and while most Chum Salmon adults return after three years, they can return after as few as two years or as many as five years at sea (Armstrong-Keta Inc. 2016; NSRAA 2016a). For eleven incomplete cohorts of Chum Salmon and Chinook Salmon, we used the return-to-date to predict eventual marine survival by establishing correlations between partial and full cohort returns using recent historical data specific to each species and release site. This is similar to the method used by NSRAA to generate internal predictions of run strength (NSRAA 2016a). Incomplete cohort marine survivals were calculated from linear regressions with a minimum  $R^2$  value of 0.72 and a mean  $R^2$  value of 0.88. Return data from Port Armstrong in 2016 was not yet available. Therefore, for 2010 through 2013, we had complete or estimated marine survivals for all released cohorts; for 2014, estimates for Chum Salmon were unavailable; and estimates for Chinook Salmon and Chum Salmon were unavailable for 2015. Among all species and sites, a total of 54 cohorts were included in analysis including the projected marine survival for 11 incomplete cohorts (Table 2.1).

Covariates were considered to account for the influence of environmental conditions and hatchery management decisions on marine survival. Variables were selected to optimize fit of the model and the degrees of freedom determined by comparing the value of the AICc statistics



(Burnham et al. 2011). Explanatory variables included mean individual mass (g/juvenile salmon) at release, the total number released with each cohort, the release site, and the first day of release as a measure of seasonal release timing (Table 2.2). To account for interannual variability in environmental conditions, we considered using year as a factor in the model, or using environmental covariates thought to be important indicators of ocean conditions. Year has the advantage of reflecting differences in productivity caused by variations in a suite of latent environmental factors operating through unobserved processes but suffers from inutility as a predictive variable. The advantage of specifying environmental forcing mechanisms is that doing so produces a model that is suitable for simulations involving those factors. The disadvantage is that it requires *a priori* knowledge of the factors and nature of the processes they influence; therefore we considered both approaches. The environmental time series observations we considered were spring sea surface temperature (SST; corresponding to the release year), summer SST (1<sup>st</sup> summer at sea), winter SST (1<sup>st</sup> winter at sea), and catch per unit effort (CPUE) an index of early marine survival of juvenile Chum Salmon.

Summer catch per unit effort of juvenile Chum Salmon in Icy Strait, Alaska (*CPUE*) was used as an index of early marine survival (Orsi and Fergusson 2015). Chum Salmon have the largest biomass released from hatcheries in Southeast Alaska and 64% are of hatchery origin (Orsi and Fergusson 2015). The Southeast Alaska Coastal Monitoring Program ([https://www.afsc.noaa.gov/ABL/EMA/EMA\\_SECM.htm](https://www.afsc.noaa.gov/ABL/EMA/EMA_SECM.htm)) conducts annual tows for juvenile salmon in Icy Strait, thought to be the main outmigration corridor for northern Southeast Alaska (Orsi and Fergusson 2015). Effort was measured in the number of standardized tows performed that year.

Sea surface temperatures were obtained from oceanographic station GAK 1 in the Gulf of Alaska, south of Resurrection Bay (59°50.7'N, 149°28.0'W) (<http://www.ims.uaf.edu/gak1/>, accessed June 2017) and modeled as a polynomial for each year with station held constant (Figure 2.1;  $F_{(45,18)} = 12.45$ ;  $\text{Adj } R^2 = 0.89$ ;  $p < 0.001$ ).

$$SST_{ijk}^{1/3} = \beta_0 + year_j (DOY_i + DOY_i^2 + DOY_i^3) + station_k + e_i \quad [\text{Equation 2.1}]$$

where  $SST_{ijk}$  is the sea surface temperature on day  $i$  in year  $j$  at station  $k$ ,  $DOY$  is the day of the year (1-365) and  $station$  is the standardized site along a transect where the measurement was taken. For each year, spring SST (*Spr.SST*) was represented as the mean modeled value from March 1 – June 30 because this time period corresponds to the release season. Summer SST (*Sum.SST*) was expressed as the mean modeled SST from June 1st – September 18th, corresponding the ocean conditions during outmigration and the first summer at sea for juvenile salmon. Winter SST (*Win.SST*) was characterized as the mean modeled SST from January 1 – March 31 the year following the release, including the minimum temperatures from the first winter at sea.

Here we present the results of preliminary analysis to identify the best model of marine survival, which will be used to determine the impact of whale depredation on the marine survival and the value of juvenile hatchery salmon cohorts. Model selection preceded iteratively since the number of candidate covariates and relationships among them meant that all candidate covariates could not be included in a full model. We used AICc for model selection and that we used F statistics and p-values as measures of model fit and confidence in coefficient estimates. A comparison of alternative models of particular interest is presented in Table 2.3. The preferred model explained the  $i$ -th observation of marine survival (*MarSurv*) in year  $j$  for salmon species  $k$  as a function of the interaction of *WDPI* and a binary variable (*Coho*) indicating whether the

species was or was not Coho Salmon, a factor (*MistCove*) that differentiated Mist Cove from all other release sites, *Species*, *CPUE*, *Sum.SST*, and *Win.SST*. The interaction between Coho Salmon and *WDPI* was included because the influence of *WDPI* on marine survival was not statistically significant for other species. Similarly, Mist Cove was the only release site that exerted a statistically significant effect on *MarSurv*. A Box-Cox technique was used to identify a transformation to ensure normality (Box and Cox 1964). The preferred model:

$$MarSurv_{ijk}^{1/4} = \beta_0 + WDPI_i \times Coho_j + MistCove + Species_k + \beta_1(CPUE_i) + \beta_2(Sum.SST_i) + \beta_3(Win.SST_i) + e_i \quad [\text{Equation 2.2}]$$

This model accounted for 86% ( $F_{(11,42)} = 30.8$ ,  $p < 0.001$ ) of the observed variation in marine survival. Coefficient estimates, standard errors, and p-values are reported in Table 2.4. This model was used to identify and describe important aspects of marine survival and to estimate costs in terms of revenue lost to humpback whale depredation.

Lost revenues were estimated from the difference between modeled marine survival under observed conditions for all explanatory variables and under a scenario of zero *WDPI*. Average ex-vessel prices (*ExvP*) per pound for each species and year for Southeast Alaska were obtained from the Alaska Department of Fish and Game (<http://www.adfg.alaska.gov>). Prices were adjusted to account for inflation (*rExvP*) using a Consumer Price Index deflation factor to ensure comparability across years. We treat ex-vessel price as exogenous to the influence of whale depredation because the ex-vessel price of salmon is determined by an interplay of global supply and demand, in which small variations in salmon production from Southeast Alaska hatcheries plays a minor role (Herrmann 1993). For each cohort, revenue (*TR*) was estimated as:

$$TR_{k,j} = \left( \sum_{m=j+1}^{2016} PropRet_{k,m} \times rExvP_{k,m} \times W_{k,m} \right) \times MarSur_{k,j} \times N_{k,j}$$

[Equation 2.3]

where the total revenue of catches from a cohort of species  $k$  released in release year  $j$  equals the sum product of the proportion returning ( $PropRet$ ) in each subsequent year ( $m$ ), the inflation-adjusted average ex-vessel price  $k$  in return year  $m$ , the average weight ( $W$ ) of returning individuals of species  $k$  in year  $m$ , the total marine survival of that cohort, and the total number of salmon released from that cohort ( $N$ ). Where cohorts were incomplete, marine survival was the predicted value of the total return, and price and weight are calculated based on the completed return years.

We also examined the costs of production among species and the effect of whale depredation on operational costs and efficiency. NSRAA provided information on costs of production by species and facility. We compared the mean costs and revenues for each species (Coho Salmon, Chum Salmon, and Chinook Salmon) and two rearing sites (Hidden Falls or Mist Cove) in the 7 years since whale depredation pressure at the release sites was first noted (2008 – 2015) to the 7 years prior (2000 – 2007). Chum Salmon incubated at Hidden Falls are released in Kasnyku and Takatz Bays.

## 2.4. Results

Salmon cohorts in this study demonstrated high variability in whale depredation pressure, with values of  $WDPI$  ranging from zero to 1.5 whale observations per day. There was also contrast in  $WDPI$  within *Site* and *Species*. Cohorts of each species at every site included one or

more observations with zero *WDPI* and one or more with non-zero *WDPI*. However, non-zero *WDPI* was not included in the analysis for Pink Salmon. This species was only released from Port Armstrong and first experienced non-zero *WDPI* in 2015, for which return data was not yet available for analysis. Regular Chum Salmon experienced the highest level of humpback whale depredation pressure and Coho salmon had the highest average marine survival (Table 2.5).

Coho Salmon was the only species for which estimated reductions in marine survival due to *WDPI* were statistically significant (Table 2.4, Figure 2.2). Juvenile Chum Salmon *CPUE* had a positive relationship to marine survival, while the marine survival declined with increasing SST in summer and winter of their first year at sea. Mist Cove Coho Salmon had higher marine survivals than Kasnyku Bay and Port Armstrong, the other release sites for that species.

The model predicted whale depredation losses to the hatcheries of \$992,000 per year (95% CI \$666,000 – \$1,326,000, Table 2.7). Although releases of Chum Salmon were observed to have suffered the greatest depredation, economic losses were small compared to the losses for Coho Salmon, due to a much stronger relationship between *WDPI* and marine survival in that species. Mist Cove and Kasnyku Bay were estimated to have suffered disproportionately large losses to whale depredation due to their reliance on Coho Salmon at Mist Cove and the previously documented high frequency of whale depredation at both sites (Table 2.7; Chenoweth et al. 2017).

The absolute effect of humpback whales on numbers of returning salmon and value depended on other release conditions. Whales had the largest impact where conditions such as site and summer temperature were favorable (Figure 2.4). The model predicted Coho Salmon marine survival under favorable conditions of summer temperature and release site but with a

hypothetical *WDPI* value of one to be roughly equivalent to marine survival with zero *WDPI* when site and summer temperature are unfavorable.

## 2.5. Discussion

Humpback whale depredation is having a measurable economic impact, estimated at approximately \$1 million per year (95% CI \$665,000 – \$1,325,000) and 12% of total revenue) on salmon fisheries supported by hatcheries located in Chatham Strait. This estimate includes average losses across cohorts and release sites. Humpback whale depredation had the strongest effect on Coho Salmon in terms of both reductions in marine survival and lost revenue.

Environmental covariates and the site of release also affected these losses. Significant losses may be currently restricted to Coho Salmon because they have the highest marine survival and have the greatest absolute variability in marine survival. For other species, marine survival was about 1% for cohorts with zero *WDPI*, therefore detecting further declines due to whale depredation is unlikely.

To interpret these results, it is best to consider humpback whales as among the first predators in a predator gauntlet faced by juvenile hatchery salmon, beginning at the release site and continuing along the outmigration corridor to offshore waters before they are harvested (Petersen and DeAngelis 2000). The effect of humpback whale predation on juvenile salmon appears to be greatest where conditions indicate marine survival would otherwise be high. This is logical, as a larger proportion of the salmon consumed by whales would be expected to survive to harvest under these otherwise favorable conditions. In particular, we detected an effect of whale depredation in Coho Salmon, which typically have much higher return rates than other species and spend less time at sea and thus susceptible to predation (1 year). Taking measures to

reduce whale depredation at the time of release, for example using a trickle release strategy rather than releasing en masse, might be particularly useful at Mist Cove or in years of favorable environmental conditions where non-whale mortality is expected to be relatively low. Ims (1990) predicts that for a generalist predator capable of prey switching, such as a humpback whale, predator swamping strategies may increase total predation, an outcome exacerbated by the high satiation threshold for these large animals (Klumov 1963; Witteveen et al. 2006). Conversely, filter-feeding baleen whales, like humpback whales, rely on dense aggregations of prey to forage efficiently (Piatt and Methven 1992; Deméré et al. 2008; Goldbogen et al. 2011; Chapter 3). Therefore, a trickle release strategy may reduce their foraging efficiency.

These results indicate that mitigating humpback whale depredation at release sites would not be sufficient to increase marine survivals in Chum Salmon and Chinook Salmon, though it may be necessary, in concert with other measures. It may be that humpback whales are consuming a large number of Chum Salmon but that those salmon were unlikely to return as adults even in the absence of whales, due to other sources of depredation or the influence of adverse environmental conditions. Whale depredation of Chum Salmon remains a concern, as whales were most commonly sighted after releases of Chum Salmon cohorts, which have historically generated the highest revenue for hatcheries (McDowell Group 2010).

Humpback whale depredation is likely having a larger impact on hatchery economics than just consuming a portion of fish at the point of release. Humpback whales may be causing a non-consumptive mortality, for example by interfering with the foraging efficiency or energetics of juvenile salmon (Preisser et al. 2005). Also, due to the bulk lunge filter-feeding style of predation by humpback whales, they are likely less selective than most predators in targeting specific individuals of low fitness. Therefore, on average, fish consumed by whales may have

been more likely to survive to harvest than juvenile salmon consumed by other predators. In addition, avoiding whale depredation affects the rearing costs. In the eight years (2008-2015) since humpback whales were first reported feeding near release sites during or shortly after releases, there has been an overall decrease in the economic performance of hatchery operations as determined by the costs of production per adult returning (personal communication Chip Blair NSRAA 2017; Table 2.8). While costs per adult return increased substantially, there were also small increases in the cost per smolt released. The Mist Cove Coho Salmon program is the only one for which mean costs of production were less than the mean value of the catch for cohorts released after 2007, although this was the case for some individual cohorts of each program.

The relatively higher marine survival and less frequent observations of whale depredation for late Chum Salmon compared to regular Chum Salmon is encouraging (see also NSRAA 2015). Moreover, these gains in marine survival appear to offset a substantial increase in rearing costs (1.7-1.9 times that of the regular Chum Salmon program) based largely on increased feed and personnel costs (Personal communication Chip Blair NSRAA 2017). Whether the improvement in marine survivals is due to a reduction in humpback whale depredation is not clear. It is likely that these larger juvenile salmon fare better against a range of marine predators (Beamish et al. 2004; Farley et al. 2007). One caveat is that because the late Chum Salmon program is new, projections of returns for incomplete cohorts in this study were based on the age composition of regular Chum Salmon. Since early data indicates that late Chum Salmon may tend to return at a younger age, these projections may overestimate the eventual marine survival of the partial cohorts (NSRAA 2015).

Hatcheries could be subsidizing populations of non-whale predators near the release sites, as occurs with many other types of anthropogenic subsidies (Boarman et al. 2006; Oro et al.



2013; Heath et al. 2014). However, they are probably not significantly subsidizing the humpback whale population, due to the low number of whales that feed there (Chenoweth et al. 2017). Salmon reared at Hidden Falls and released at other sites show improved survival, suggesting that local conditions (including local predators) rather than rearing practices or ocean conditions are primarily responsible for poor returns at Kasnyku Bay and Takatz Bay. To avoid these local conditions, NSRAA is expanding production to more facilities and transporting salmon to other sites prior to release, a strategy analogous to pest control through crop rotation (NSRAA 2016b, 2017). Initial returns of three-year-old chum salmon to one of these sites in 2017 exceeded expectations, suggesting high future returns from this cohort (personal communication Scott Wagner NSRAA, 2017).

This study also points to environmental conditions affecting marine survival of juvenile salmon that are outside of the control of managers. Juvenile salmon catch per unit effort in Icy Strait, an important outmigration corridor, is an indicator of early marine conditions. In particular, freshwater discharge has been shown to be particularly important for juvenile salmon cohort strength in this region (Kohan et al. *in press*). Early marine growth is an important contributor to overall marine survival with mortality particularly high during the early marine period and first winter (Holtby et al. 1990; Beamish and Mahnken 2001; Beamish et al. 2004; Moss et al. 2005; Farley et al. 2007). Cohort strength of salmon has been shown to have a positive relationship with the abundance of congeners in the nearshore environment (LaCroix et al. 2009) due to predator sheltering (i.e., strength in numbers), and a negative relationship in the offshore environment (Debertin et al. 2016; Yasumiishi et al. 2016) due to resource competition. This study does not address broader effects including cyclic temperature regimes (Hare et al.

1996; Kilduff et al. 2015) and global climate change, which could affect salmon cohort strength in years to come (Shanley et al. 2015).

Whale depredation on released juvenile salmon is not addressed in federal U.S. Department of Agriculture programs intended to cover disasters and depredations that affect agriculture, including aquaculture (Agricultural Act of 2014). Livestock ranchers can be compensated up to 75% of the cost of lost animals due to depredation by wild predators through the USDA Livestock Indemnity Program, but this benefit does not extend to aquaculture losses. Fishing and aquaculture losses can be covered under the Non-insured Crop Disaster Assistance Program (Herrmann et al. 2004); however, this program provides for depredation losses of crops due to insects but not wild animals. Finally, the Emergency Assistance for livestock, honeybees, and farm-raised fish provides relief for losses resulting from severe weather events but applies only to confined fish and does not extend to losses due to depredation. A revision of the Agricultural Act of 2014, which is up for reauthorization in 2018, could modify one of these programs to provide support to hatcheries for depredation losses from humpback whales.

The environmental and economic benefits of healthy marine mammal populations are well documented (Estes and Duggins 1995; Croll et al. 2007; Cisneros-Montemayor et al. 2010; Roman and McCarthy 2010; Roman et al. 2014) and many populations worldwide remain depleted or in danger of extinction (Magera et al. 2013; Roman et al. 2013; Rojas-Bracho and Reeves 2013). While in some areas where marine mammal populations are growing they do not appear to be limiting fishery productivity (Corkeron 2009), hatchery release sites are among the places where they do pose quantifiable management challenges (Larson et al. 2013; Peterson et al. 2013, 2014).

## 2.6. Figures

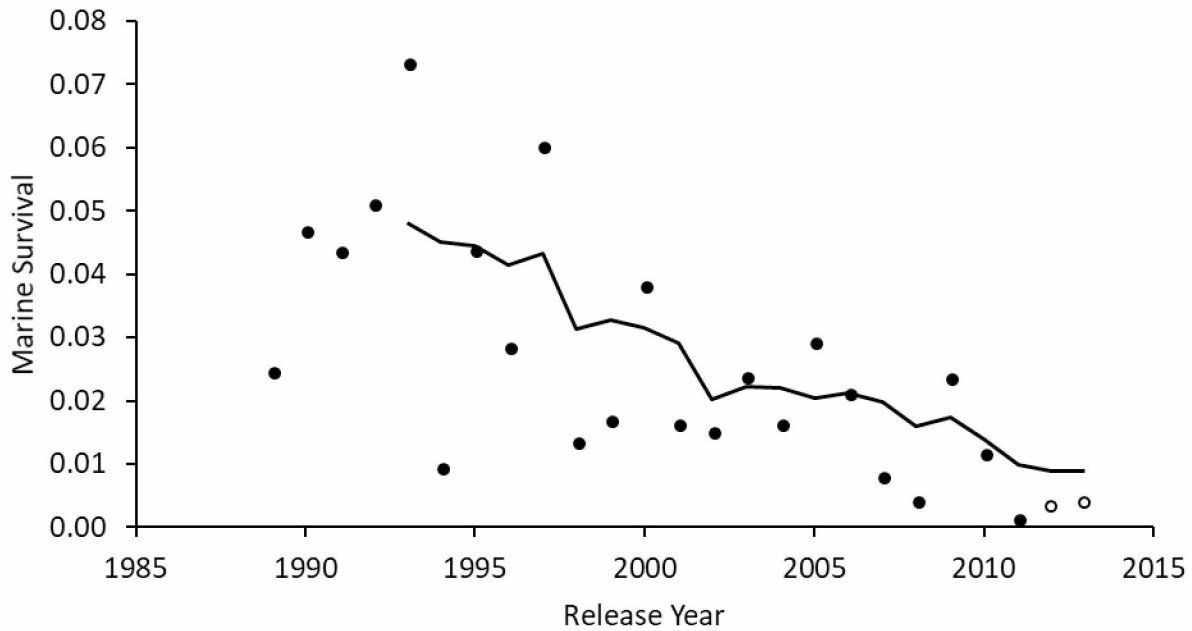


Figure 2.1 Five-year moving average of marine survival for juvenile Chum Salmon smolts raised at Hidden Falls hatchery and released in Kasnyku and Takatz Bays. Open circles represent incomplete cohorts of Chum Salmon whose total marine survivals have been estimated using methods described in this document. Data from NSRAA (2016a).

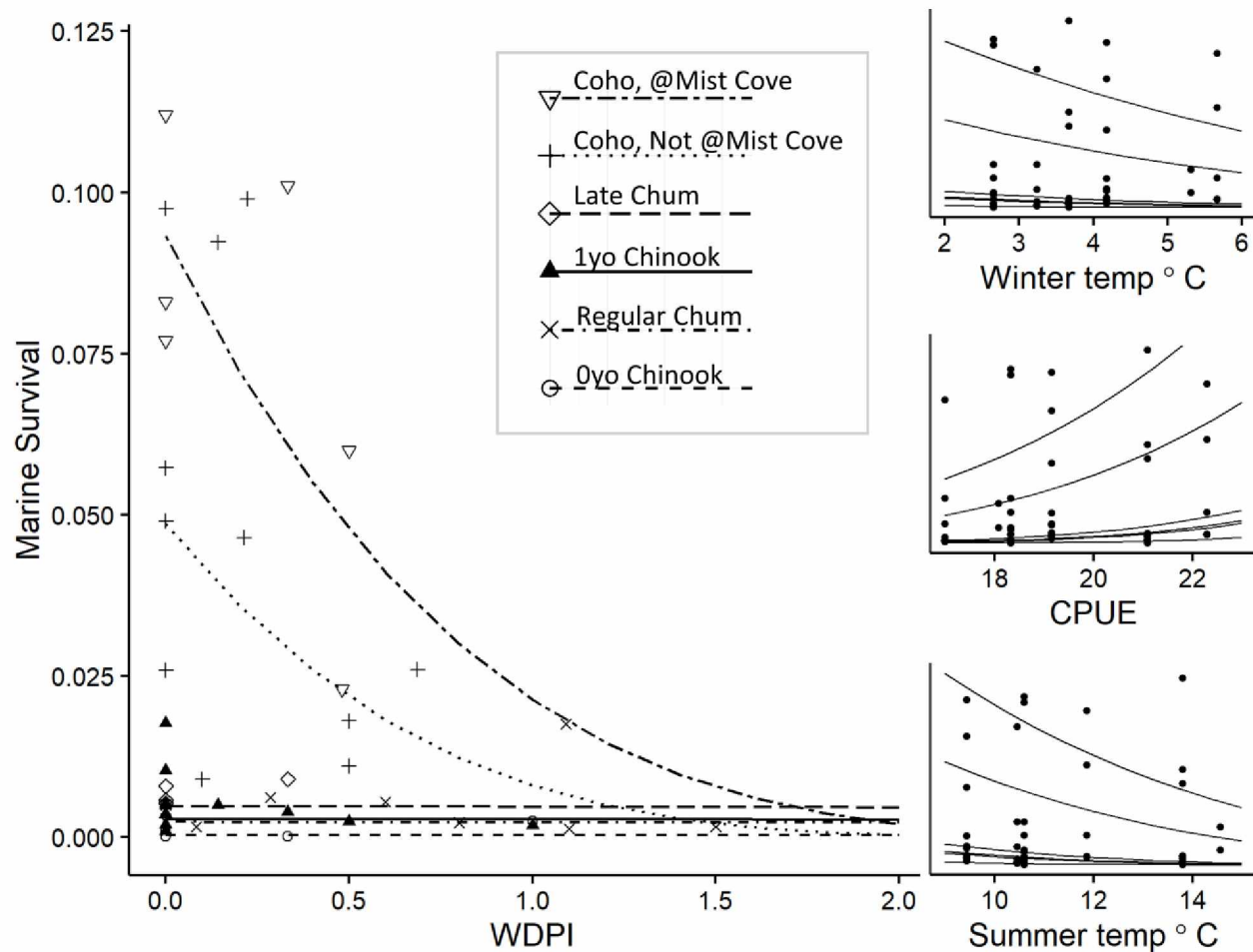


Figure 2.2 Fitted relationships between marine survival of hatchery salmon (y-axis of all subplots) and the Whale Depredation Pressure Index (*WDPI*) by *Species* (subdivided by release strategy) and covariates (Equation 2.2). Lines indicate fitted values for marine survival across a range of three different covariates when the others are held constant at their means. *Species* are ordered in the main panel's legend by the magnitude of the intercepts. Since this order is consistent across all covariates, they are shown as solid lines in the side panels. Coho @ Mist Cove/ Not @ Mist Cove refers to the site of the release, while Chum Salmon are subdivided by the seasonal timing of their release, and Chinook Salmon are subdivided based on their age at release. Pink Salmon are not included in these figures for ease of interpretation since they were not observed to experience whale depredation.

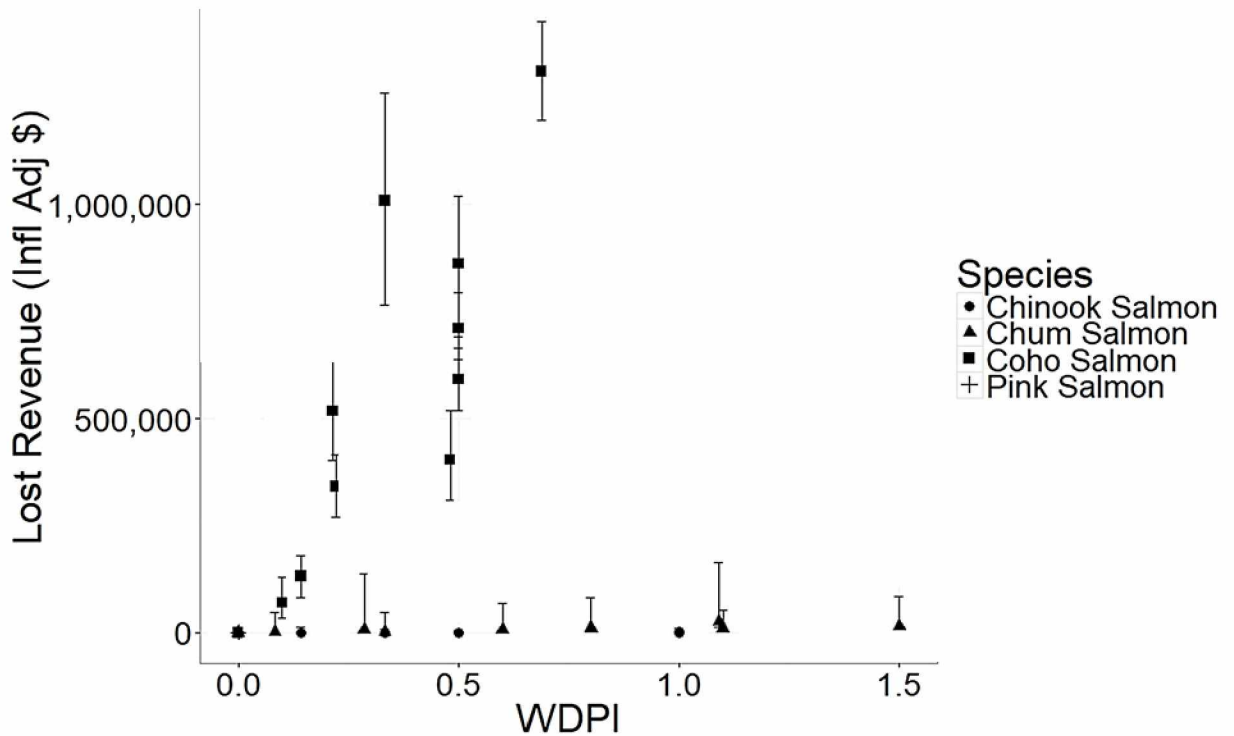


Figure 2.3 Lost revenue at five release sites attributed to whale depredation pressure index (*WDPI*) by release cohort. Lost Revenue is defined as the difference between the predicted value for marine survival of each cohort under observed values for the *WDPI* and the predicted value if all covariates remained the same but the *WDPI* is set to zero over the same period. Revenues are derived from marine survivals by multiplying by the total number of released fish per cohort, the average inflation-adjusted ex-vessel price, and the average weight for each species of salmon in each returning year weighted by the proportion of the total return that occurred in that year (Equation 2.3).

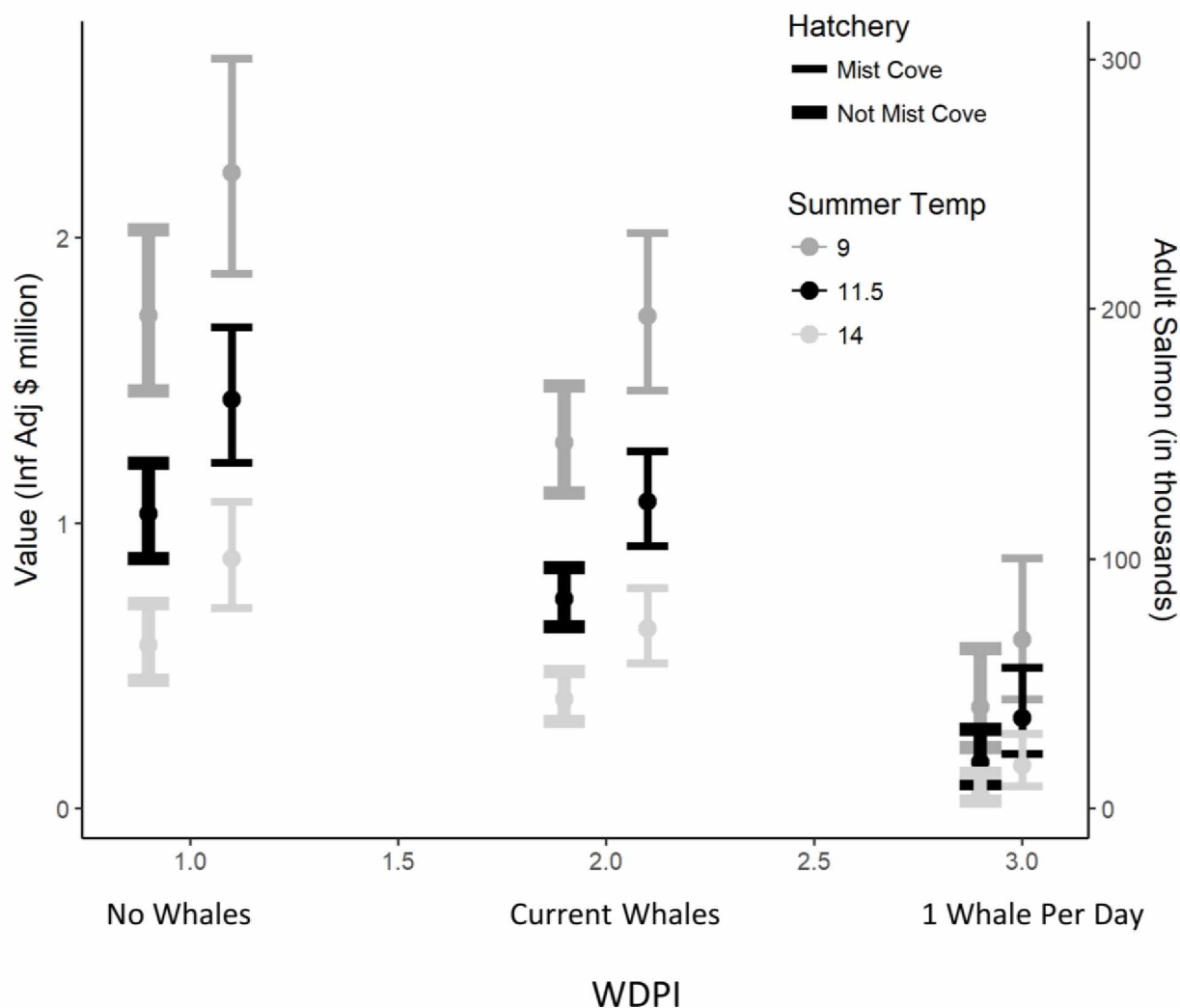


Figure 2.4 Effects of site, temperature, and whale depredation pressure index (*WDPI*) on total value of Coho Salmon cohorts. Value of Coho Salmon returns under different whale depredation scenarios including the mean for cohorts in the study (current whales) and 1 whale observed for each day. Observation days include all release days for a cohort and the two days following each release. Winter temperature = 4.1 °C, the mean for the 6-year dataset. Error bars are calculated from the model (Equation 2.2) standard errors for estimated marine survival. Marine survival is converted to adult salmon numbers and value using (Equation 2.3). Since Coho Salmon all return in the same year, value is a linear transformation of the total number of returning adult salmon for that year.

## 2.7. Tables

Table 2.1 Summary of cohorts by *Species* and *Site*. Years indicated are the year in which the cohort was released (as opposed to the brood year or return year). Cohorts indicated with italics are partial cohorts: a multi-age run that had not completed at the time of analysis or for which data for the final year is not available. Partial cohorts were included in the dataset by using regression of historical data from those sites and the to-date cumulative return to predict the total marine survival.

<i>Site</i>	0 yo Chinook	1 yo Chinook	Coho	Regular Chum	Late Chum	Pink	Total cohorts by <i>Site</i>
Kasnyku Bay	--	2011-12 <i>2013-14</i>	2010-15	2010-11 <i>2012-13</i>	<i>2012-13</i>	--	16
Takatz Bay	--	--	--	2010-2011 <i>2012-'13</i>	<i>2012-13</i>	--	6
Mist Cove	--	--	2010-15	--	--	--	6
Little Port Walter	--	2010-12 <i>2013-14</i>	--	--	--	--	5
Port Armstrong	2010-11 <i>2012-13</i>	2010-12 <i>2013</i>	2010-14	2010-11 <i>2012</i>	--	2010-14	21
Total cohorts by <i>Species</i>	4	13	17	11	4	5	54

Table 2.2 Candidate model variables. All management variables are specific to cohort, defined by variables *Site*, *Species* and *Year*. All environmental variables are specific to year (all cohorts released in the same year have the same values for all environmental variables)

Variable Type	Name	Explanation	Source
Predictor	<i>WDPI</i>	Humpback whale depredation pressure index	1,2
Response	<i>MarSurv</i>	proportional marine survival to adult harvest	2,3
	<i>Species</i>	Levels = 0yo Chinook, Age 1yo Chinook, Coho, Pink, Regular Chum, Late Chum	2,3
	<i>Site</i>	Levels = Kasnyku, Takatz, Mist Cove, Little Port Walter, Port Armstrong	2,3
Management covariate	<i>Mass</i>	Average mass of juvenile salmon at release (g)	2,3
	<i>DOY</i>	Day of year of first release	2,3
	<i>Release</i>	Number of juvenile salmon released	2,3
	<i>Sum.SST</i>	Mean modeled Gulf of Alaska sea surface temperature Jun 1 – Sep 18 of release year	4
	<i>Spr.SST</i>	Mean modeled Gulf of Alaska sea surface temperature Mar 1 – Jun 30 of release year	4
Environmental covariate	<i>Win.SST</i>	Mean modeled Gulf of Alaska sea surface temperature Jan 1 – Mar 31 year after release (1 <sup>st</sup> marine winter)	4
	<i>CPUE</i>	Total juvenile wild and hatchery chum captured in Icy Strait per sampling haul during release year	5
	<i>Year</i>	Factor levels = 2010-2015	--

References: [1] see Chenoweth et al. (2017); [2] Courtesy of NSRAA, Armstrong Keta Inc, NOAA [3] Armstrong-Keta Inc 2016, NSRAA 2016a; [4] <http://www.ims.uaf.edu/gak1/> [5] Orsi and Fergusson 2015



Table 2.3 Candidate models describing marine survival of juvenile salmon cohorts released from Southeast Alaska salmon hatcheries. The response variable for all models is marine survival ( $MarSurv^{1/4}$ ).

	Parameters	Adj R <sup>2</sup>	K	AICc	ΔAICc
1	<i>WDPI x Coho + MistCove + Species + CPUE + Sum.SST + Win.SST</i>	0.86	12	-155	0
2	<i>WDPI x Coho + MistCove + Species* + CPUE + Sum.SST + Win.SST + Mass</i>	0.85	11	-154	1
3	<i>WDPI x Coho + MistCove + Species + CPUE + Sum.SST + Win.SST + Release</i>	0.86	13	-153	2
4	<i>WDPI x Coho + MistCove + Species + Year</i>	0.86	14	-152	3
5	<i>WDPI x Coho + MistCove + Species + CPUE + Sum.SST</i>	0.84	10	-151	4
6	<i>MistCove + Species + CPUE + Sum.SST + Win.SST</i>	0.83	10	-149	6
7	<i>WDPI x Coho + MistCove + Species + CPUE + Sum.SST + Win.SST + DOY</i>	0.84	13	-149	6
8	<i>WDPI x Coho + MistCove + Species* + CPUE + Sum.SST + Win.SST</i>	0.82	10	-145	10
9	<i>WDPI x Coho + MistCove + Species + Spr.SST + Sum.SST + Win.SST</i>	0.78	11	-132	23
10	(Intercept only)	-----	1	-67	88

Adj R<sup>2</sup> is the coefficient of determination adjusted for the number of parameters. K is the number of estimated parameters for each model. AICc is the Akaike's information criteria bias-corrected for small sample size, ΔAICc is the AICc for each model minus the AICc for the best model. Models include the best model (1) and the best model plus each of the rejected covariates: *Mass*, (2); *Release* (3); *DOY* (7); and *Spr.SST* (9), which replaced *CPUE* as they both are proxies for to spring conditions. Also included is the best model without the least significant covariate (*Win.SST*, 5), a model without the predictor of interest (*WDPI*, 6), and a model where *Year* as a factor replaces all annual-scale environmental covariates (4). Other models include a redefinition of *Species* without subdividing by release strategy (noted here as *Species\**) (2,8) and a null model (10).

Table 2.4 Parameter estimates and significance values for equation (2.2) with marine survival ( $MarSurv^{1/4}$ ) as the response variable.

	Estimate	S.E.	p value
Intercept (0yo Chinook)	-0.04	0.08	0.6
<i>Coho</i>	0.34	0.03	<0.001
<i>1yo Chinook</i>	0.10	0.03	<0.001
<i>Late Chum</i>	0.13	0.03	<0.001
<i>Pink</i>	0.17	0.03	<0.001
<i>Regular Chum</i>	0.09	0.03	0.003
<i>MistCove</i>	0.08	0.02	0.001
<i>CPUE</i>	0.03	0.01	<0.001
<i>Sum.SST</i>	-0.03	0.005	<0.001
<i>Win.SST</i>	-0.02	0.01	0.01
<i>WDPI x Coho</i>	-0.17	0.05	0.004
<i>WDPI</i>	-0.012	0.02	0.95

Table 2.5 Marine survival and whale depredation pressure index (*WDPI*) by species of salmon 2010-2015 at five sites.

<i>Species</i>	n	Marine Survival (mean ± SD)	<i>WDPI</i> (mean ± SD)	<i>Sites</i>
<i>Coho at Mist Cove</i>	6	7.6 ± 3.2 %	0.22 ± 0.25	MC
<i>Coho at other site</i>	11	4.8 ± 3.4 %	0.22 ± 0.24	KB, PA
<i>Pink</i>	5	1.4 ± 1.0 %	0	PA
<i>Late Chum</i>	4	0.7 ± 0.2 %	0.08 ± 0.17	KB, TB
<i>1 yo Chinook</i>	13	0.5 ± 0.4 %	0.15 ± 0.30	KB, PA, LPW
<i>Regular Chum</i>	11	0.4 ± 0.5 %	0.50 ± 0.55	KB, TB, PA
<i>0 yo Chinook</i>	4	0.1 ± 0.1 %	0.33 ± 0.47	PA

MC = Mist Cove, KB = Kasnyku Bay, PA = Port Armstrong, TB = Takatz Bay, LPW = Little Port Walter

Table 2.6 Lost revenue by species 2010-2013. Lost revenue is the difference between the predicted revenue under observed conditions (fitted value) and the predicted value under 0 *WDPI*. However, total revenue is calculated using the observed values (equation 2.3).

Species	Lost Revenue	Lost Revenue 95% CI	Total Revenue	Percent Lost
Coho Salmon	\$3,890,000	\$2,990,000 - \$4,820,000	\$16,577,757	23%
Chum Salmon	\$77,800	\$0 - \$646,000	\$10,692,091	0.7%
Chinook Salmon	\$3,700	\$0 - \$47,500	\$832,134	0.4%
Pink Salmon	\$0	-----	\$5,828,507	0%
	\$3,970,000	\$2,660,000-\$5,300,000	\$33,930,489	12%

Table 2.7 Lost revenue by *Site* 2010-2013. Lost revenue is the difference between the predicted revenue under observed conditions (fitted value) and the predicted value under 0 *WDPI*. However, total revenue is calculated using the observed values (equation 2.3).

<i>Site</i>	Lost Revenue	Lost Revenue 95% CI	Total Revenue	Percent Lost
Kasnyku Bay	\$2,410,000	\$1,910,000- \$2,920,000	\$10,489,730	23%
Takatz Bay	\$35,300	\$0 – \$377,000	\$3,044,184	1%
Mist Cove	\$1,010,000	\$21,300 - \$1,650,000	\$5,997,024	17%
Little Port Walter	\$931	\$0 – \$17,000	\$107,001	<1%
Port Armstrong	\$518,000	\$0 – \$1,430,000	\$14,292,549	4%
	\$3,970,000	\$2,660,000-\$5,300,000	\$33,930,489	12%

Table 2.8 Hatchery production costs by salmon species and *Site* for cohorts released before and after targeted whale predation from the Northern Southeast Regional Aquaculture Association. Cost per smolt is through 2014 release season for Chum Salmon and 2015 release season for Coho Salmon.

Site	Species	Pre-whales (Release years 2000-2007)			Post-whales (Release years 2008-2014/2015)		
		Cost per smolt (mean $\pm$ se)	Cost per adult	Cost as % of adult value	Cost per smolt	Cost per adult	Cost as % of adult value
Mist Cove	Coho Salmon	\$0.66 $\pm$ 0.14	\$5.19 $\pm$ 1.00	110 $\pm$ 28 %	\$0.39 $\pm$ 0.065	\$6.30 $\pm$ 1.3	87 $\pm$ 18 %
Kasnyku Bay	Coho Salmon	\$0.11 $\pm$ 0.0031	\$2.01 $\pm$ 0.88	33 $\pm$ 18 %	\$0.13 $\pm$ 0.0047	\$6.10 $\pm$ 1.8	130 $\pm$ 48 %
Kasnyku Bay/ Takatz Bay	Chum Salmon	\$0.011 $\pm$ 5.7 $\cdot$ 10 <sup>-4</sup>	\$0.74 $\pm$ 0.18	15 $\pm$ 1.5 %	\$0.014 $\pm$ 5.1 $\cdot$ 10 <sup>-4</sup>	\$3.70 $\pm$ 1.6	100 $\pm$ 55 %
Kasnyku Bay	Chinook Salmon	\$0.23 $\pm$ 0.013	\$28.00 $\pm$ 5.5	85 $\pm$ 19 %	\$0.36 $\pm$ 0.025	\$154.00 $\pm$ 79	410 $\pm$ 200 %

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## Chapter 3: Using a Process Model to Predict and Understand Net Energy Gain of Humpback Whales on Typical and Novel Prey Patches.<sup>1</sup>

### 3.1. Abstract

1. Humpback whales (*Megaptera novaeangliae*) feed on a wide range of prey types, but their modes of prey selection are poorly understood. Scientists lack an integrated framework for understanding how characteristics of these prey, such as patch density, depth, energy content and mobility interact to affect the energy humpback whales gain from feeding.
2. Animal-borne tags were deployed to record humpback whale behaviour while feeding and measure *in situ* prey patch characteristics for four taxa in Southeast Alaska: krill, herring, and two novel prey: juvenile coho and chum salmon released from hatcheries. A process model was developed to determine the proportion of the prey energy density per volume in a prey patch the whale is likely to capture and the energetic costs based on the observed predator behaviour and constraints on prey escape.
3. Among nine distinctive foraging targets considered, predicted net energy gain ranged from -1859 to 3,632 kJ/min. No single species was universally energetically superior, with patch density playing the largest role in determining profitability. Notably, coho salmon tended to be too diffusely distributed for humpback whales to profitably feed, underscoring the importance to whales of behaviours that aggregate prey, notably the production of bubble nets.

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4. Whales may forage on prey that only partially offset metabolic losses when energetically profitable prey are not available. Our process model provides a framework to predict diet shifts of baleen whales due to a wide range of changes in prey and predator characteristics.

### 3.2. Introduction

Due to baleen whale's superlative size and energetic demands, highly-specialized anatomy, and persistent conservation concern, their foraging ecology is a topic of acute interest for evolutionary biologists, morphologists, conservationists, marine ecologists, and fisheries managers. The development of archival short-term animal-borne tags has enabled the direct fine-scale study of subsurface cetacean foraging for the first time (Goldbogen *et al.* 2013). Data from these tags have allowed for the modelling of baleen whale hydrodynamics with particular focus on the metabolic costs of foraging lunges (Goldbogen, Potvin & Shadwick 2010; Goldbogen *et al.* 2011, 2012; Potvin, Goldbogen & Shadwick 2010, 2012). Many studies have investigated baleen whale foraging behaviours and documented the characteristics of their prey, such as depth, patch density, and energy content. However understanding how different prey patch characteristics and foraging behaviours affect foraging efficiency and prey selection are major outstanding questions in baleen whale ecology (Goldbogen *et al.* 2017b). Determining the relative advantages of foraging on different types of prey patches requires integrating the effects of these different factors into a single mathematical framework.

Optimal foraging theory offers such a framework to understand energetic considerations when generalist predators select different prey. This theory posits animals that select prey that maximizes a fitness-related currency such as net energy gain have an adaptive advantage (Pyke 1984; Stephens and Krebs 1986). This framework has been used to interpret observed foraging behaviour (Mittelbach & Osenberg 1994; Thums *et al.* 2013; Watanabe *et al.* 2014) and to predict circumstances in which animals will forage, how they will forage, and for how long (MacArthur & Pianka 1966; Charnov 1976). Optimal foraging theory has also been invoked to explain when whales forage or rest (Friedlaender *et al.* 2016), how whales target prey within a

prey patch (Burrows *et al.* 2016), and foraging dive duration (Doniol-Valcroze *et al.* 2011). Humpback whales have been identified as “energy maximisers” meaning that whales are expected to prefer prey with characteristics that allow for high net energy gain as opposed to others that optimize some other currency, for the time spent foraging (Dolphin 1988).

The role of prey escape is probably the least studied aspect central to energy gain in baleen whales. Previous models of baleen whale foraging have assumed whales capture a quantity of prey equal to the patch density of prey in the water column times the engulfment volume (Goldbogen *et al.* 2011) or avoid the issue by making relative comparisons only among prey patches of the same species (Hazen, Friedlaender & Goldbogen 2015). However, the effectiveness of predator avoidance behaviours and speeds of prey have been invoked to explain the effectiveness of foraging (Heintz *et al.* 2010; Potvin, Goldbogen & Shadwick 2010) and baleen whale foraging manoeuvres (Goldbogen *et al.* 2015; Cade *et al.* 2016). Humpback whales in particular use a variety of behaviours such as bubble net feeding, surface feeding, echelon feeding, and flick feeding, presumably to minimize escape and increase capture proportion (Jurasz & Jurasz 1979; Sharpe 2001; Acevedo *et al.* 2011; Chenoweth, Gabriele & Hill 2011; Chenoweth *et al.* 2017; Goldbogen *et al.* 2013; Cade *et al.* 2016).

Humpback whales (*Megaptera novaeangliae*) are generalist predators known to feed on diverse prey but most commonly on krill (euphausiids) and small schooling fishes (Nemoto 1957, 1973; Straley *et al.* 2017). These prey vary widely in characteristics central to foraging energetics including size, swimming speed, energy density, patch density and depth. Modes of humpback whale prey selection are of growing interest as humpback whale populations increase in many other regions of the world (Calambokidis *et al.* 2008; Fleming & Jackson 2011; Hendrix *et al.* 2012; Smith *et al.* 2015; Surma & Pitcher 2015). Humpback whales prey on important

commercial species, notably herring (*Clupea palasii*; Boswell *et al.* 2016; Straley *et al.* 2017) but also northern anchovies (*Engraulis mordax*), Pacific sardines (*Sardinops sagax*; Fleming *et al.* 2016) and juvenile walleye pollock (*Gadus chalcogrammus*; Krieger & Wing 1986). Humpback whales are innovative foragers with diverse feeding tactics (Werth 2000), capable of inventing and transmitting new foraging behaviours throughout their population (Allen *et al.* 2013). Within the last decade, humpback whales have been reported for the first time feeding on juvenile Pacific salmon (*Oncorhynchus* spp.) at hatchery release sites (Chenoweth *et al.* 2017).

The goal of the present study is to develop a comprehensive process model to assess the relative adaptive advantages to humpback whales of various foraging opportunities. A process model integrates current knowledge and assumptions about the mechanisms and generates predictions under different initial conditions. Though often labour-intensive for complex processes, and sometimes lacking a clear framework for assessing model precision (unlike stochastic models), process models are necessary for generating predictions of a quantity, such as net energy gain, that cannot be directly observed (Peck 2000). Process models are also useful for confronting assumptions about the process they model, identifying priorities for improving our understanding of the system, and for making predictions about how the system will respond to novel conditions. (Cuddington *et al.* 2013). Our primary objective of this study is to: 1) develop a model to compare expected net energy gain from different types of prey patches in Southeast Alaska. One of the advantages of our proposed model is that it integrates the effects of many different variables simultaneously to evaluate complex trade-offs in real-world foraging conditions. However, that complexity can obscure the mechanistic understanding of the variables at play. Therefore, we also 2) conduct a sensitivity analysis to determine the most influential variables in the model and 3) apply the model to inform our understanding of why and how some



humpback whales feed on a relatively recent and distinctive foraging opportunity--juvenile salmon from hatchery release sites--demonstrating the practical application of such a tool.

### 3.3. Methods

We developed a process model (Cuddington *et al.* 2013) to calculate and compare the relative energetic benefits to humpback whales feeding on different prey targets. Energetic benefits were measured in terms of net energy gain per lunge (or feeding event) and net energy gain per time. Net energy gain per lunge was used for judging the relative energetic advantage of lunges on different types of prey (Stephens & Krebs 1986; Friedlaender *et al.* 2016). This metric is simply the energy obtained and assimilated from prey captured during a lunge minus the metabolic costs of the lunge [Equation 3.1].

$$\frac{\text{Net Energy Gain}}{\text{lunge}} = \frac{\text{Gross energy gain (kJ)} - \text{Energy lost (kJ)}}{\text{lunge}} \quad [\text{Equation 3.1}]$$

Net energy gain per time is similar but accounts for differences in lunge rate (feeding rate) and non-feeding energy expenditures among foraging opportunities [Equation 3.2].

$$\frac{\text{Net energy gain}}{\text{time (min)}} = \frac{\text{Gross energy gain (kJ)} - \text{Energy lost (kJ)}}{\text{time (min)}} \quad [\text{Equation 3.2}]$$

The model is best conceptualized as consisting of three sub-models: the patch energy density model, the capture proportion model, and the metabolic costs model (Figure 3.1). First, the patch energy density model calculates the distribution of energy the environment (in the form of prey items; kJ/m<sup>3</sup>) in using a simple deterministic equation [Equation 3.3].

$$\text{Patch energy density } \left(\frac{\text{kJ}}{\text{m}^3}\right) = \text{School density } \left(\frac{\text{ind}}{\text{m}^3}\right) * \text{Prey mass } \left(\frac{\text{g}}{\text{ind}}\right) * \text{Prey energy density } \left(\frac{\text{kJ}}{\text{g}}\right)$$

$$[\text{Equation. 3.3}]$$

Second, the capture proportion model calculates the amount of the energy in the water column that a whale would actually capture and accounts for differences in the ability of different types of prey to escape from a whale. This sub-model determines the proportion of prey in the path of a lunging whale that are captured at each time step during engulfment. Key parameters for this model include the size, initial, and final speed of the whale during engulfment; the speed of the prey; and the distance at which they react to predators (bold or skittish prey). The patch energy density model and the proportion captured model were multiplied together to estimate the total energy ingested by a whale per lunge and then scaled by the assimilation efficiency to yield the gross energy gain per lunge [Equation 3.4].

$$\frac{\text{Gross energy gain}}{\text{lunge}} = \frac{\text{Patch Energy Density} * \text{Proportion Captured} * \text{Engulfment Volume} * \text{Assimilation Efficiency}}{\text{Engulfment Volume} * \text{Assimilation Efficiency}} \quad [\text{Equation 3.4}]$$

Third, the model accounted for energy lost during foraging. The energetic losses during a lunge are a function of both the speed and mass of the whale. When calculating net energy gain per time we accounted for the costs of three behaviours: lunging (feeding events), swimming, and gliding (Goldbogen *et al.* 2012).

This three-part model was parameterized to a large degree with *in situ* measurements of prey patch characteristics and observations of humpback whale foraging behaviour on a variety of prey in Southeast Alaska. For comparison, observations of whale feeding behaviours and the characteristics of the prey they were targeting were grouped together into broad foraging targets defined by the prey species, the location of observations, dates of the observations, and significant differences in prey size or energy content. These foraging targets may consist of dozens of similar prey schools measured over a week or a single distinctive school (Table 3.1).

Net energy gain for each foraging target is determined using mean characteristics of prey in that target as well as characteristics of the behaviours whales used to exploit them.

#### 3.3.1.1. Prey patch energy density

We determined the energy density of prey schools actively exploited by humpback whales. Ultimately, this value, when combined with the humpback whale's engulfment volume, indicates the maximum quantity of prey that could be obtained in a single lunge if the prey made no effort to escape. The patch energy density model used acoustic prey surveys as well as species-specific relationships between individual length and acoustic target strength of individual prey items to determine the school density (individuals per space). Individual prey items collected at each site were measured for length and mass and analysed for energy density using bomb calorimetry.

#### 3.3.1.2. School density

Acoustic prey surveys were conducted near foraging whales in four locations in Southeast Alaska from 2012 - 2014 (Figure 3.2). In Tenakee Inlet, Sitka Sound and Seymour Canal, humpback whales were tagged with animal-borne dataloggers (tagging deployment and analysis protocols described in section 3.3.3: *Determining the metabolic costs of foraging*) and our surveys focused on mapping around, and directly behind the tagged animal as it was tracked with a VHF transmitter and receiver. A towable dual-frequency split-beam SIMRAD EK 60 scientific echosounder was used to assess depth and acoustic density of prey in the water column. The echosounder operated at 38 and 120 kHz about 1 m below the surface of the water.

In Kasnyku Bay, humpback whales were not tagged concurrently with prey mapping, but were observed feeding intermittently near net pens and in Bear Cove to the north (Figure 3.3). To assess prey density and distribution, hydroacoustic surveys were conducted using a 4 m

electrically powered Autonomous Surface Vessel (ASV; SeaRobotics Corp.), instrumented with a 120 kHz SIMRAD EK60 echosounder. The instruments were deployed at approximately 0.5 m below the surface and aimed downward. Hydroacoustic surveys were performed in a zig-zag design around the main dock and coho salmon net pens where humpback whales were commonly observed feeding (Figure 3.3). Detailed survey characteristics are listed in Table A-3.10 in Appendix 3.1)

Acoustic data were processed in Echoview software 6.1 - 7.1 (Echoview, Hobart, Tasmania, Australia). Decibel differencing was used to filter the data for krill prior to analysis as described in Burrows *et al.* (2016) (Appendix 3.1). When prey were sufficiently dense, schools were detected using the school detection algorithm in Echoview. Because herring form dense aggregations that attenuate acoustic energy, we applied a correction factor to avoid underestimating density of fish toward the bottom of the school (Foote 1990; Zhao & Ona 2003) (Appendix 3.1). Coho salmon were too diffuse for school detection so repeated survey data was analysed using a spatial generalized additive model to determine expected prey densities. These modelled densities were highest in the area where whales were most commonly observed feeding following the release of coho salmon.

#### 3.3.1.3. Prey energy density

Prey were captured using a variety of methods at each of the four locations to determine their morphometrics and energy content (Table 3.2). Prey samples were processed at the NOAA Ted Stevens Marine Research Institute in Juneau, Alaska using established protocols (Siddon, Heintz & Mueter 2013). Samples were divided into strata by species and collection date. Fork lengths were measured for all fish and a subsample of krill. A maximum of eight fish per stratum was weighed and analysed. Krill were analysed as composites of multiple individuals. Where

more than eight samples were available (chum salmon), individual fish were selected for calorimetry to represent a range of observed sizes. For juvenile salmon, a linear regression was used to determine the relationship between length and kJ/fish with collection date and an interaction between length and collection date included as predictors (Appendix 3A).

### 3.3.2. Estimating capture proportion

We designed a capture proportion sub-model to estimate the proportion of the prey in the path of an engulfing humpback whale we expect to be captured. This was a key component of our overall net energy gain model as humpback whales feed on prey that vary in size and mobility. The model estimates different capture probabilities for prey encountered by a whale at each time step during engulfment and, within each time step, at different locations across the plane of the whale's mouth. Our model builds on a previous model of the kinematics of humpback whale engulfment (Potvin, Goldbogen & Shadwick 2012), an animal-borne video detailing the stages of engulfment (Cade *et al.* 2016), and assumptions about how prey react to an oncoming whale informed by observations and physical limitations of each taxa. In addition, the model accounts for differences in the behaviour of whales as they feed. When whales lunge at high speeds, prey have less time to react, resulting in a greater capture proportion. In addition, the surface can impede the escape of prey, leading to greater capture proportions during surface feeding. Finally, when whales feed in a coordinated manner, fish escaping from one whale are likely to be captured by another whale, further increasing the net capture rate.

When the whale opens its mouth to feed, the combined forces of engulfment drag in the mouth and shape drag around the body begin to slow the whale. The engulfed water with prey and the whale form an inelastic collision, modelled by Potvin, Goldbogen & Shadwick (2012) to compare the metabolic expenditures during engulfment across rorqual species. This model

calculates the (negative) acceleration of the whale at each time step by finding the net force acting on the whale at each time step divided by the mass of the whale and engulfed water (Acceleration = Force/Mass, from first principles). Forces considered include the drag due to engulfment, the drag due to the whale's shape, thrust, and weight-subtracted buoyancy (Potvin, Goldbogen & Shadwick 2012). This model forms a useful framework to develop a model of capture proportion because it produces dynamic predictions of engulfment area, gape angle, and whale speed at different time steps within the engulfment based on initial conditions of engulfment duration, initial speed, and size of the whale. This model is parameterized assuming a humpback whale of average length for the North Pacific, 12.3 m, (Nichol & Heise 1992) and scaling relevant morphometries accordingly (Table 3.3).

The Potvin, Goldbogen & Shadwick (2012) model includes only a mouth-opening phase and a mouth-closing phase; here the model has been modified to include an additional "mouth-open" phase (Figure 3.4). Observations of foraging events from animal-borne camera tags indicate that the mouth does not immediately close once it reaches maximum gape, but rather is frequently held at maximum gape for seconds or before beginning to close around prey (Cade *et al.* 2016). Consistent with Cade *et al.* (2016), the mouth-opening phase for krill was set at 35% of the total engulfment duration, the mouth open phase at 25% and the mouth-closing phase at 40%. For all piscine prey, the mouth-opening phase was 25% of the engulfment duration, the mouth-open phase was 44% and the mouth-closing phase was 31%. Total engulfment duration is inversely related to initial speed of engulfment (Potvin, Goldbogen & Shadwick 2012).

Whale speed prior to engulfment is important for determining how much time prey have to react. The initial velocity of a whale foraging was estimated as the mean velocity of the peak speed during foraging lunges at each foraging opportunity, as determined by animal-borne tags

(described in the next section). Different initial speeds were calculated for whales feeding on each prey patch at the surface and subsurface because our tag data indicated a substantial reduction in lunge speed at the surface. Average initial lunge speeds for surface ( $< 22.5$  m and subsurface  $\geq 22.5$  m) for each prey group were determined as well as the proportion of lunges occurring in surface or subsurface waters (Table 3.4)

Tag data were not available for all prey targets (Kasnyku Bay herring and all juvenile salmon). Lunge speeds were approximated using lunges from the entire dataset that occurred at similar depths and whale group sizes where tags were not available. The proportion of surface and subsurface lunges for herring in Kasnyku Bay was determined from the mean depth of prey schools. Lunge rates were observed and recorded for whales feeding on juvenile salmon, but for whales feeding on herring, lunge rates were approximated from other tagged whales feeding on herring in small groups or as individuals.

In addition to differences in whale behaviour during a lunge, the capture proportion is affected by the ability of different types of prey to escape (Figure 3.5). These probabilities are estimated at each time step of engulfment where the distance a prey item can swim to avoid a whale (the escape distance) is determined by the following equation:

$$D_{escape}(t) = \frac{V_p \cdot R_{xn}}{\bar{V}_{capture}(t)} \quad [\text{Equation 3.5}]$$

Where  $V_p$  is the speed of the prey and  $R_{xn}$  is the reaction distance, or the distance from a whale at which a prey item will begin to swim away. This can be conceptualized as a quantification of how skittish a prey item is in the face of predators.  $\bar{V}_{capture}(t)$  is the average speed of the whale as it approaches over that prey's reaction distance and is specific to each time step (moving average). Escape distance enters the model as a distribution based on variance in the prey speed and reaction distance, with variances assumed to be independent (Figure 3.5).

The model accounts for differences in the probability of escape for individual prey centred in the whale's path compared to those on the margins. Individuals nearer to the edge of the whale's path and will not need to swim far to escape. This model assumes that prey will move in the direction that minimizes the escape distance based on the orientation of the whale at the point when it will encounter the prey. At each time step, we modelled the distance a prey item would need to swim to escape capture at evenly spaced locations along a 15 by 15 grid superimposed on the capture area of a humpback whale (defined as a half-ellipse). The vertical radius of the capture area increases during the mouth-opening phase, remains the same during the mouth-open phase, and decreases during the mouth-closing phase. For each point, the distance to the closest escape point is identified mathematically. Escape probability for a prey item at that location is then assigned based on where the distance required to escape falls along the distribution of escape distance for that prey at that time step. At each time step, these probabilities are averaged to yield the proportion of the prey at that location in the path of the whale prior to engulfment that will be captured at that time step. The proportions at each time step are multiplied by the volume of water engulfed during that time step and summed to yield the capture proportion for that engulfment.

When whales feed at the surface, particularly in coordinated large groups, there are fewer routes for the prey to successfully escape. Here we model three simplified scenarios observed in this study: subsurface lunges, group surface lunges, or individual surface lunges and model prey escape routes unique to each type of lunge (Figure 3.5). When a whale lunges below the surface, prey may escape by swimming laterally or ventrally with reference to the orientation of the approaching whale. The positioning of the upper jaw prevents escape dorsally. Toward the end of a lunge, as the whale decreases in speed, escape forward is also possible. When a whale is



group feeding and lunging vertically at the surface, forward escape is prevented by the surface. In addition, ventral and lateral escape is minimized by close proximity to other whales such that escaping from one whale results in being captured by another whale. Therefore, net escape approaches zero and the capture volume will equal the engulfment volume. Whales also frequently perform individual lateral surface lunges. In this case, escape is reduced along the side of the whale that is out of the water during the lunge however; escape along the length of the submerged jaw is still possible. Forward escape is typically impeded, therefore, unlike a subsurface lunge, the model of surface feeding does not include a point at which escape = 100%. Variables and formulas for the capture proportion model are provided in Table 3.5.

### 3.3.3. Determining the metabolic costs of foraging

Here we describe the sub-model developed to account for differences in the metabolic costs associated with foraging on different types of prey patches. To estimate the overall metabolic costs of foraging, we need to consider the costs of three main activities (gliding, swimming and lunging) and the differences in how much time whales at different prey patches spend on each activity. Lunging is the most energetically costly, but also the only behaviour by which energy is obtained. Swimming is the primary activity between lunge events, with gliding providing a metabolic savings for transport to deeper prey. The metabolic costs of a foraging lunge are a function of the size of the whale and the speed of the lunge. Across a foraging period, we also account for the lunge rate, how often a whale performs a lunge. Here we describe how we determined the metabolic costs associated with each of these major components and then describe how we applied those costs across foraging periods on different prey.

The total cost of a dive is equal to the sum of the costs associated with swimming, gliding and lunging during a dive (Table 3.6). We assumed that the costs of swimming and gliding were

functions of basal metabolic rate (BMR), which is determined from an allometric relationship with whale mass ( $M_c$ ) (Ahlborn 2004). The cost of gliding, being the least costly behaviour, was assumed to be equal to 1.4 BMR (Sparling & Fedak 2004). Hence, the total cost of gliding in a dive is equal to 1.4 BMR times the amount of time spent gliding. The amount of time spent gliding is a function of dive depth (Williams *et al.* 2000). Swimming is assumed to be equal to the active metabolic rate, calculated as three times the BMR (Potvin, Goldbogen & Shadwick 2012). Any time in the dive that was neither gliding nor lunging is assumed to be swimming, including surface time.

Lunging is the most costly component of a dive because it is characterized by a rapid pre-engulfment acceleration and high exposure to drag during engulfment (Potvin, Goldbogen & Shadwick 2012). Pre-engulfment acceleration ( $\Delta Q_{pre}$ ) occurs as the whale increases its speed, typically abruptly, prior to lunging. This is added to the costs of work associated with overcoming shape and engulfment drag ( $\Delta Q_d$ ). The sum is scaled by a constant to account for the combined efficiency of converting mechanical energy to metabolic energy (Goldbogen *et al.* 2012, Table 3.6)

We used data collected from field observations to estimate the metabolic costs associated with an individual foraging period, defined as a continuous series of dives where a whale appears to be focused on foraging (as opposed to social, traveling or resting behaviours) in a somewhat consistent manner in terms of target prey, dive or lunge depth and group size. Three or more dives without any lunges indicated the end of a foraging period for the purposes of our analysis and typically coincided in changes to target prey or group composition. Tags were deployed on whales to collect kinematic data (described below), which we then used to determine the number of dives per foraging period and quantify the energy cost for each dive. A new dive was assigned

to the tag record when a whale would descend to greater than 10 m and remain below the surface for more than 25 seconds.

#### 3.3.3.1. Tag deployment

Animal-borne tags were deployed on foraging whales in Tenakee Inlet, Sitka Sound and Seymour Canal. While the tag remained on a whale (1- 24 hours) and during daylight hours, the whale was tracked either from a small skiff or from a larger vessel that was also conducting the prey survey. At each surfacing, laser rangefinders were used to determine the range and bearing of the whale or group of whales from the vessel. Observers also recorded the time, GPS position of the vessel, group size, and any notable surface behaviours following Altmann, Loy, and Wagner (1973). When tags detached from the whale, either haphazardly or due to a pre-programmed deployment duration, they floated to the surface and were recovered. Tag data were downloaded from the flash memory storage for analysis.

Tag data were not available at hatchery release sites (Kasnyku and Takatz Bays), because manoeuvring of the deployment vessel was hampered by small areas and unpredictable whale movement. Observers noted the frequency of surface lunges. To be included in the analysis, an observed feeding period required a minimum of three lunges with frequent respirations of the whale in between to indicate that no lunges had occurred outside of the view of observers. For humpback whales feeding on herring in Kasnyku Bay, lunge rates were not available because whales were neither tagged nor feeding at the surface. For this foraging opportunity, we used the depth of prey patches as a proxy for lunge depth and dive depth (for estimating gliding behaviour). The mean lunge rates from small groups of whales feeding on herring in Tenakee Inlet and Seymour Canal were used to model foraging costs for surface feeding on herring in

Kasnyku Bay, where lunge rates were not directly observed. Lunge speeds were taken from the average lunge speeds of whales feeding near the surface from across all tag records.

#### 3.3.3.2. Tag data analysis

Three different tag designs were used in this study: DTAGs (Johnson & Tyack 2003), Acousonde tags (Greenridge Sciences, [acousonde.com](http://acousonde.com)), and an early prototype of a CATS tag (Goldbogen *et al.* 2017a). Tag data were calibrated, oriented, and georeferenced prior to analysis. We georeferenced each track and interpolated locations of all lunges between focal follow locations using Trackplot software available at <https://ccom.unh.edu/vislab/projects/trackplot.html> (Ware, Arsenault & Plumlee 2006) with technical support from Colin Ware, (2017, University of New Hampshire). Mean error of location estimates is about 400m based in part on the frequency of surface observations (Colin Ware, pers comm, Jan 3, 2017).

To approximate speed on DTAGs and Acousonde tags, we used accelerometer jiggle (stochastic motion of the tag in flow in complete dataset prior to downsampling; Cade *et al.* 2017) that has been shown to scale with speed. The prototype CATS tag included a paddle wheel, which allows speed to be inferred by the rate of paddle rotations. These metrics were calibrated *in situ* with data from each deployment by dividing vertical velocity ( $\Delta$  depth/time) by the sine of the pitch angle upon ascent (where greater than 30°). Thereby we account for differences in flow rate over the sensors at different swimming speeds due to tag placement on the body and orientation (calibrations by David Cade & Jeremy Goldbogen, Stanford University). Speed data were drawn from only tags with a high sampling rate. Lunges were detected from visual scrutiny of several synchronized metrics including pitch, roll and heading,

depth profiles, speed profiles, and jerk, the derivative of acceleration (Simon, Johnson & Madsen 2012; Cade *et al.* 2016; Appendix 3C).

Energetic costs of lunging varied due to differences in the pre-engulfment acceleration phase ( $\Delta Q_{pre}$ ) whereas costs due to work against drag were presumed constant (Goldbogen *et al.* 2012). Pre-engulfment acceleration occurs as the whale increases its speed, typically abruptly, prior to lunging. The difference between the maximum speed and minimum speed of each lunge was used to determine the cost of the pre-engulfment acceleration phase. For each lunge, we found the maximum and minimum speed within 2 seconds prior and 12 seconds following for use in determining the metabolic costs of each lunge. Minimum speeds less than 1 m/s were all reported as 1 m/s since speed methods are considered unreliable below 1 m/s (Cade *et al.* 2017). While speed estimates can be unreliable in the top 2 m of the water column, we found no significant difference in mean speeds between 0 – 2 m and 2 – 22.5 m depth. Because both terms are squared in the equation to determine pre-engulfment energy cost (Table 3.6) this calculation is much more sensitive to variability in the maximum value. Other terms, such as the cost of work against shape and engulfment drag, and the combined efficiency converting mechanical energy to metabolic energy, are provided by Goldbogen *et al.* (2012) and detailed in Table 3.6.

#### 3.3.3.3. Sensitivity analysis

We performed a sensitivity analysis to determine the variables with the greatest influence on our model output. This analysis served both to identify 1) in a biological sense, the most influential prey characteristics in determining the expected net energy gain and 2) in a mathematical sense, the relative effect of uncertainty in the value of different parameters. Sensitivity is the average increase in standard deviations of the model output for every one

standard deviation increase in the independent variable. Sensitivity analysis was undertaken using the differential or direct method (Hamby 1994).

$$\text{Sensitivity of the model to parameter } x = \left| \frac{\partial z}{\partial x} \right| \cdot \frac{\sigma(x)}{\sigma(z)} \quad [\text{Equation 3.6}]$$

Where  $\frac{\partial z}{\partial x}$  is the partial derivative of z with respect to x, where x is the input values and z is the model output, net energy gain/min (Hamby 1994). A steeper average slope indicates a variable has more influence, as the effect of a small change in the predictor on the response is acute. The model is sensitive to independent variables that are influential but also have large natural variability because these parameters have more range over which to affect the model output.

To determine the mean of the partial derivatives, it was necessary to have a deterministic equation for each part of the model. The patch energy density sub-model and the metabolic costs sub-model are already deterministic, as is the framework connecting major model components (Eq 3.1 – 3.3). However, the proportion captured sub-model was derived iteratively so the underlying function is unknown. To approximate the deterministic function and measure the model sensitivity, we used a software Eureqa 1.24.0 (build 9367) available through Nutonian Inc. ([www.nutonian.com](http://www.nutonian.com) Schmidt & Lipson 2013). Each sub-model was entered into Eureqa as a separate data file to improve computational efficiency and interpretability. The formula search was assisted with combinations of terms known to be important, such as the allometric formulas, as well as formulas for the reaction distance and the standard deviation of the reaction distance. The models were then combined by multiplying the sensitivity of the sub-model to each variable by the sensitivity of the overall model to that sub-model output. Therefore, some variables that

contribute to multiple parts of the model (lunge rate, whale length, whale speed) had these effects assessed separately.

When comparing the sensitivity of the model to multiple variables, it is important that the independent variables do not covary. In this model, acoustic target strength and prey mass are related in that both vary with prey length. Therefore, we modelled the relationship of each variable with respect to length and used the residuals from that relationship to measure the effects of each variable. The residuals were also rescaled to a proportion of the original true unit to address heteroscedasticity in the relationship. Finally, acoustic volume backscatter was regressed against acoustic target strength and the residuals of this relationship were entered into the sensitivity analysis since the acoustic volume backscatter even a high density of krill could produce is limited by the low acoustic target strength of the individuals.

To conduct the sensitivity analysis, the formula search in Eureqa successfully identified the equations for the simpler energy density and metabolic costs sub-models; however, after 341 computational hours (4 CPU cores), the Eureqa software failed to identify a deterministic equation to exactly reproduce the proportion captured model. However, the top models, which included all variables, had very similar values for the sensitivity to each of the parameters and low total error in the model with the best fit (maximum error = 0.02;  $R^2 = 0.9998$ ). After first identifying this model, the software ran for a more than 140 hrs without any additional improvement. Therefore, this model was incorporated with the energy density and metabolic costs sensitivity analyses and used to calculate the overall sensitivity analysis.

Finally, although all reported values assumed a humpback whale of average length for the North Pacific (12.3 m), we calculated values for larger and smaller whales to determine the model sensitivity to whale length. Whale size is particularly important to consider as it affects

both the capture proportion and the metabolic costs of foraging (Goldbogen *et al.* 2012). We recalculated capture proportion and metabolic costs for each prey target for humpback whales 10 m, 12.3 m and 14.4 m, which is sometimes used as the average length of humpback whales in other parts of the world (Potvin, Goldbogen & Shadwick 2012).

### 3.4. Results

For the nine distinctive foraging targets considered, a wide range of values were predicted for net energy gain, ranging from more than 3,600 kJ/min for whales feeding on krill in Sitka Sound in 2012 to -1,900 kJ/min for a whale feeding on more diffuse krill in Seymour Canal in 2014 (Figure 3.6, Table 3.7). Expected net energy gain for humpback whales feeding on juvenile chum salmon (895-1,960 kJ/min) was higher than for juvenile coho salmon (-431 - -407 kJ/min), though both fell within the range of more typical prey (Table 3.7). The model was parameterized using 21 foraging periods identified from two surface observations and 17 tags (Table 3.8). These foraging periods occurred during three years and across four sites. Foraging periods were included from 15 different humpback whales. The duration of foraging periods ranged from 15 minutes to over nine hours. During these tagged periods, 1,530 lunge events were identified on the tag record and analysed for speed, depth, and feeding rate.

Prey patch energy density was the sub-model with the largest influence on net energy gain per minute (Table 3.9). An increase by one standard deviation in the prey patch energy density leads on average to a four standard deviation increase in net energy gain per time (sensitivity = 4.00). Prey patch energy density has a linear relationship with net energy gain per time with a slope equal to the product of capture proportion, assimilation efficiency, engulfment volume, and lunge rate (Table 3.9). The model was more sensitive to all the parameters in this sub-model than any other parameters. Overall, the model was most sensitive to acoustic volume



backscatter followed by target strength. Both of these parameters are related to the density of individuals within a school and have an exponential relationship with net energy gain.

Variability in acoustic target strength has more influence when it is small; acoustic volume backscatter has more influence when it is large. Prey patch energy density of prey targets ranged widely, from a maximum of 3,300 kJ/m<sup>3</sup> of herring Kasnyku Bay to a minimum of 33 kJ/m<sup>3</sup> measured for coho salmon released from Kasnyku Bay (Table 3.7, Figure 3.6). Juvenile coho salmon had low patch energy density due to diffuse distribution of individuals.

Changes in capture proportion had a greater influence on the model output when prey energy density and lunge rate are high. Our modelled estimates of average capture proportion ranged widely from 0.05 – 0.99 (Table 3.7). Both the lowest and highest capture proportions were for humpback whales feeding on herring, depending on the type of lunges observed. Herring had the quickest swim speeds and by far the largest reaction distances of any prey. Whales feeding subsurface on herring caught relatively few, primarily due to that large reaction distance. The sub-model was most sensitive to this parameter. Because group size was only a factor for whales feeding on herring in Tenakee Inlet, it was not included in the sensitivity analysis, although in this case the effect was large, increasing capture proportion from 0.07 for single or small group subsurface feeders to 0.95 for large group subsurface feeders and 0.8 for surface feeding to one for group surface feeders. Krill capture rates approached 0.99 due to krill's low mobility relative to the whale. Capture proportions were higher for chum salmon than coho salmon due to lower swimming speeds, despite larger reaction distances. Within salmon species, capture proportions were higher for smaller fish that were either released earlier in the season (chum salmon) or were sampled closer to their release time (coho salmon), due to a reduction in swimming speed with length.

Lunge rate was highly variable with prey species and group size (Table 3.8). When net energy gain per lunge is positive, net energy gain per time increases linearly with lunge rate with a slope equal to the net energy gain per lunge. Because lunges are the most energetically expensive part of a dive, higher lunge rates increase the metabolic costs of foraging per time even as they increase the gross energy gain per time (Figure 3.6). These costs are analysed separately in the metabolic costs sub-model. During feeding, whales executed an average of 0.47 (SD 0.07) lunges per minute, or a lunge about every two minutes and seven seconds. This large range was notable with the highest lunge rate (1.11 lunges/min) occurring during the shallowest surface feeding bout at the slowest lunge speed (1.9 m/s) on unknown prey in Seymour Canal. High lunges rates (0.57 - 0.9) were also seen in whales feeding on subsurface krill in some of the deepest dives recorded in this study (122 – 156 m), despite the larger surface periods necessary to recover from these dives. The lowest lunge rates (0.14 - 0.10) occurred in the large coordinated feeding group in Tenakee Inlet. Lunge rates on juvenile salmon were intermediate, with the chum salmon-feeding whales feeding at rates similar to a tagged whale feeding on surface krill in Tenakee Inlet, while the coho salmon-feeding whale had rates more similar to those observed in herring-feeding whales.

The model was least sensitive to the metabolic costs per lunge. Again, the relationship between net energy gain per time and metabolic costs was linear (slope = -1). Larger whales lunging at higher rates and higher speeds incurred greater metabolic costs. Because whale size and speed increase capture proportion, lunge speed must have an energetic optimum specific to the size of the whale and the escape ability of prey and the energy density of the prey patch. Metabolic costs were greatest for krill-feeding whales in Seymour Canal (2,574 kJ/lunge) due to high lunge rates and fast lunging speeds (Table 3.6).

### 3.5. Discussion

Our model successfully predicts reasonable values of net energy gain, indicating that humpback whales can feed profitably on both typical prey and novel prey where they occur in sufficiently dense aggregations. The density of prey aggregations has been demonstrated as particularly important for larger baleen whales (Goldbogen *et al.* 2011, 2012) but our results indicate that prey density is also the most important factor for humpback whales (Burrows *et al.* 2016). This finding underscores the need to better understand how humpback whales locate these aggregations. The model also identifies large differences in the capture proportion of different prey taxa, lending support to its importance as a key consideration for foraging energetics and for interpreting humpback whale foraging behaviour. Surface and group feeding are important methods for increasing prey capture and require more study to better incorporate their effects, particularly group feeding subsurface, where little data are available. Finally, our results indicate the importance of considering lunge rate, as it is variable across prey types. The role of prey and predator characteristics in restricting lunge rate are not well understood, but our results suggest it may be inversely related to prey mobility and group size.

The most counter-intuitive implication of this model is that humpback whales sometimes feed on prey patches that are unprofitable, where the energetic benefits of feeding do not entirely compensate for the energetic costs. Some whales may be minimizing their losses by feeding in a prey patch which has a negative net gain over time, as has been suggested for blue whales using lower cost foraging strategies to target diffuse aggregations of krill (Hazen, Friedlaender & Goldbogen 2015). However, this model suggests that whales that fed on krill in Seymour Canal and coho salmon fed where the metabolic costs of the foraging lunge itself exceeds the benefits of the lunge, which would be a counter adaptive behaviour in a purely energetic framework

(assuming perfect knowledge on the part of the whale) (Stephens & Krebs 1986). However, as noted by Potvin, Goldbogen & Shadwick (2012), at small sizes (~10 m) of related balaenopterid whales, the costs of lunging approach the costs of active swimming, meaning that there is little to no additional metabolic cost from lunging. For 12.3 m humpback whales, the metabolic costs of foregoing a lunge and instead swimming during the 12.2 sec allotted for pre-engulfment acceleration and engulfment is approximately 250 kJ. Here, assuming surface feeding lunges on coho salmon are similar in lunge speed to surface feeding on other prey, we assume a metabolic cost per lunge of only 807 kJ (Table 3.7). If we were to redefine our foraging currency to consider the effective cost of engulfment as the cost above the alternative behaviour (swimming) and reduce metabolic costs of a lunge by this amount, all prey groups with the exception of the whale feeding on krill in Seymour Canal have lunge efficiencies greater than 1, the intuitive baseline for an energetically adaptive behaviour. In the case of the single whale feeding on krill in Seymour Canal, it is likely that because the whale was feeding nearshore and we were sampling from a large vessel, we were unable to sample the densest part of the prey patch leading us to underestimate of the net energy gain per lunge. Regardless, this prey target demonstrates that humpback whale prey can naturally occur in densities that are not suitable for foraging, underscoring an assessment of patch density as an important aspect of prey selection.

The consistent observation of humpback whales feeding in an area without acoustically discrete prey patches, as we observed in Kasnyku Bay with coho salmon as the target prey, is anomalous (Hazen *et al.* 2009; Nowacek *et al.* 2011; Boswell *et al.* 2016; Burrows *et al.* 2016). Coho salmon are known for territorial and agonistic behaviours which can persist in the nearshore environment (Paszkowski & Olla 1985), resulting in distributions in lower densities than chum, pink (*O. gorbuscha*), and sockeye (*O. nerka*) salmon in Southeast Alaska (Jaenicke

& Celecwydz 1994). Reflecting this difference in behaviour, juvenile coho salmon are sometimes considered non-schooling fish, in contrast to schooling juvenile chum salmon (Hoar 1951; Davis & Olla 1987). Despite the low densities, whales commonly fed around the main dock where our spatial model indicated the greatest consistency in fish density. Humpback whales at hatcheries typically use bubbles to feed and feed near shoreline, floating salmon holding pens and docks, which likely impede escape allowing whales to feed on prey that are more densely aggregated than they appear in a neutral water column (Chenoweth *et al.* 2017; Appendix 3D). Nonetheless, it is likely that coho salmon represent a low-ranking resource for humpback whales. Despite high abundances the nearshore waters of Southeast Alaska in the spring (Orsi *et al.* 2007), juvenile salmon had not been previously documented as prey for humpback whales prior to Chenoweth *et al.* (2017). Likely, the release of large numbers of these salmon at individual sites provides a dense enough aggregation to attract whales. The main advantage of feeding at hatchery release sites may be that these sites release juvenile salmon beginning in April and May before other humpback whale prey reach peak abundance (Straley *et al.* 2017). Chum salmon are a more highly ranked prey, but it should be noted schools were small, patchy and ephemeral compared to krill and herring. This perhaps explains the small number of whales that feed at release sites and the decline in foraging at release sites observed later in the 2014 season (Appendix 3D, Figure 3.D-1), despite continued releases of chum salmon.

Our model highlights many areas for future study. Future models should refine estimates of reaction distance and the variability in reaction distance, as this is given little attention but has a large influence on the model outputs. We also need a better understanding of the effects of bubble net feeding on prey aggregation prior to a lunge. These secondary barriers likely have a large effect on capture proportion under the right conditions. Previous studies have shown that a

humpback whale's lower jaw can change shape during the course of a lunge, increasing capture area at specific gape angles (Lambertsen, Ulrich & Straley 1995). For prey with the ability to narrowly escape, this change of shape may make an importance difference in capture proportion. Here we model swimming costs as uniform. How does modulation of swimming speed, use of flippers (Segre *et al.* 2017), or speed gained during gliding affect energetic costs? Finally, more data is needed on the variables influencing lunge rate. This has a large effect on net energy gain, particularly when gross energy gain per lunge is large. Yet this variability in lunge rate is not well understood. In particular, the high lunge rate on krill, including relatively deep krill, was essential for elevating krill in Sitka Sound to the highest net energy gain among prey targets.

The increasing humpback whale population in Southeast Alaska and worldwide (Fleming & Jackson 2011; Barlow *et al.* 2011; Hendrix *et al.* 2012; Gabriele *et al.* 2017) will ultimately result in an increase in intraspecific competition for prey. Although the prey are more diffuse at hatchery release sites than at the sites of many other humpback whale foraging studies, foraging studies tend to focus on “hot spots,” areas with large aggregations of humpback whales, for efficient data collection (Hazen *et al.* 2009; Nowacek *et al.* 2011; Burrows *et al.* 2016). It is possible that this study describes a more typical range of prey fields. The seasonal nature of these prey resources suggest that humpback whale foraging is likely uneven, with whales making minimal gains or even suffering energetic losses during some of the feeding season, but being able to compensate for these energetic shortfalls during shorter windows when higher quality prey is available (Baker *et al.* 1985; Straley *et al.* 2017). Optimal foraging theory predicts that humpback whales will increasingly rely on less preferred prey and more on specialized feeding behaviours (Estes *et al.* 2003) as intraspecific competition increases. It is also possible that hatchery fish will become more important should krill or herring in this region suffer population

declines. Process models like this one are essential for modelling quantities that cannot be directly observed (e.g. net energy gain) and for which current observations are outside the range of historical ecosystem conditions.

### 3.6. Figures

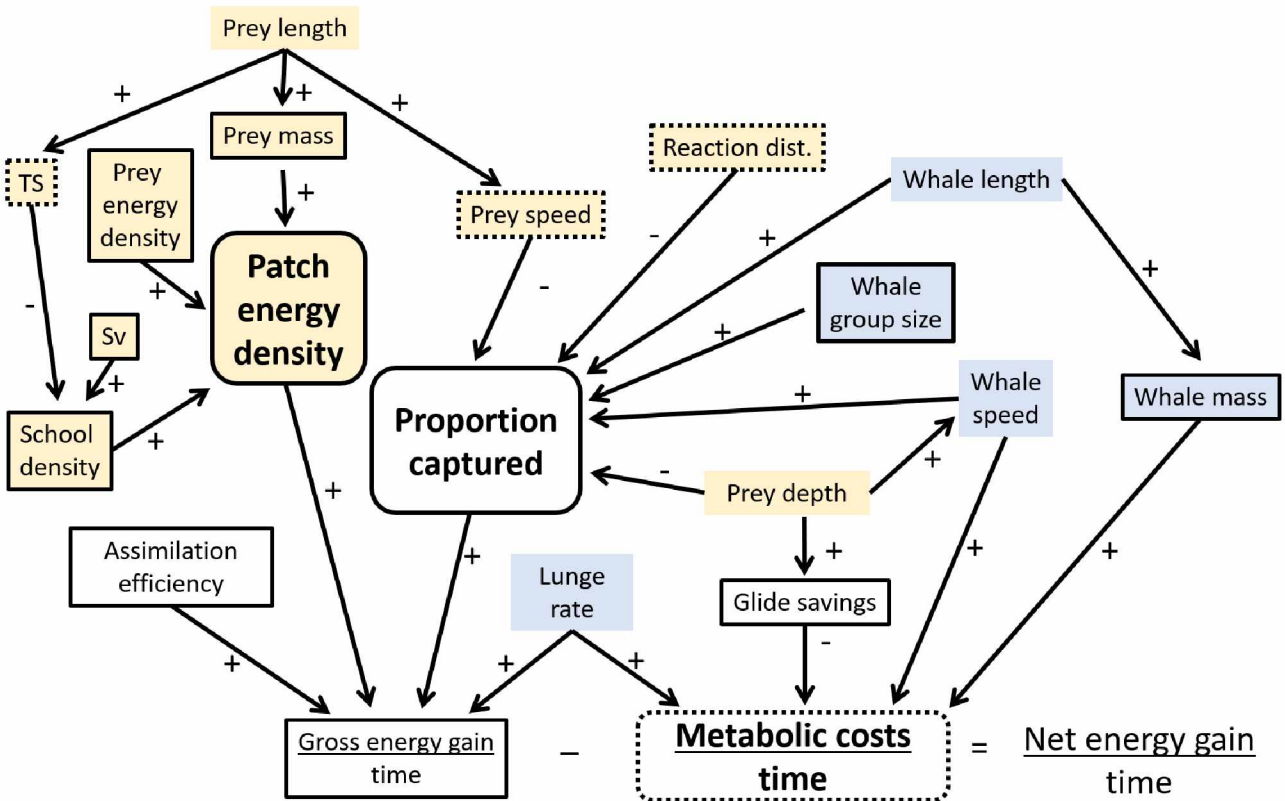


Figure 3.1 A conceptual diagram of the process model calculating net energy gain per time for humpback whale foraging. White boxes indicate factors that are affected by whale and prey characteristics or behaviour. The output of each of the three main sub-models are identified by boxes with rounded corners. Positive linkages are indicated with a “+” and negative relationships with a “-.” Boxes with thick lines indicate factors that contribute positively to net energy gain, boxes with dashed lines indicate factors that contribute negatively to net energy gain, and boxes with thin solid lines indicate factors that react with both sides of the model and whose net effect is dependent on other factors.  $S_v$  = acoustic volume backscatter and TS = acoustic target strength.

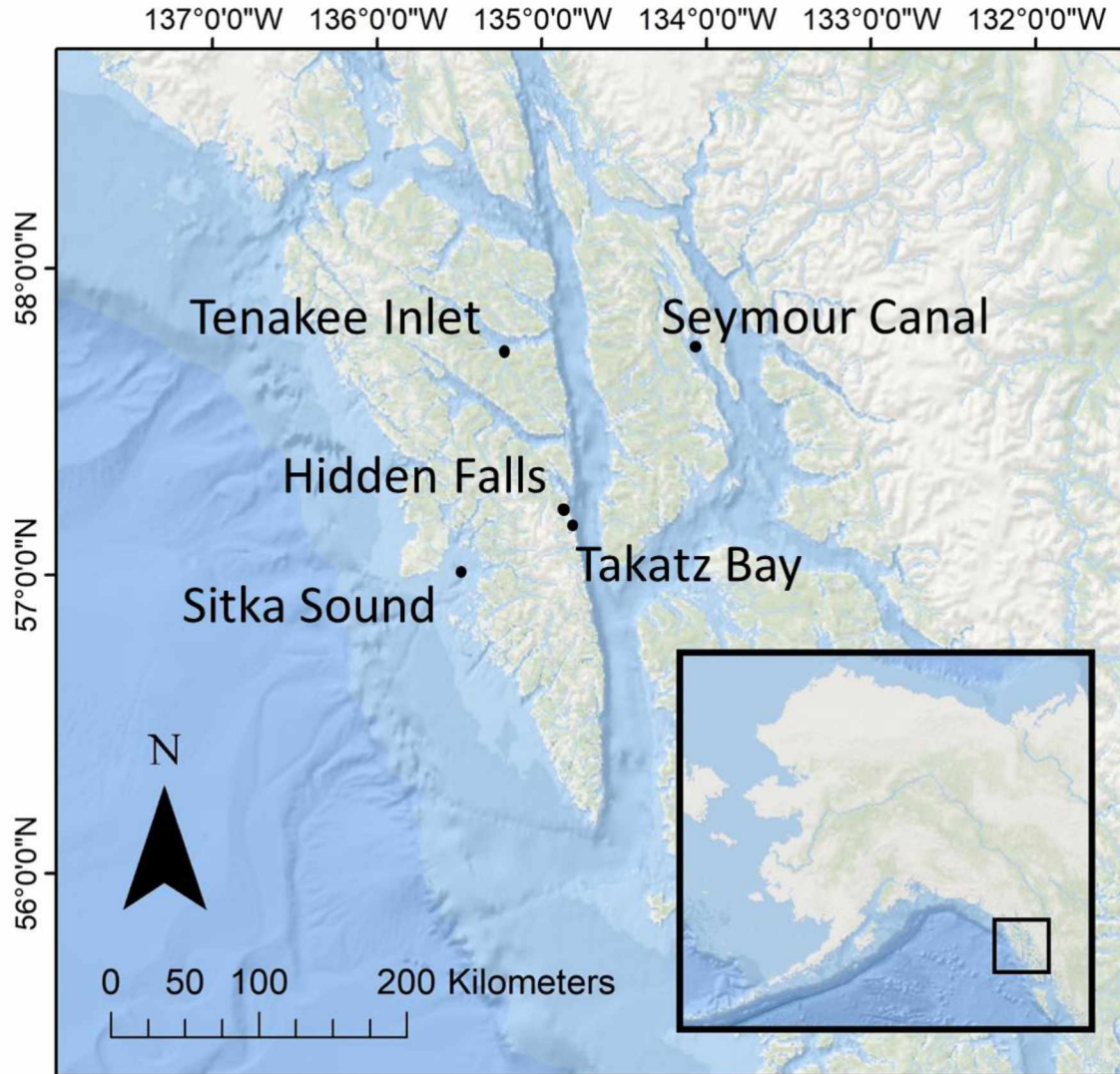


Figure 3.2 Study region. Humpback whales were tagged or observed, and prey patch characteristics were determined through prey sampling and acoustic prey density surveys at five locations in Southeast Alaska.



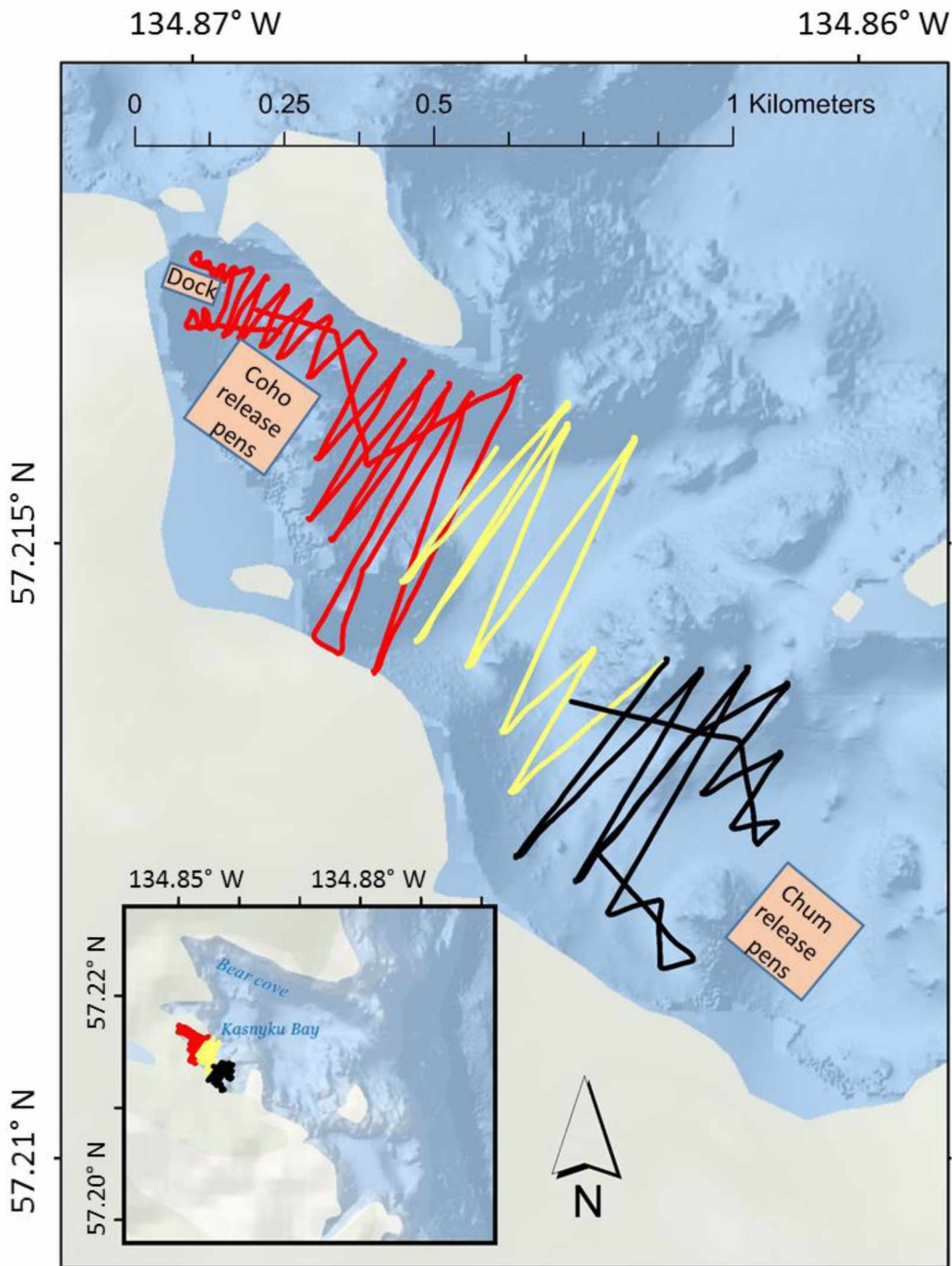


Figure 3.3 Location of the Hidden Falls hatchery release area within the southernmost of three main coves in Kasnyku Bay. Tracklines from the acoustic surveys (120 kHz EK 60 transducer on an autonomous surface vessel) are also shown: red indicates the “inner pens” survey, yellow indicates the “middle” survey between the pens, and black indicates the “outer pens” survey.

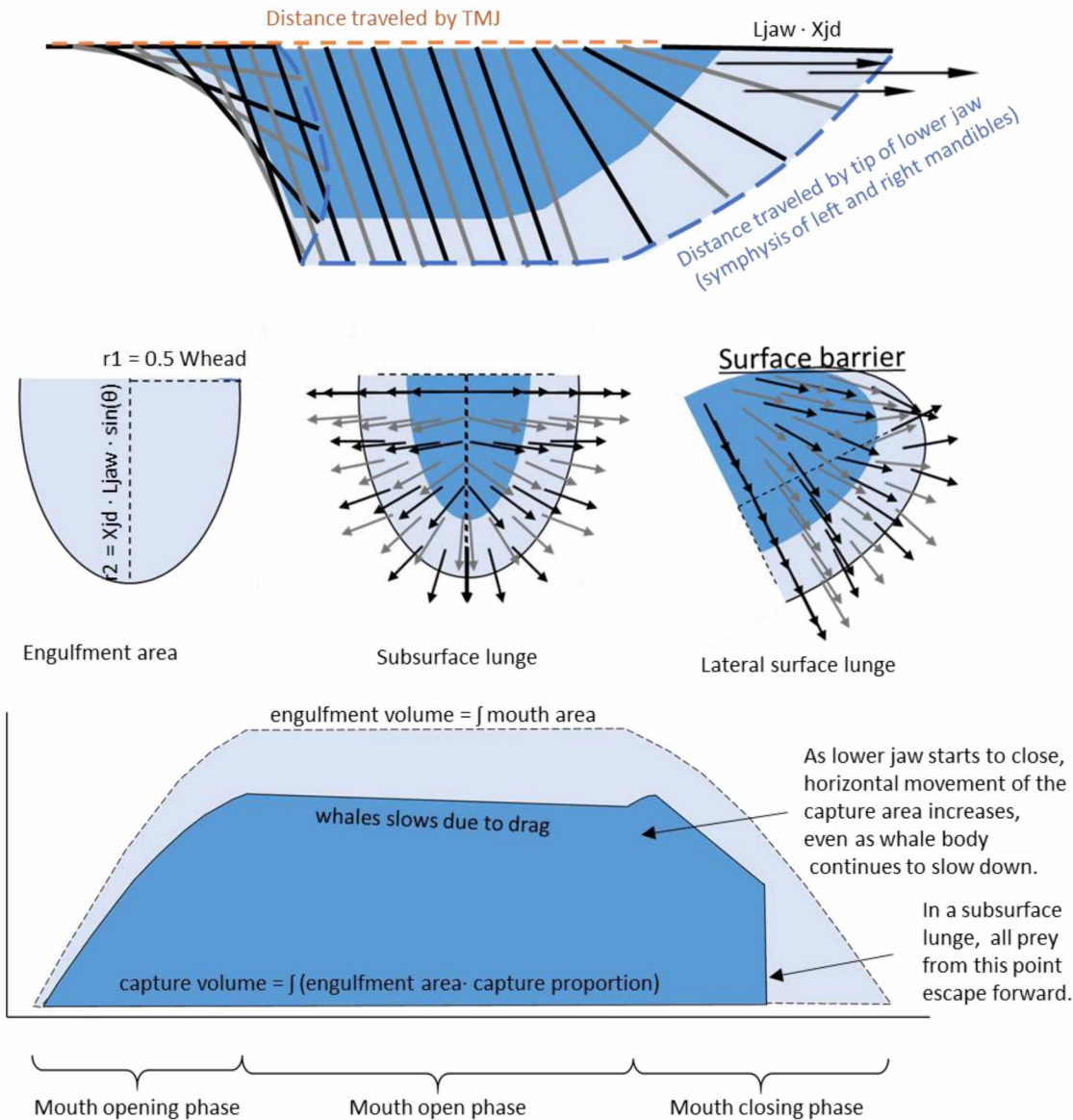


Figure 3.4 Conceptual model of whale engulfment with engulfment phases. In all panels, light blue indicates the engulfment volume and dark blue indicates the area or volume from which there is, on average, no escape. TOP PANEL: The whale is moving left to right. Alternating black and grey lines indicating the position of the lower jaw during engulfment. Orange dashed line indicates the distance travelled by the transmandibular joint or main body of the whale. The blue dashed line indicates the route travelled by the tip of the lower jaw. MIDDLE PANEL: Engulfment area formula from Potvin, Goldbogen & Shadwick (2012) Black arrows indicate the direction of escape for prey at various locations within the path of the approaching whale. An adjustment is provided for a lateral surface lunge where prey can only escape along one mandible. BOTTOM PANEL: Results of modelling prey capture on an individual subsurface lunge.

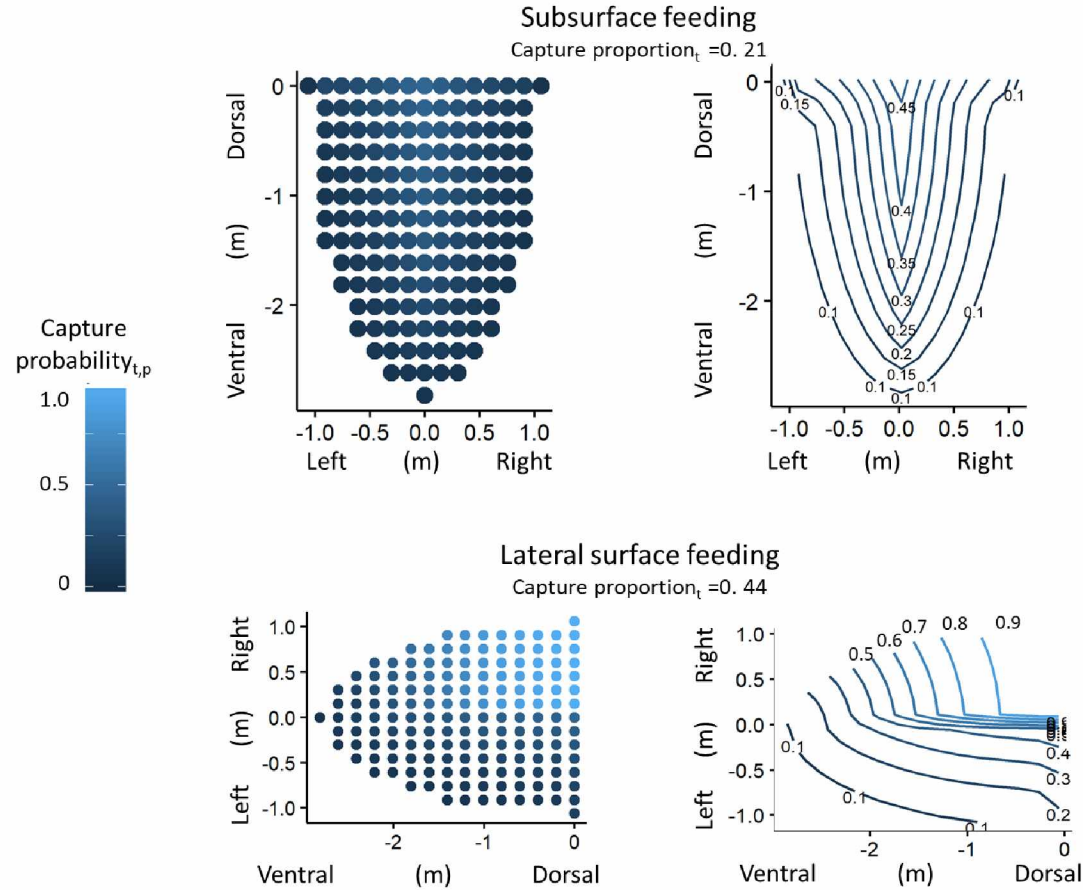


Figure 3.5 Probability of prey capture for surface and subsurface feeding at different points (p) across the capture plane at a particular time step (t). Capture probability at each time step is modelled as the average of the probability of escape at evenly spaced locations on a 15 by 15 grid of points within the half-ellipse engulfment area, on the plane of engulfment at each time step. At each point, the distance to the nearest edge of the plane (escape distance) was determined. The probability that prey would achieve that distance was determined by the mean and standard deviation of the prey speed ( $V_p$ ) and reaction distance ( $Rxn$ ) modelled as independent random variables and the average whale speed within the reaction distance.

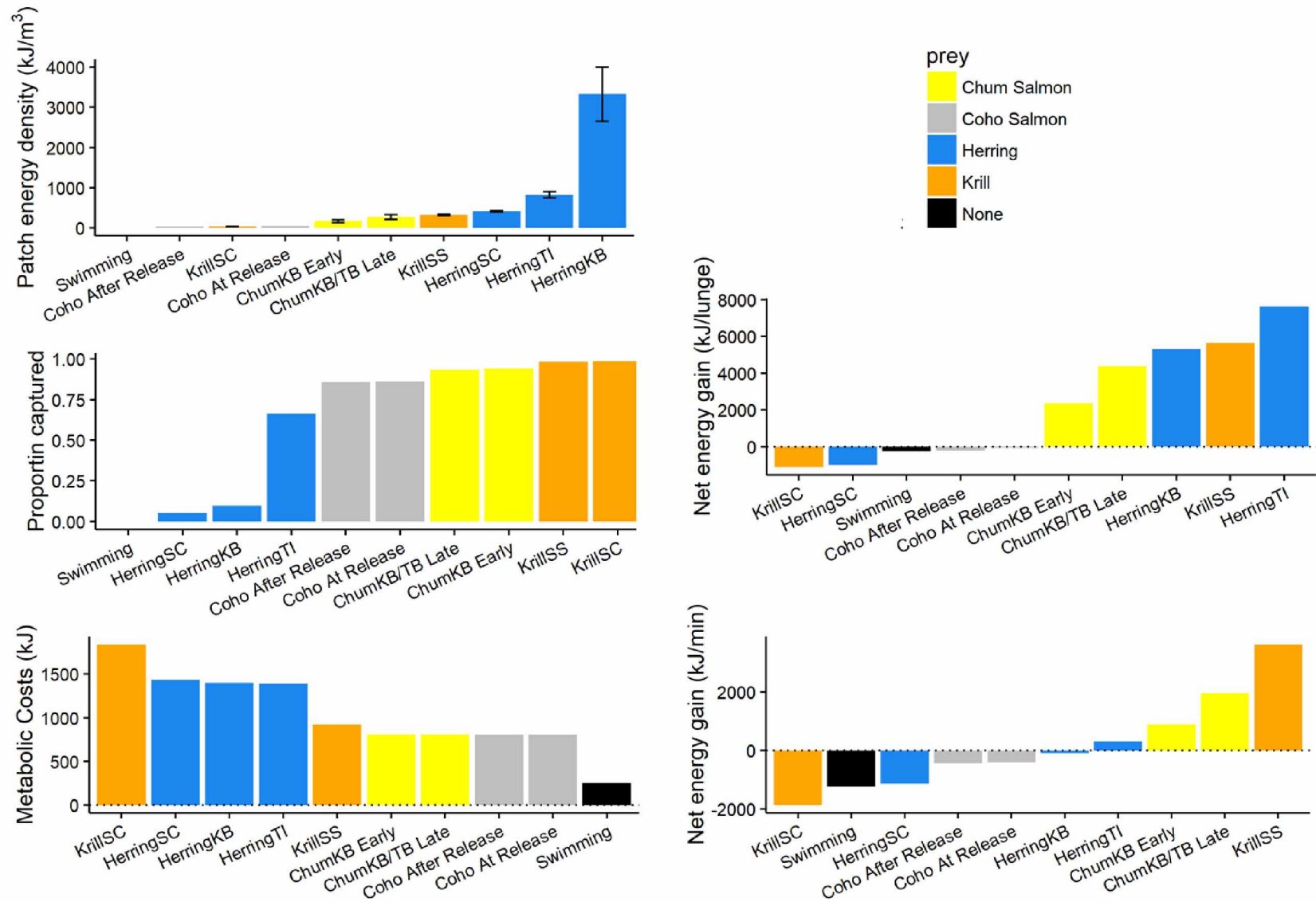


Figure 3.6 Comparing sub-model outputs and net energy gain among prey targets. SC = Seymour Canal, KB = Kasnyku Bay (the site of Hidden Falls hatchery), TI = Tenakee Inlet, TB = Takatz Bay

### 3.7. Tables

Table 3.1 Summary of foraging target characteristics.

Foraging Target	Taxa	Year	Lunge type	Group Size	Location	Date
HerringTI	Herring	2013	Surface/Subsurface/ Large group surface	1-15	Tenakee Inlet	April 18 -24
HerringSC	Herring	2014	Surface/Subsurface	1-4	Seymour Canal	April 20 - 25
HerringKB	Herring	2014	Surface/Subsurface	3*	Kasnyku Bay	June 2
KrillSS	Krill	2012	Subsurface	1-3	Sitka Sound	Sept 18 - 25
KrillSC	Krill	2014	Subsurface	2	Seymour Canal	April 14
ChumKB early	Chum	2014	Surface	1	Kasnyku Bay	May 21 – June 7
ChumKB/TB late	Chum	2014	Surface	1	Kasnyku/Takatz Bays	May 25 – June 6
CohoKB At Release	Coho	2014	Surface	1	Kasnyku Bay	May 16 - 27
CohoKB After Release	Coho	2014	Surface	1	Kasnyku Bay	May 16 - 27

\*Group size for HerringKB is uncertain because there were multiple whales feeding at night. ChumKB early refers to chum salmon released in Kasnyku Bay early in the release season of a higher energy content and smaller length than Chum KB/TK late. Juvenile salmon released late from both Kasnyku Bay and Takatz Bay were collected to determine the length, TS, mass and energy content for this foraging target.

Table 3.2 Parameter values for modelling prey patch energy density. Each prey group was parameterized with the best available data, though methods vary. See details in Appendix 3A.

Foraging Target	Prey length N	Capture method	Prey length $\mu$ (mm)	Prey length $\sigma$ (mm)	Energy & mass N	Wet mass $\mu$ (se) (g)	Energy (kJ/g)	TS $\mu$ (dB)	Sv $\mu$ (se) (dB)
HerringTI	9	jig	217	21	9	117.23 (11.2)	5.40	-40	-41 (0.3)
HerringSC	6	jig	202	8	6	88.79 (3.4)	5.76	-41	-49 (0.5)
HerringKB	211	trawl*	196	20	3	44.07 (4.5)	6.61	-42	-34 (1.3)
KrillSS	74	trawl	16	4	4 composites	0.11 (0.1)	3.80	-86	-59 (0.3)
KrillSC	6	dipnet	18	3	2 composites	0.07 (0.0)	2.94	-85	-62
ChumKB early	36	dipnet	58	5	7	2.19 (0.2)	3.19	-52	-39 (1.2)
ChumKB/TB late	136	dipnet	66	9	9	3.16 (0.3)	4.57	-51	-39 (1.2)
CohoKB At Release	9	jig	121	6	9	17.57 (1.1)	5.93	-46	-50
CohoKB After Release	9	jig	128	11	9	21.22 (1.1)	4.98	-45	-50

\*We did not capture a representative size distribution of herring in Kasnyku Bay. Instead, we used a size distribution from a trawl of multiple age classes captured in May and June in various locations around Southeast Alaska used curtesy of NOAA.  $S_v$  = acoustic volume backscatter, TS = acoustic target strength. SC = Seymour Canal, KB = Kasnyku Bay (the site of Hidden Falls hatchery), TI = Tenakee Inlet, TB = Takatz Bay

Table 3.3 Humpback whale morphology and scaling.

Parameter	Symbol	Unit	Value	Formula	Source of value
Whale length	$L_c$	m	12.3		[1]
Whale mass	$M_c$	kg	26,942	$0.7683 \cdot L_c^{4.17}$	[2], in [3] using coefficients of allometric scaling from [4].
Engulfment volume	$Vol_{engulf}$	$m^3$	24.8	$0.007852 \cdot L_c^{3.21}$	[4] assuming a density of seawater ( $1020 \text{ kg/m}^3$ )
Maximum gape	$Gape_{max}$	°	78		[3]
Width of the head	$W_{head}$	m	2.11	$0.155 \cdot L_c^{1.04}$	Scaled from $W_{head}$ of 14m whale [3] using coefficient of allometric scaling from [4].
Length of the lower jaw	$L_{jaw}$	m	2.80	$0.134 \cdot L_c^{1.21}$	Scaled from $L_{jaw}$ of a 14m whale [3] using coefficient of allometric scaling from [4].
Length of ventral groove blubber	$L_0$	m	7.45	$0.376 \cdot L_c^{1.19}$	Scaled from $L_0$ of a 14m whale [3] using coefficient of allometric scaling from [4].
Cross-sectional area of body	$A_{body}$	$m^2$	6.70	$0.00674 \cdot L_c^{2.75}$	Scaled from $A_{body}$ of a 14.4m whale [3] using coefficient of allometric calculated from [3].
Jaw disarticulation factor	$X_{jd}$	m	1.03		[3]

Source: 1. Nichol & Heise (1992) 2. Lockyer (1976) 3. Potvin, Goldbogen & Shadwick (2012) 4. Goldbogen *et al.* (2012)

Table 3.4 Prey input parameter values for modelling capture proportion. Source data and analyses for calculating parameter values are included in Appendix 3B.

Foraging Target	Whale group size	Prey speed $\mu$ (m/s)	Prey speed $\sigma$ (m/s)	Reaction distance $\mu$ (m)	Reaction distance $\sigma$ (m)	Whale initial speed (surface) (m/s)	Whale initial speed (subsurface) (m/s)	Proportion surface lunges
HerringTI	small	1.241	0.31	4.0	0.1	2.3	4.4	0.63
HerringTI	large	1.241	0.31	4.0	0.1	3.4	4.0	0.51
HerringSC	small	1.161	0.31	4.0	0.1	2.1	3.7	0.03
HerringKB	small	1.131	0.31	4.0	0.1	2.4	3.9	0.65
KrillSS	small	0.056	0.014	0.9	0.6	---	3.1	0.00
KrillSC	small	0.063	0.011	0.9	0.6	---	4.2	0.00
ChumEarly	small	0.223	0.23	1.3	0.03	2.5	---	1.00
ChumLate	small	0.253	0.23	1.3	0.03	2.5	---	1.00
Coho At Release	small	0.984	0.84	0.7	0.2	2.5	---	1.00
Coho After Release	small	1.034	0.84	0.7	0.2	2.5	---	1.00

Small group size is 1-4. Large group size is 11-15.

Herring: Mean=5.746 lengths/s, SE = 0.2, SD=1.4

Krill: Mean=3.5 lengths/s, SD=0.14 (Strand & Hamner 1990)

Chum salmon: Mean=3.8 lengths /s, SE = 0.5, SD=3.2

Coho salmon: Mean=8.1 lengths /s, SE = 1.3, SD=6.6 (Puckett & Dill 1984) salmon is the average of all tags < 22.5m.

SC = Seymour Canal, KB = Kasnyku Bay (the site of Hidden Falls hatchery), TI = Tenakee Inlet, TB = Takatz Bay



Table 3.5 Model specification for capture proportion model.

Variable or Parameter	Symbol	Unit	Formula
Capture proportion Subsurface	CP	unitless	$\frac{\sum_{t=0}^{t=t_{forward.escape}} Ac_t \cdot V_{capture.area_t} \cdot dt \cdot \overline{capture.prob_t}}{\sum_{t=0}^{t=Dur_{engulf}} Ac_t \cdot V_{capture.area_t} \cdot dt}$
Surface			$\frac{\sum_{t=0}^{t=Dur_{engulf}} Ac_t \cdot V_{capture.area_t} \cdot dt \cdot \overline{capture.prob_t}}{\sum_{t=0}^{t=Dur_{engulf}} Ac_t \cdot V_{capture.area_t} \cdot dt}$
Group Subsurface			$\frac{\sum_{t=0}^{t=Dur_{engulf}} Ac_t \cdot V_{capture.area_t} \cdot dt \cdot 1}{\sum_{t=0}^{t=Dur_{engulf}} Ac_t \cdot V_{capture.area_t} \cdot dt}$
Group Surface			= 1
Capture probability (t)	$\overline{capture.prob_t}$	unitless	$\frac{\sum_{p=1}^{p=n} capture.prob_p}{n}$ where n = number of points inside the capture area at time t from a 15 by 15 grid of dimensions $2w_{head}$ by $X_{jd}L_{jaw} \sin \theta_{gape}(t)$
Capture probability (p)	$capture.prob_p$	unitless	$P(D_{escape}(t) < -D_{required}(p,t))$
Engulfment area	$Ac_t$	m <sup>2</sup>	$\frac{\pi}{2} \cdot \frac{w_{head}}{2} X_{jd}L_{jaw} \sin \theta_{gape}(t)$
Gape angle Mouth opening phase	$\theta_{gape}(t)$	°	$\frac{\theta_{gape.max+t}}{Dur_{open}}$
Mouth open phase			$\theta_{gape.max} = 78$
Mouth closing phase			$\frac{-\theta_{gape.max+t}}{Dur_{engulf} - Dur_{open} - Dur_{gape.max}} + \theta_{gape.max}$
Time after which all prey may escape forward	$t_{forward.escape}$	s	t where $D_{escape}(t) > \bar{V}_{capture}(t_{max})$
Distance from position p to the nearest edge of the lower jaw	$D_{required}(p,t)$	m	Arrived at by minimizing the distance between each point along the edge of the entire lower jaw (subsurface feeding) or half the lower jaw (surface feeding)
Distance prey can travel to escape capture	$D_{escape}(t)$	m	$N(\mu, \sigma^2), \text{ where:}$ $\mu = \frac{V_p \cdot Rxn}{\bar{V}_{capture}(t)}$ $\sigma^2 = \frac{Vp.sd^2 \cdot Rxn.sd^2 + Vp.sd^2 \cdot Rxn^2 + Vp^2 \cdot Rxn.sd^2}{\bar{V}_{capture}(t)^2}$

Table 3.5 Continued

Variable or Parameter	Symbol	Unit	Formula
Mean approach speed	$\bar{V}_{capture}(t)$	m/s	$\frac{\sum_{i=t_0}^t V_{capture}(i)}{(t-t_0)/dt}$ where $D_{capture}(t_0) = D_{capture}(t) - Rxn$
Speed of the capture area	$V_{capture}(t)$	m/s	
Mouth opening & open phases			$V_c(t)$
Mouth closing phase			$V_{ij}(t)$
Absolute forward movement of the tip of the lower jaw	$V_{ij}(t)$	m/s	$V_c(t) + V_{horz}(t)$
Forward movement of the tip of the lower jaw with respect to the whale.	$V_{horz}(t)$	m/s	$[L_{jaw} \cdot X_{jd} \cdot \cos(\theta_{gape}(t)) - L_{jaw} \cdot X_{jd} \cdot \cos(\theta_{gape}(t - dt))]/dt$
Prey speed	$V_p$	m/s	See Table 3.4
Distance at which prey react to approaching whale	$Rxn$	m	See Table 3.4
Speed of the whale at time t	$V_c(t)$	m/s	See Potvin, Goldbogen & Shadwick (2012)
Total distance travelled by capture area at time t	$D_{capture}(t)$	m	See Potvin, Goldbogen & Shadwick (2012)
Engulfment duration	$D_{engulf}$	s	See Potvin, Goldbogen & Shadwick (2012)

Table 3.6 Model specifications for metabolic costs model.

Variable or Parameter	Symbol	Unit	Formula	Source
Metabolic costs per foraging period (p)	$MC_p$	kJ	$\sum MC_d$	
Metabolic costs per dive (d)	$MC_d$	kJ	$MC_{lunge_d} + MC_{swim_d} + MC_{glide_d}$	
Total metabolic cost of lunging per dive	$MC_{lunge_d}$	kJ	$\overline{MC_l} \cdot n_{lunges_d}$	
Number of lunges in a dive	$n_{lunges_d}$		-----	Measured from tag data
Metabolic cost of lunge	$MC_l$	kJ	$\frac{\sum Q_{lunge}}{\eta_{combined}}$	
Mechanical cost of a lunge	$\sum Q_{lunge}$	kJ	$\frac{\Delta Q_{pre} + \Delta Q_D}{1000}$	Goldbogen <i>et al.</i> (2012) (Supplemental Material 2 divided by 1000 to correct for units)
Cost of pre-engulfment acceleration	$\Delta Q_{pre}$	J	$0.5M_c(V_{c_{max}}^2 - V_{c_{end}}^2)$	
Combined efficiency	$\eta_{combined}$		0.16	Goldbogen <i>et al.</i> (2012) Supplemental Material 2
Cost of work against drag (shape and engulfment)	$\Delta Q_D$	J/kg	$2.4 \cdot M_c$	Goldbogen <i>et al.</i> (2012) Supplemental Material 2
Maximum speed during lunge	$V_{c_{max}}$	m/s	-----	Measured from tag data
Minimum speed during lunge	$V_{c_{end}}$	m/s	-----	Measured from tag data
Metabolic cost of gliding in a dive	$MC_{glide_d}$	kJ	$GMR \cdot t_{glide_d}$	

Table 3.6 Continued

Variable or Parameter	Symbol	Unit	Formula	Source
Metabolic cost of swimming in a dive	$MC_{swim_d}$	kJ	$SMR \cdot t_{swim_d}$	
Total time of dive and recovery	$t_{dive_d}$	s	$t_{recovery_d} + t_{subsurface_d}$	Measured from tag data
Total time subsurface	$t_{subsurface_d}$	s	-----	Measured from tag data
Total recovery time	$t_{recovery_d}$	s	-----	Measured from tag data
Time gliding in a dive	$t_{glide_d}$	s	$\max\left(0.859 - \frac{28.203}{\max.\ depth_d}, 0\right)$	Williams <i>et al.</i> (2000)
Maximum depth in a dive	$\max.\ depth_d$	m	$\frac{\cdot t_{subsurface_d}}{\text{-----}}$	Measured from tag data
Time swimming in a dive	$t_{swim_d}$	s	$t_{recovery_d} + (t_{subsurface_d} - t_{glide_d}) - t_{lunge_d}$	
Time lunging in a dive	$t_{lunge_d}$	s	$12.2 \cdot n_{lunges\ d}$	Potvin, Goldbogen & Shadwick (2012)
Metabolic rate while gliding	GMR	kJ/s	$9.6 = 1.4BMR = 0.00504M_c^{0.74}$	Sparling & Fedak (2004)
Metabolic rate while swimming	SMR	kJ/s	$20.5 = 3BMR = 0.0108M_c^{0.74}$	Goldbogen <i>et al.</i> (2012)

Table 3.7 Foraging energetics by foraging target. Foraging targets are ordered in decreasing order of net energy gain (kJ/min)

Foraging Target	Patch energy density (kJ/m <sup>3</sup> )	Proportion captured	Gross energy gain (kJ/lunge)	Lunge rate (lunge/min)	Metabolic costs (kJ/lunge)	Metabolic costs (kJ/min)	Net energy gain (kJ/lunge)	Net energy gain (kJ/min)
KrillSS	321 (17)	0.99	6,585 (343)	0.83 (0.05)	923 (259)	1,808 (299)	5,661	3,632
ChumKB/TB Late	267 (62)	0.93	5,178 (1,210)	0.53 (NA)	807 (13)	795 (NA)	4,371	1,960
ChumKB Early	163 (38)	0.94	3,177(743)	0.53 (NA)	807 (13)	795 (NA)	2,370	895
HerringTI	820 (73)	0.66	9,034 (596)	0.18 (0.03)	1,390 (146)	1,325 (40)	7,644	316
HerringKB	3,330 (673)	0.10	6,722 (1359)	0.18 (0.02)	1,403 (111)	1,294 (40)	5,319	-88
Coho At Release	41 (NA)	0.86	744 (NA)	0.16 (NA)	807 (13)	528 (NA)	-63	-407
Coho After Release	33 (NA)	0.86	596 (NA)	0.16 (NA)	807 (13)	528 (NA)	-212	-431
HerringSC	405 (16)	0.05	437 (17)	0.17 (0.01)	1,438 (169)	1,210 (52)	-1,001	-1,134
KrillSC	36 (NA)	0.99	734 (NA)	0.97 (NA)	1,840 (NA)	2,574 (NA)	-1,106	-1,859

Table 3.8 Results of tag deployments and surface observations of humpback whales feeding. Where whale speeds are not available, speeds from similar foraging periods are used to estimate metabolic costs. \*/\*\* indicates tag deployments on the same animal.

Tag ID	Foraging Target	Duration (min)	Group size	Lunge depth (m)	Dive depth (m)	Mean max speed per lunge (m/s)	Meta. Costs $\mu$ (se) (kJ/lunge)	Lunge rate (lunge/min)	Meta. costs (kJ/min)
Surface obs1	ChumTB	15	1	5	10	NA	807 (13)	0.53	795
Surface obs2	CohoKB	18	1	5	10	NA	807 (13)	0.16	528
mn14_113b	HerringSC	364	~2	61	66	3.8	1,531 (41)	0.20	1,242
mn14_113a	HerringSC	70	3	68	83	3.2	1,110 (18)	0.16	1,061
mn14_110a*	HerringSC	239	2	64	68	4.1	1,674 (42)	0.16	1,164
mn13_113d	HerringTI	143	~14	20	59	3.7	1,429 (43)	0.10	1,122
mn13_112a	HerringTI	299	~11	24	36	4.2	1,828 (82)	0.14	1,402
mn13_113a	HerringTI	180	~11	23	42	4.5	2,044 (122)	0.12	1,334
mn13_111a	HerringTI	563	~11	19	54	3.1	1,102 (27)	0.11	1,129
mn13_108a	HerringTI	70	3	32	37	3.8	1,490 (223)	0.23	1,385
mn13_108a	HerringTI	76	7	21	40	3.3	1,193 (70)	0.16	1,238
mn13_109a	HerringTI	77	~2.5	10	17	2.2	738 (37)	0.35	1,404
mn13_109a	HerringTI	66	2.5	17	31	3.3	1,294 (172)	0.24	1,426
mn14_114a*	KrillSC	54	2	46	57	4.3	1,840 (48)	0.97	2,530
mn12_263a**	KrillSS	150	1.5	129	134	NA	923 (15)	0.96	1,547
mn12_264a	KrillSS	104	2	151	156	NA	923 (15)	0.57	1,335
mn12_264b**	KrillSS	153	2	117	122	NA	923 (15)	0.91	1,542
mn12_265a	KrillSS	196	2.3	135	140	NA	923 (15)	0.82	1,479
mn12_262b	KrillSS	339	1	135	135	NA	923 (15)	0.83	3,289
mn12_262a	KrillSS	330	1	135	135	3.1	923 (15)	0.85	1,657
mn13_110a	KrillTI	91	2	16	21	2.1	702 (12)	0.53	1,450
mn13_110a	KrillTI	197	2.5	17	23	2.2	728 (8)	0.62	1,538
mn14_113b	UnkSC	253	unk	4	10	1.9	614 (3)	1.11	1,493

SC = Seymour Canal, KB = Kasnyku Bay (the site of Hidden Falls hatchery), TI = Tenakee Inlet, TB = Takatz Bay

Table 3.9 Sensitivity of model output net energy gain per time (NEG/T) to model parameters.

Parameters	Symbol	Unit	Sub-model sensitivity	Overall sensitivity	Description of influence
<b>Prey patch energy density</b>	<b>PPED</b>	<b>kJ/m<sup>3</sup></b>		<b>+ 4.00</b>	<b>Linear. slope = CP·AA·EV·LR</b>
Acoustic vol. backscatter (ind)	S <sub>v</sub> .ind	dB	+ 1.07	+ 4.29	<b>Positive Exponential</b>
Acoustic target strength (ind)	TS.ind	dB	- 0.35	- 1.38	<b>Negative Exponential</b>
Mass (ind)	Mp.ind	g	+ 0.28	+ 1.11	<b>Linear</b>
Length	Lp	mm	+ 0.19	+ 0.74	<b>Negative Power</b>
Prey energy density	Energy	kJ/g	+ 0.17	+ 0.67	<b>Linear</b>
<b>Capture proportion</b>	<b>CP</b>	<b>unitless</b>		<b>+ 0.62</b>	<b>Linear. slope = PPED·AA·EV·LR</b>
Reaction distance	Rxn	m	- 0.67	- 0.26	<b>Complex.</b> Influence increases with whale speed.
Prey speed	Vp	m/s	- 0.35	- 0.24	<b>Complex.</b> Influence increases with whale speed.
Whale lunge speed (max)	Vc_max	m/s	+ 0.21	+ 0.14	<b>Complex.</b> Influence greater for subsurface lunges & higher values Vp. (See opposing effects on MC.)
Lunge type	L_Type	(cat)	+ 0.18	+ 0.13	<b>Complex.</b> More influence at intermediate Vp and Rxn.
Prey speed (SD)	Vp.sd	m/s	- 0.13	- 0.09	<b>Complex</b>
Whale body length	Lc	m	+ 0.09	+ 0.06	<b>Complex.</b> (see opposing effects on MC)
Reaction distance (SD)	Rxn.sd	m	- 0.02	- 0.01	<b>Complex</b>
<b>Lunge rate (GEG effects only)</b>	<b>LR</b>	<b>lunge/min</b>		<b>+ 0.58</b>	<b>Linear. slope = NEG/L</b>
<b>Metabolic costs</b>	<b>MC</b>	<b>kJ/min</b>		<b>- 0.43</b>	<b>Linear. slope = -1</b>
Whale body length	Lc	m	+ 0.63	- 0.27	<b>Power (4.17).</b> More influence at large values of whale lunge speed
Lunge rate (MC effects only)	LR	lunge/min	+ 0.49	- 0.21	<b>Linear.</b> slope = MC. When NEG/L >1, GEG increases more steeply than MC.
Whale lunge speed (max)	Vc_max	m/s	+ 0.37	- 0.16	<b>Negative Quadratic.</b> Increased costs at larger body size.
Max dive depth	pmax	m/s	- 0.08	+ 0.03	<b>Step function.</b> Slope = 0 at shallow pmax. Correlated with Vc_max and Lunge type.
Whale lunge speed (min)	Vc_min	m/s	- 0.03	+ 0.01	<b>Positive Quadratic</b>

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### 3.9. Appendices

#### Appendix 3A: Parameter values for modelling prey patch energy density

##### Prey lengths and standard deviations

Herring were captured in Tenakee inlet on 19 April 2013 ( $n = 9$ ) and on 25 April 2014 in Seymour Canal ( $n = 6$ ) during our tagging and acoustic surveys at each site. In Kasnyku Bay, on 2 June 2014, three herring were extracted from the stomach of a cod (species unknown) to verify the species composition of the acoustic volume backscatter. For each location, unbiased estimates of population standard deviation were calculated from these samples. For the model, the estimate of mean length (187 mm  $\pm$  16.5 SE) of herring in Kasnyku Bay was determined by taking the grand mean of mixed age class herring trawl surveys ( $n = 8$ ) in Southeast Alaska during the month of May in 2001, 2002, and 2003 collected by the Ted Stevens Marine Research Institute in Fredrick Sound and Auke Bay (NOAA unpublished data). Capture numbers per trawl ranged from 4 – 42 individual herring (26  $\pm$  8.8 se). To estimate the standard deviation of herring length in Kasnyku bay (21 mm), we calculated the mean and unbiased standard deviation of all eight individual trawls. The standard deviations for each trawl were then expressed as a proportion of the mean for that trawl (0.11  $\pm$  0.2 se). That proportion was then applied to the overall mean.

All juvenile salmon were captured at Kasnyku and Taktaz Bays in spring 2014. Coho salmon were captured with jigs on 16 May 2014 directly following a release in Chatham Strait ( $n = 20$ ) and on 28, May 2014 near the main Hidden Falls dock ( $n = 9$ ). Chum salmon were dip-netted by hatchery staff from saltwater net pens prior to immediate release on 23 May 2014 ( $n = 36$ ) and 3 June ( $n = 46$ ) at Kasnyku Bay and 7 June at Takatz Bay, an alternative release location ( $n = 133$ ; Figure 3.2). Fish captured live were euthanized with a mixture of 95% ethanol and

clove oil (approx. 1:10) mixed in a bucket of salt water (Cho & Heath 2000; Nickum 2014). One to three mL of clove oil/ethanol mixture was added to the salt water until the fish ceased opercular movement and floated, generally within 5 minutes. All fish samples were frozen individually to be measured (fork length) and weighed in the lab. All lengths are fork lengths. We assumed a normal distribution for all length measurements and, for chum salmon with a larger sample size, the sample distribution visually supported this assumption.

Krill lengths from Seymour Canal 2014 were measured from a photograph of krill in a dish of known diameter. Six individuals that were mostly extended in a straight posture were measured relative to the diameter. Mean (18 mm +/- 1 SE) and unbiased standard deviation of lengths (3 mm) were calculated. Seventy-four krill from Sitka Sound were measured. The length distribution for krill entered into the model was centred on the mode of this left skew of the distribution (about 16.4) of sampled krill because of the expectation that larger krill would not be sampled. Standard deviation was recalculated based on this assumed mean (16.4).

#### Target Strength (TS)

TS is the target strength (dB) of fish in the school, either determined by capturing individuals and calculating their expected target strength with different formulas for juvenile salmon (Love 1971; Burczynski & Johnson 1986):

$$TS = 19.1 \log_{10} \text{fork length (cm)} - 66.57 \quad \text{[Equation 3.A-1]}$$

And for herring (Ona 2003; Boswell *et al.* 2016):

$$TS = 20 \log_{10} \text{fork length (cm)} - 2.3 \log_{10} \left( 1 + \frac{Z}{10} \right) - 65.4 \quad \text{[Equation 3.A-2]}$$

Where  $Z$  is the mean water depth of the acoustic target. For krill, we used the distorted-wave Born approximation (DWBA) scattering model (Lawson *et al.* 2006) with material



properties that specified in Becker & Warren (2014) and the mean and distributions of length from Sitka Sound and Seymour Canal.

#### Wet mass

For herring and coho salmon, wet mass is simply the mean mass of the samples used for calorimetry analysis. Because we had many more chum salmon samples, we chose to represent a size distribution rather than a random sample for those used in calorimetry analysis. Therefore, the mean mass of chum salmon was determined by a regression of 17 juvenile chum salmon  $mass = 0.1214 \times length - 4.848$  ( $R^2 = 0.8733$ ) where *mass* is expressed in grams and *length* is expressed in millimetres. The mean value of length for ChumKB Early was 58 mm (SE = 0.83, N = 36) and ChumKB/TB Late was 66 (SE = 0.77, N = 136).

#### Energy density

For herring and krill, the energy density (kJ/wet g) was the mean energy density of the samples used for bomb calorimetry. For juvenile coho and chum salmon, a linear regression was used to determine the relationship between length and kJ/fish with collection date and an interaction between length and collection date included as predictors (Figure 3.A-1):

$$\frac{kJ}{fish_{ij}} = \beta_0 + \beta_1(length_i) + \beta_2(collection\ date_j) + \beta_3(length_i \times collection\ date_j) + e_i$$

[Equation 3.A-3]

where for each species *collection date* is a factor with two levels. A Box-Cox procedure was used to determine an appropriate transformation of the response to ensure normality (Box & Cox 1964; Faraway 2005). Akaike Information Criteria for small samples sizes (AICc) was used to determine which terms to retain for the best model for each species (Burnham *et al.* 2011).

Energy density was determined for coho and chum salmon by calculating the total energy of a

fish of the mean fork length for each prey group and dividing by the mean mass for that prey group.

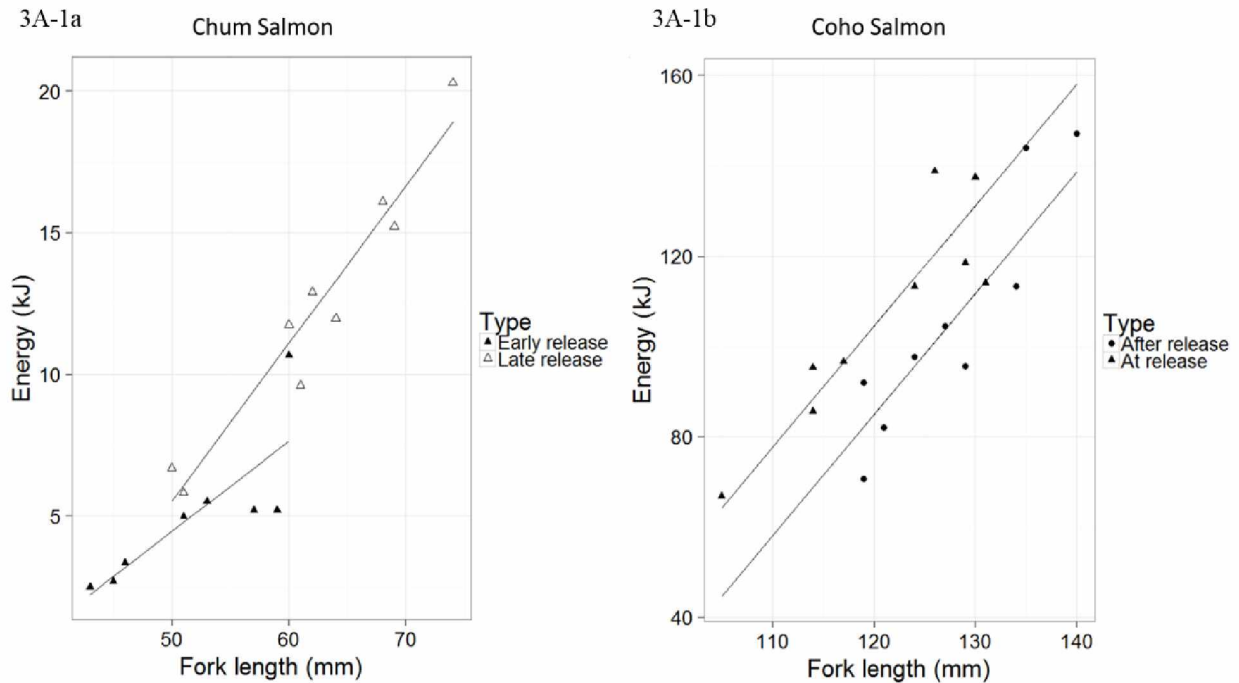


Figure 3.A-1 Energetic content of juvenile salmon. a. Energetic content of chum salmon released early and late in the season. Early in the season Energy (kJ) =  $0.31802 \cdot \text{Length (mm)} - 11.45264$ . Late in the season, Energy (kJ) =  $0.55862 \cdot \text{Length (mm)} - 22.42915$ .  $F = 32_{2,15}$   $p < 0.001$ ,  $\text{Adj } R^2 = 0.78$  b. Energetic content of coho salmon on the day of release and captured from the release area. At the time of a releases: Energy (kJ) =  $2.6848 \cdot \text{Length (mm)} - 237.2978$ ; wild caught after a release: Energy (kJ) =  $2.6848 \cdot \text{Length (mm)} - 217.8102$ .  $F = 65_{2,15}$   $p < 0.001$ ,  $\text{Adj } R^2 = 0.92$ . Models were selected using AICc criteria from a full model with predictors length, type, and the product of length and type.

#### Acoustic volume backscatter ( $S_v$ )

Each echosounder was calibrated at least once during each research cruise following the standard sphere protocol (Demer *et al.* 2015) with target strengths for specific water properties calibrated using the NOAA Southwest Fisheries Science Center Standard Sphere Target Strength Calculator (<http://swfscdata.nmfs.noaa.gov/AST/SphereTS/>). To control for the effect of ocean temperature and salinity on acoustic transmissions, oceanographic data were collected using a

conductivity, temperature, and pressure recorder (SBE 19plusV2 SEACAT Profiler, Sea-bird Electronics, INC 13431 NE 20th St. Bellevue Washington 98005). Acoustic absorption and sound speed coefficients for each survey were determined from the mean salinity and temperature of the profiles closest in space and time to the survey using R package oce (Kelley 2014).

Data were analysed in Echoview software (v. 6.1 – 7). The top 1 m below the transducer was removed from analysis as well as any acoustic scatter contiguous with the surface, to eliminate near field effects and entrained air bubbles. An acoustic volume backscatter ( $S_v$ , in dB) threshold of -60 dB was used to exclude zooplankton or fish smaller than juvenile salmon. Each cell was integrated, and acoustic fish density was expressed in terms of  $s_a$  (area scattering coefficient;  $m^2/m^2$ ). Notation follows descriptions details by MacLennan Fernandes & Dalen (2002). We then used zero-inflated generalized additive models (Zeileis Klieber & Jackman 2008) to locate areas of highest density by depth and location for areas where distinctive schools were not detected despite whale feeding.

When prey were sufficiently dense, schools were detected using the school detection algorithm in Echoview using the following parameters: minimum school length 5 m, minimum school height 5 m for Seymour Canal and Kasnyku Bay; minimum school length 20 m, minimum school height 8 m for larger spawning aggregations in Tenakee Inlet. Parameters were selected iteratively to identify aggregations visibly apparent on echograms where individual tracks are overlapping substantially so as to be not individually distinguishable (Burgos & Horne 2007). Echo intensity signals within each school were integrated to determine the acoustic density of the school expressed as the mean nautical area scattering coefficient ( $s_A$ ):

$$s_{A\_adj} = \frac{1}{K \cdot \gamma} \ln \left( \frac{1}{1 - K \cdot \gamma \cdot s_A} \right) \quad [\text{Equation 3.A-4}]$$

where  $K = 2/18522$  and  $s_A$  is the nautical area scattering coefficient for each school. We used the extinction factor  $\gamma = 0.97$  (SE 0.27) previously calculated for Pacific herring in Southeast Alaska (Boswell *et al.* 2016). Prey patches were then included in analysis if they were the closest patch to a tagged whale at the time of a lunge. To estimate the biomass density in terms of  $\text{g/m}^3$  of schools or cells, we used:

$$\text{Biomass density} = \frac{s_{A\_adj} / 4\pi(1852)^2}{10^{(TS/10)}} \text{ } mh^{-1} \quad [\text{Equation 3.A-5}]$$

Typically, there was a single prey dominating the seascape, however. In Kasnyku Bay, likely chum salmon schools were distinguished from herring schools also observed in the region by identifying single acoustic targets around a school and determining the mean target strength. Schools with nearly targets less than -47 dB were considered likely chum salmon and included in analysis based on the range of expected target strengths for the lengths of chum salmon in our study. Schools without nearby targets or with targets larger than -47 dB were excluded. Because there was no relationship found between TS of nearby targets and mean  $S_v$  of the school, the same schools were used to model the density of both early and late release chum salmon.

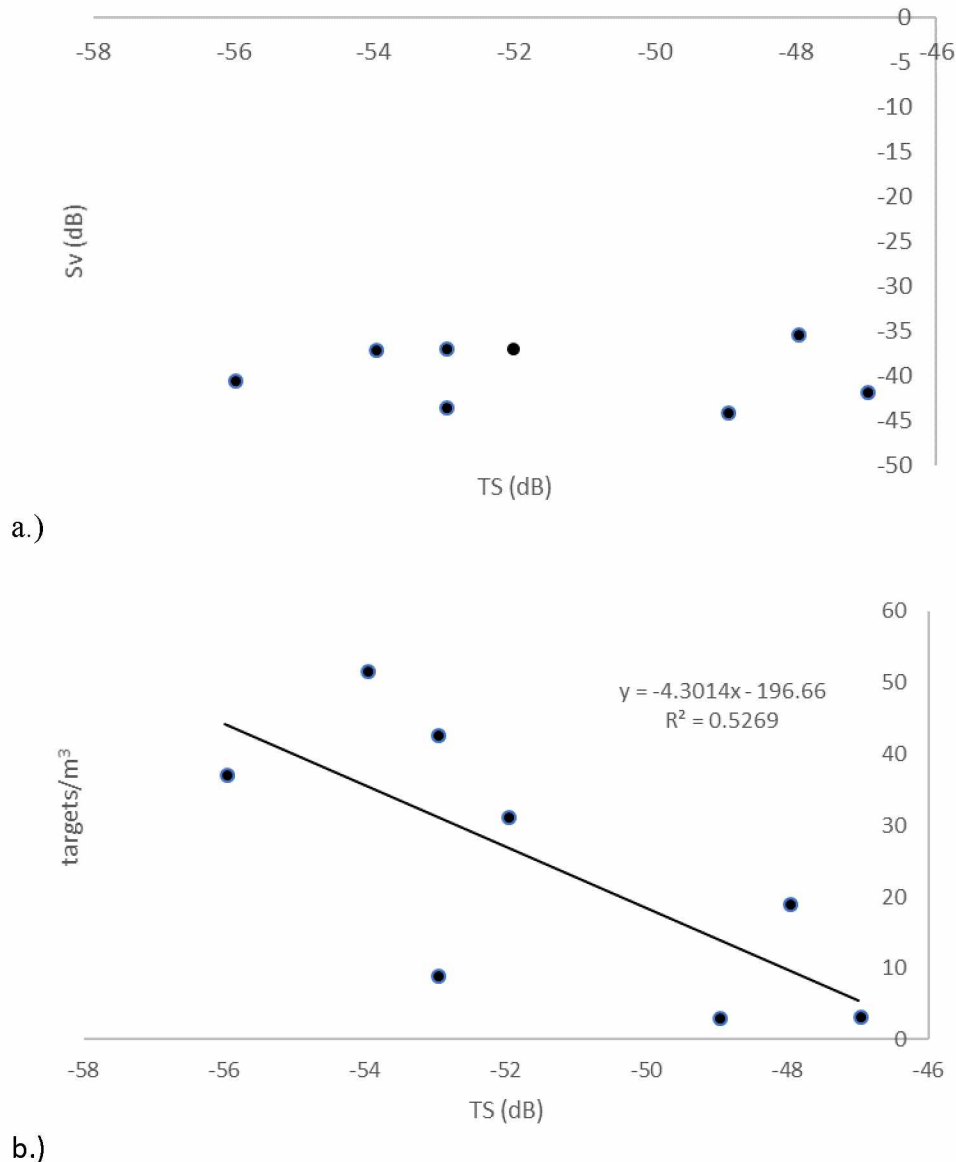


Figure 3.A-2 Evidence for a negative relationship between school density and fish size in juvenile chum salmon. If larger chum salmon (with larger target strengths) packed as densely in schools as smaller chum salmon, we would expect an increase in  $S_v$  as TS increases, but this is not observed (3.8a). Therefore as TS increases, targets per space decrease (3.8b). Because TS scales with individual length and  $S_v$  with density, this implies a negative relationship between chum salmon size and school density.

For coho salmon, densities were too diffuse for acoustic school detection. Therefore, densities were modelled in space and time to determine the density where whales were frequently feeding, which was also the maximum density. Surveys were repeated during the

release season and all surveys were included in the model (Table 3.A-1). To identify areas of highest acoustic fish density, we modelled the area scattering coefficient ( $s_a$  in  $m^2 \cdot m^{-2}$ ) as a function of latitude and longitude using a zero-inflated generalized additive model (Zeileis Klieber & Jackman 2008). This model had two parts: a binomial model to determine the probability of a positive  $s_a$  value, and a gamma-distributed model for cells with non-zero values of  $s_a$ .

$$\mu = (1 - \hat{\pi})(\hat{S}_a) = \frac{e^{\hat{b} + \hat{g}}}{1 + e^{\hat{b}}}$$

$$b_i = \ln\left(\frac{\pi_i}{1 - \pi_i}\right) = \beta_0 + f_i(\text{Latitude}, \text{Longitude}) + e_i, \text{ For } s_{a_i} > 0$$

$$g_i = \ln(s_{a_i}) = \beta_0 + f_i(\text{Latitude}, \text{Longitude}) + e_i \quad [\text{Equation 3A.6}]$$

where:  $s_a$  = fish density (area scattering coefficient;  $m^2 \cdot m^{-2}$ ), a continuous variable measured from acoustics;  $b_i$  = probability for location  $i$  that  $s_a = 0$ ;  $g_i$  = the predicted value at location  $i$  of the binomial model on the logit scale; and  $\mu$  = the predicted value at location  $i$  of the gamma model on the log scale.

Table 3.A-1 Summary statistics of acoustic surveys in Kasnyku Bay

Survey location	Mean min depth (m)	Mean max depth (m)	Mean depth (m)	Length of transect (km)	Area covered (km <sup>2</sup> )	Approx. distance between neighbouring transects (m)	n	Start/End dates
Inner Pens	3	40	23	5.5	142	24	9	5/16 – 6/5
Outer Pens	8	19	31	4.2	167	30	6	5/23 – 6/7
Middle	10	41	33	3.5	133	51	4	5/23 – 6/7

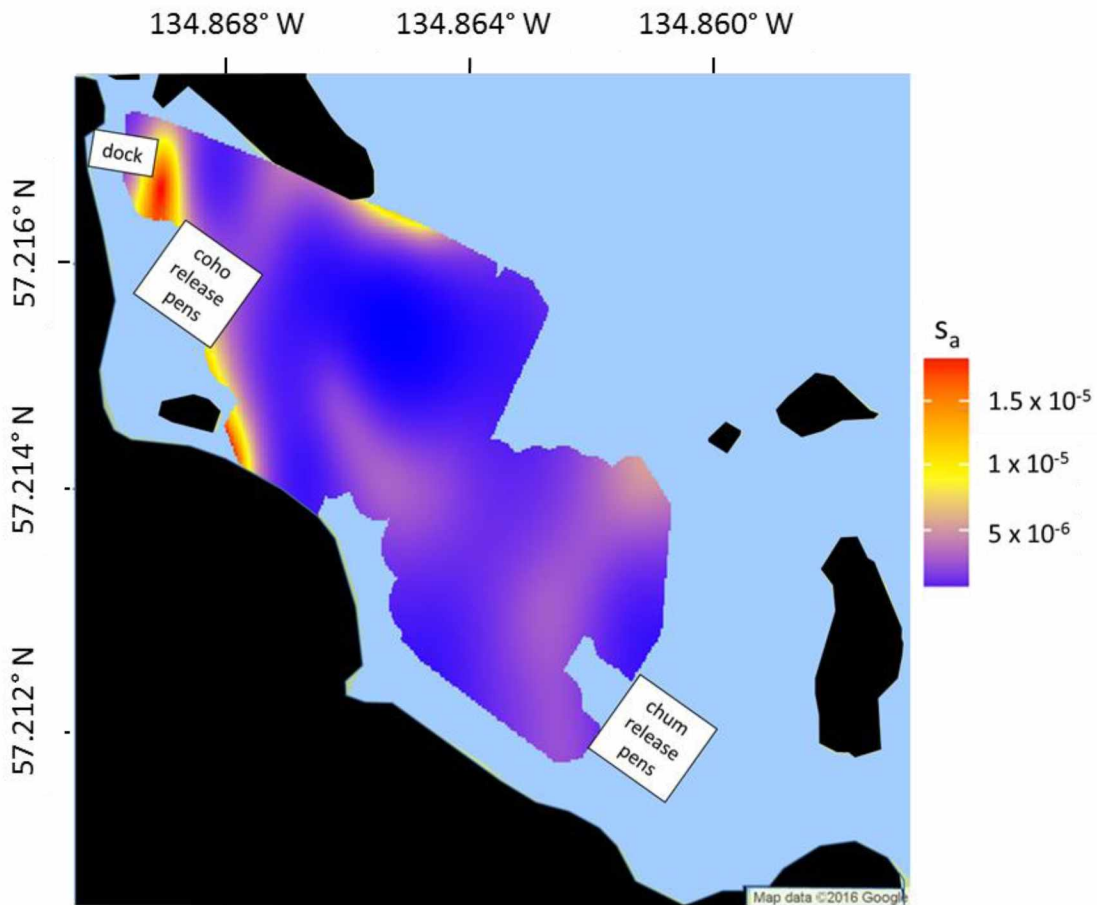


Figure 3.A-3 Contour plot of fish density ( $s_a$ ) in the acoustic survey area. Salmon densities were modelled using data from nineteen surveys in the area between 16 May and 7 June 2014, with the most survey effort concentrated around the coho release pens and dock. Fish density values were modelled from processed acoustic data using a zero-inflated generalized additive model with a gamma distribution and allowed to interpolate between track lines but not extrapolate outside of a convex hull formed by the tracklines. Shoreline is indicated in black.

Where whales with georeferenced tracks (Trackplot 3.0) and acoustic data available (Herring TI, HerringSC, KrillSS and Krill SC), we identified acoustically detected schools that were closest in time and space to each individual lunge. Spatial and temporal proximity was balanced and combined into a single metric using units of 30 min and 300 m. For Kasnyku Bay chum salmon and herring, no whales were tagged while feeding. Therefore,  $S_v$  measurements are of prey schools where whales were feeding.

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## Appendix 3B Parameterizing model capture proportion (including detailed methods for Table 3.4)

### Herring

Herring reaction distances and escape response swim speeds were determined by measurements of herring responses ( $n = 61$  speed;  $n = 2$  reaction distance) to predation by sea lions in Fritz Cove near Juneau, Alaska in January 2007. Observations were made at a depth of approximately 50 m with a high-definition (1.1/1.8MHz) imaging sonar (DIDSON) (Moursund, Carlson & Peters, 2003) on a remotely controlled platform (Boswell, Miller & Wilson, 2007). The DIDSON was configured to operate in high-frequency mode (1.8 MHz) with max range of 12 m. Length estimates of herring were derived from the in situ DIDSON data; herring had an average length of 218 mm (0.32 SE). Average escape response speed was 5.7 fork lengths/s (0.2 SE, SD = 25%). Reaction distance was measured from two sea lion approaches where approach trajectories toward the prey were parallel to the instrument field of view. Because herring began to escape before the sea lion entered the frame, the reaction distances were extrapolated using the time between the herring reaction and the entrance of the predator into the frame and the average speed of the predator once detected in the frame. The average (4.0) and standard deviation (0.1) of the extrapolated reaction distance from the two encounters (4.1m and 3.9 m) was used to parameterize the model.

### Juvenile Chum Salmon

To measure in-situ swimming speeds, single acoustic targets were detected on the EK60 echosounder, (a minimum threshold of -60 dB, pulse length determination level of 6 dB, and minimum and maximum normalized pulse length of 0.7-1.5 ms). Echoview target

tracking algorithm identified likely repeated detections of the salmon individual fish and linked them into a single track (Blackman 1986). Only tracks with two or more targets within five consecutive pings were included. Single targets were georeferenced to account for the movement of the autonomous surface vessel (ASV). For each selected track, speed was calculated by the track detection algorithm using 4-dimensional geometry (Arrhenius *et al.* 2000, McQuinn & Winger 2003).

Fish swimming speeds were measured acoustically as an indicator of avoidance behaviours and ease of capture. Thirty-four individual fish tracks met our criteria of a mean target strength within each track less than -47.8 dB and greater than -57.3 dB, consistent with the size of chum salmon just prior to release (31 mm – 96 mm). Within this range of target strengths, target strength was not a significant predictor of swimming speed ( $F_{1,41} = 2.9$ ,  $p = 0.1$ ). The maximum speed recorded was 1.1 m/s with the mean top speed per track = 0.24 m/s ( $n = 33$ ). The maximum top speed was 13.9 body lengths/s and the mean top speed was 3.8 body lengths/s ( $n = 33$ ). Measured surface temperature was 10.6 °C.

Juvenile chum salmon reaction distance was determined by an acoustic observation using the ASV at the site of an active chum salmon release from hatchery net pens. An echogram and visual inspection of a high frequency Didson sonogram indicated that at one point a potential predator swam into the school of juvenile chum salmon. The salmon expanded to form a buffer around the target (Figure 3.B-1). As the vertical axis is the most reliable for measuring distance, we determined salmon allowed a 1.3 m buffer around a potential threat. Since we derived this estimate from a single encounter, we assumed the same percent (2.5%) standard deviation as was measured for herring ( $SD = 0.03\text{m}$ ).

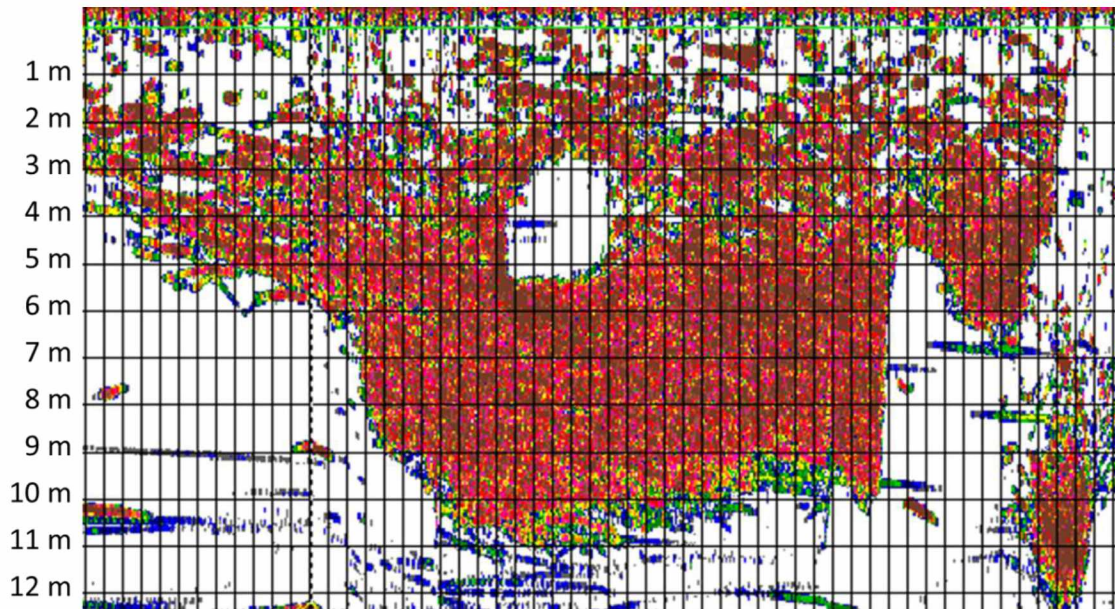


Figure 3.B-1 Echogram from 4 June 2014 in Kasnyku Bay showing chum salmon responding to a piscine predator. The vertical buffer of empty water around a presumed potential predator of unknown species (about 1.33 m) was used to parameterize the prey capture model for the predator avoidance distance of chum salmon.

### Juvenile Coho Salmon

Mean prey speed (8.1 lengths/s, 1.3 SE,  $n = 25$ ) and was taken from Puckett & Dill (1984) after removing the effect of current. Because the juvenile salmon in the study had a narrow range of length distributions (48 – 53 mm), the standard deviation of speed for the input model was calculated from the mean and standard deviation of speed in Puckett & Dill (1984) (6.6 lengths/s) and the mean and standard deviation of the length distribution assuming independence between variability in length and variability in speed. Water temperature in this experiment was 15° C.

To determine the reaction distance, we used findings from a laboratory experiment by Healey & Reinhardt (1995) that recorded the reactions of predator-experienced juvenile coho salmon to a trout. The average reactions distance was 0.66m (SD 2.62,  $n= 43$ ). The standard

deviation (0.17 m) was derived from these reported estimates. There was no relationship between predator speed and reaction distance in this study.

## Krill

Mean and standard deviation of swimming speeds were calculated based on visual inspection of figure 3 in Strand & Hamner 1990. The mean swimming speed (17 m/s, 3.5 lengths/s) and standard deviation (1 m/s, 0.14 lengths/s) was from an average of two sets of 50 individual krill with the introduction of krill extract to the water. Standard error is not calculated because only two values (17.75 m/s, 16.25 m/s) were used to produce the estimate of the mean. Values were rescaled based on lengths/s as the original experiment was conducted with larger Antarctic krill. These krill were taken from a population of 500 individuals with a mean size of 4.84 cm and standard deviation of 1.1. Because the Strand & Hamner experiment utilized krill of a range of lengths, we simply rescaled the standard deviation from that experiment without incorporating the length distribution of krill in our experiment.

The mean reaction distances of krill (0.9 m) were derived from an experimental laboratory study by Strand & Hamner (1990) which recorded the predator-avoidance distances of krill based on the size of a simulated predator (black dots). We fit a logarithmic curve was fitted to apparent mean experimental values from Strand & Hamner (1990) (Figure 3.B-2). ( $y = 17.369 \times \log_e(x) - 2.7623$ ;  $R^2 = 0.9975$ ). The standard deviation of the reaction distance (0.6 m) is calculated from the apparent standard error of the krill reaction distance (~0.04 m) to the largest simulated predator after  $n = 200$  trials. Notably, this reaction only occurred in unblinded krill in the presence of ambient light.

The relationship between simulated predator size and reaction distance (cm) (Strand & Hamner 1990) is represented here as Figure (3.B-2).

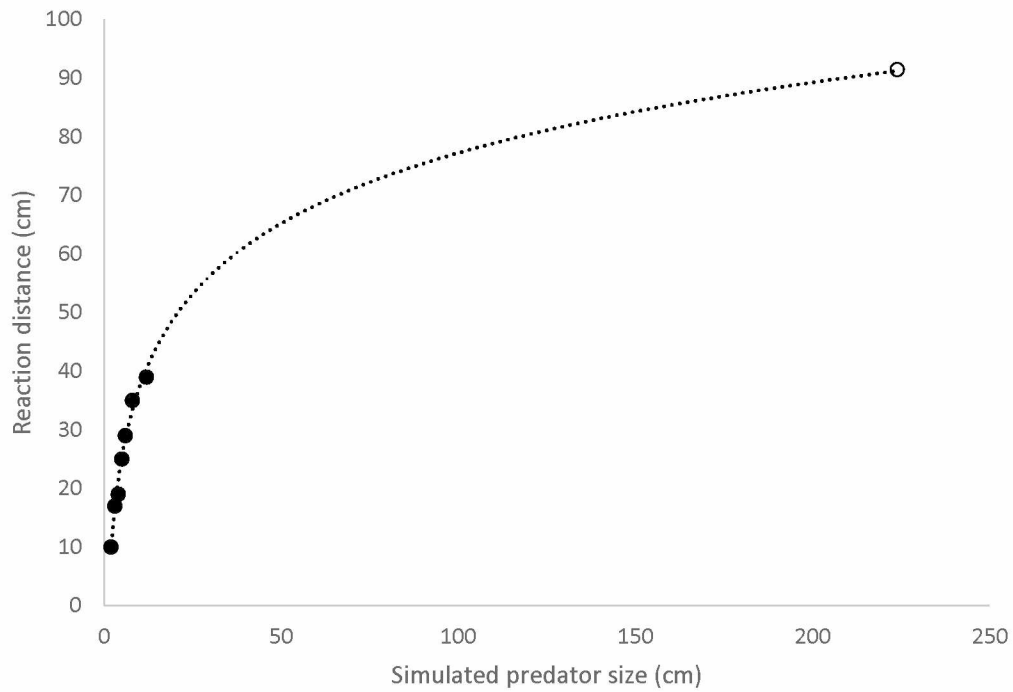


Figure 3.B-2 Relationship between simulated predator size and reaction distance (cm) curved fitted with data in Strand & Hamner (1990) (closed circles). Open circle represents the head width of a mean length humpback whale.

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### Appendix 3C: Tag deployment processing and lunge detection

Tags were deployed from a small rigid-hulled inflatable boat (RHIB) from a custom bracket at the end of an 8 m carbon fibre pole. Tags were attached to the dorsal surface of a whale forward of the dorsal fin. All tags include a VHF transmitter for real-time telemetry tracking, a hydrophone, a pressure sensor, a 3-axis accelerometer and magnetometers (sampling rate 50 Hz).

Pressure, magnetometer, and accelerometer data obtained from DTAGs were calibrated, and oriented to the whale frame using customized DTAG code written in MATLAB accounting for the orientation of the tag with respect to the whale direction of movement (Mathworks, Inc. Release 2012b; Johnson & Tyack 2003). Acousonde data were calibrated and oriented with technical assistance from David Cade, (2017, Goldbogen Lab, Stanford University). Non-acoustic sensor data was downsampled to 5Hz. Whale locations at surfacing were calculated using spherical geometry from the range, bearing observations and the position of the focal follow vessel using R package geosphere (Hijmans 2016) and Microsoft Excel add-in geometry functions (<http://www.afsc.noaa.gov/nmml/software/excelgeo.php>). In Sitka Sound in 2012, some tagged animals were outfitted with Fastloc GPS; only three of these fixes were used to supplement focal follow locations due to unreliability of the locations.

$$MSA = (\sqrt{A_x^2 + A_y^2 + A_z^2} - 1) \cdot g_{acc} \quad [\text{Equation 3.C-1}]$$

$$Jerk = \frac{\|MSA_{t+1} - MSA_t\|}{(1/fs)} \quad [\text{Equation 3.C-2}]$$

Where  $A_x$ ,  $A_y$ , and  $A_z$  are the three accelerometers and  $g_{acc}$  is gravitational acceleration and  $fs$  is the sampling frequency. Typically, lunges are identified primarily by a dramatic peak in jerk followed by a decline in speed (Simon, Johnson & Madsen 2012; Cade



*et al.* 2016). The magnitude of peak and speed changes are not constant enough for automated detection across deployments, individuals, and locations. In particular, this method of lunge detection has been unreliable for surface lunges (Owen *et al.* 2017). For some analyses, these lunges are removed due to the uncertainty. Here, however, it was preferable to include the best approximation of lunges rather than include only lunges with a high degree of certainty, which would lead to a biased estimate of lunge rate. (Note that because many surface feedings occurred at night, it was not possible to visually confirm lunges). Therefore, surface lunges were included and repeatedly compared visually across individuals to ensure consistency. We identify surface lunges by identifying, in addition to changes in jerk and speed, stereotyped repetitive manoeuvres observable through trackplot animation and scrutiny of 3 axis accelerometers (Figure 3.C-1).

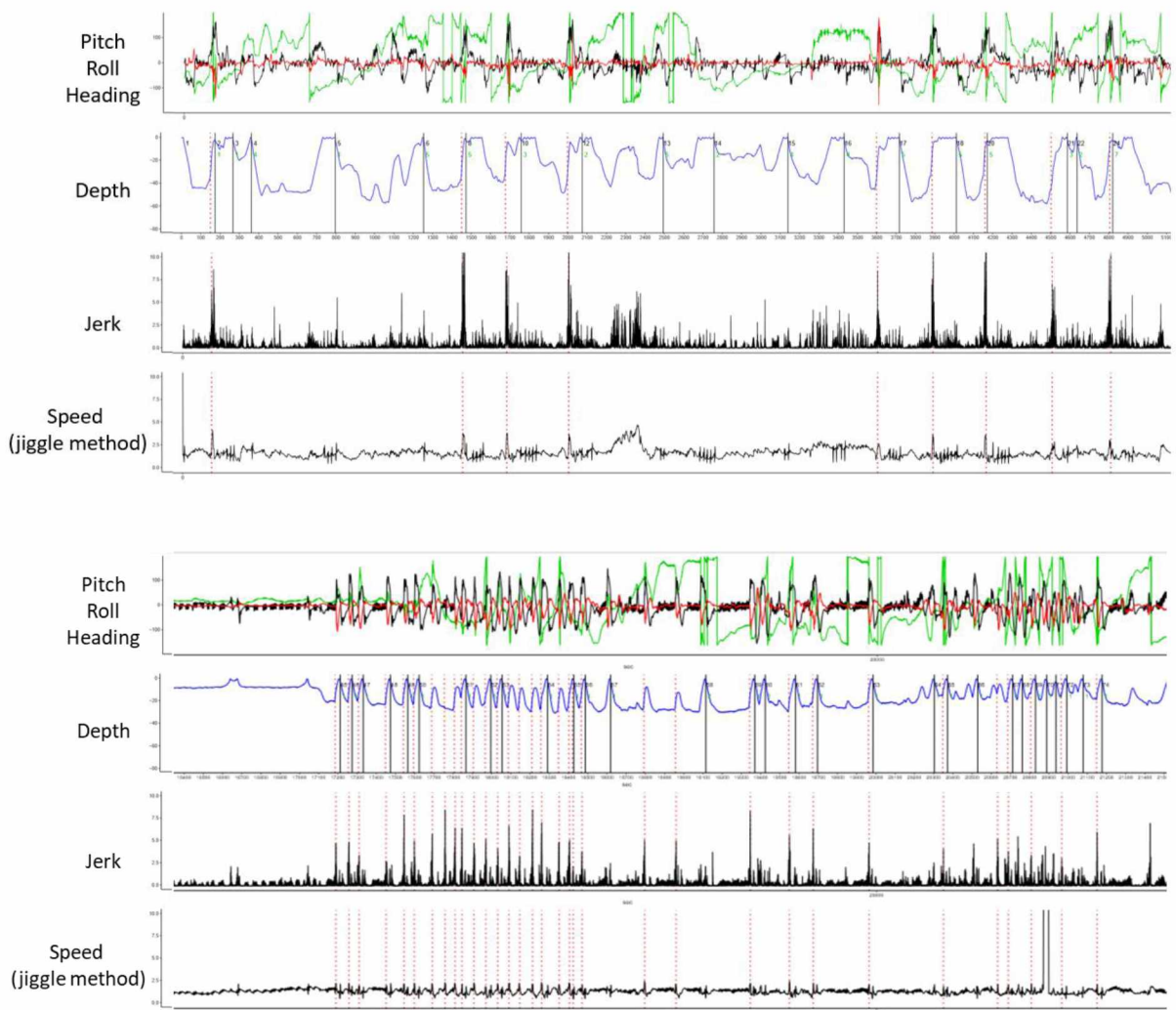


Figure 3.C-1 Sample of variables used to identify lunge feeding events. The red dotted lines denote the location of lunge events. Tag duration (in seconds) is shown along the x-axis of the depth plot. Vertical black lines denote each dive. Lunges are detected visually by a peak in lunge followed by an abrupt decrease in speed. The top tag (mn13\_112a) was deployed in Tenakee Inlet on April 22, 2013 on a whale feeding on a mix of surface and subsurface on pre-spawn herring. The bottom tag is (mn13\_110a) a whale feeding on surface krill in Tenakee Inlet on April 20, 2013.

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### Appendix 3D: Humpback whale behavioural observations at hatchery release sites

Kasnyku Bay (Figure 3.D-1) was selected for this study based on previous work showing frequent humpback whale predation associated with salmon releases from the Hidden Falls Hatchery located at this site (Chenoweth et al. 2017). Chum salmon (*O. keta*) are primarily released at this site, and to a lesser extent coho (*O. kisutch*) and Chinook (*O. tshawytscha*) salmon. Kasnyku Bay itself consists of three main coves and opens into Chatham Strait, a deep (up to 600 m), 240 km-long, 15 km-wide channel located in the Alexander Archipelago of Southeast Alaska, USA (Figure 3D.1). The hatchery and its dock are located in the southernmost cove, where salmon are released from two sets of net pens. This cove is the most protected with barrier islands separating it from the mouth of main Kasnyku Bay. This cove extends 40 m deep, sloping steeply along the northern shore and more gradually along the southern shore. The largest and northernmost cove, Bear Cove, is 60 m deep where it opens into main Kasnyku Bay; no salmon were released in Bear Cove. We also conducted observations from surveying an area around Kasnyku Bay (Figure 3.D-1) as far north as the mouth of Kelp Bay (8 km) and as far south as Takatz Bay (7 km).

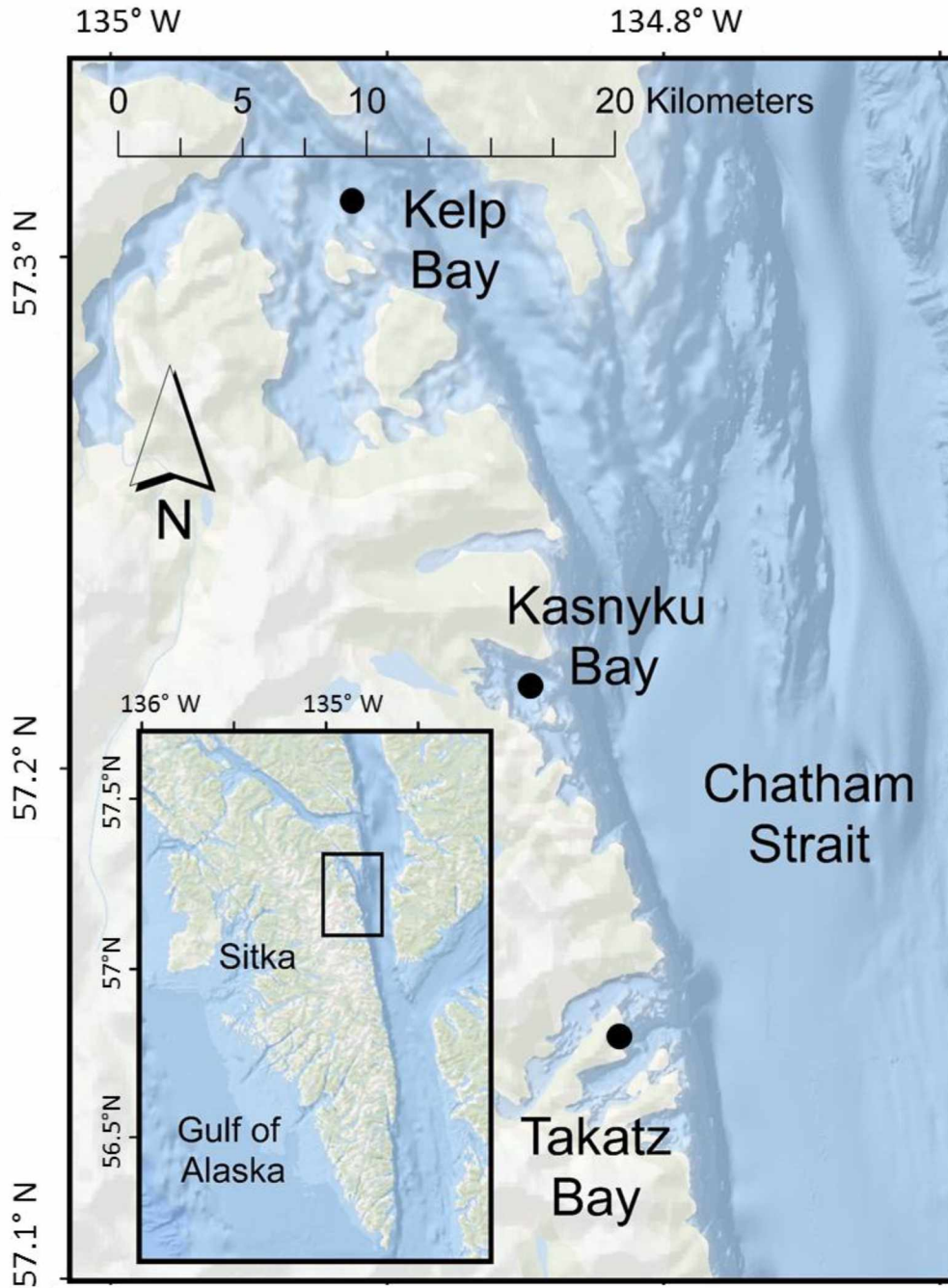


Figure 3.D-1 Humpback whale survey area off the east coast of Baranof Island, Southeast Alaska (inset), including the Takatz Bay and Kasnyku Bay release sites, as well as Kelp Bay to the north and Chatham Strait to the east.

Observations were performed throughout the day from the main Hidden Falls Hatchery site in Kasnyku Bay from 15 May to 7 June 2014. During the day, humpback whales were observed haphazardly from the Hidden Falls main dock, the net pens, a small skiff, or the *SV Bob*, a 15-m auxiliary sail vessel. Most nights, whales were observed from the sail vessel tied to either the hatchery dock or net pens in Kasnyku Bay. Humpback whale observations included identifying individual whales, assessing group composition, and documenting behaviour. Humpback whales were approached, and the ventral flukes and dorsal fins were photographed for individual identification (Katona *et al.* 1979). Identification photographs were cross-referenced with a catalogue of over 3,000 unique humpback whale flukes with individual identification numbers from northern Southeast Alaska (bordered by Frederick Sound to the south and Glacier Bay/Lynn Canal to the north) (Straley & Gabriele 2000). This catalogue has been updated to include all whale sightings up to 2012 and some from later observations (Straley & Gabriele, unpubl.). Once a whale was identified, its identification number was used to retrieve information about all the confirmed sightings of that animal back to 1979 from the Southeast Alaska Humpback Whale Database (Straley & Gabriele unpublished data; Straley & Gabriele 2000). Behaviours such as surface feeding, bubble production, traveling (short dives in a consistent direction), or resting (slow or no forward movement) were noted. Subsurface feeding was inferred when whales repeatedly dove in the same area staying submerged for more than a couple of minutes. When possible, towable EK 60 echosounders (120 and 38 kHz) were used to confirm the presence of subsurface prey and jigging was used to capture voucher samples of prey (herring or juvenile salmon).

Twenty whales were individually documented with fluke photographs captured in the whale survey area (Kelp Bay to Takatz Bay including Chatham Strait), but only four were

observed feeding on juvenile salmon. When feeding on juvenile salmon, whales were observed in shallow or nearshore areas lunge feeding at the surface, often using bubbles (Table 3.D-1). Two whales (SEAK ID 2571 and SEAK ID 2227) were seen repeatedly at the Kasnyku Bay and Takatz Bay release sites and were the only two individuals observed approaching the net pens at either site. SEAK ID 2571 was seen most frequently, observed on 11 different days and often multiple times per day in Kasnyku Bay, consistently targeting juvenile coho salmon. SEAK ID 2571 was seen most frequently earlier in the season before chum salmon had been released and fed frequently around the net pens and inner dock, where coho salmon had been released, were frequently observed, and were captured by researchers. This whale had been previously documented at the Kasnyku Bay release site in 2009 and was subsequently sighted in 2016 by our research group feeding on juvenile salmon in Kasnyku Bay, Takatz Bay, Kelp Bay, and a region south of this study, Warm Springs Bay (Kosma et al., unpublished data). SEAK ID 2227 was seen on six different days in 2014. This whale was sighted at the Kasnyku Bay release site in 2009, 2010, 2013, 2014 and 2016, despite a lack of consistent effort in those years. This whale was feeding on coho salmon on 20 and 21 May 2014 at Kasnyku Bay and chum salmon at Takatz Bay on 4 and 6 June. These whales typically fed singly but were observed around the main dock area together on 3 June. The other two salmon feeders (SEAK ID 1834 and UNK) arrived on the last day of the survey period, 7 June. Neither had been sighted at a hatchery release site in previous years. These two individuals were observed bubble net feeding on chum salmon in Chatham Strait just south of Kasnyku Bay. The whales appeared to be feeding separately but near each other and very close to shore.

Most whales were not observed to be feeding on juvenile salmon, spent little time in the area, and were most commonly seen outside of Kasnyku Bay in Chatham Strait. Thirteen of the

16 whales not noted feeding on juvenile salmon were sighted only on one day each. Prey were captured and identified as herring once in Chatham Strait (28 May 2014), once in Bear Cove where three whales were feeding (2 June 2014), and once being targeted in Bear Cove and central Kasnyku by a group of five bubble net feeding whales (7 June 2014). Near the main dock at Hidden Falls, herring schools were observed (5 June 2014) as were sand lance (15 and 17 May 2014).

Fewer whales were sighted later in the season even as more salmon were released in the area. Notably, on 19 May 2014 a whale entered the survey area at least 14 times for periods of 15 minutes to 2 hours before leaving the area (Figure 3.D-1). This whale was identified as SEAK ID 2571 and presumed to be the same whale for all sightings this day, although photographs were not taken for each sighting due to the frequency of sightings. Whales were less common at the release site in June even though chum salmon were still being released. At the Kasnyku Bay release site, whales tended to feed in periods of 15 minutes to 2 hours and concentrated feeding around the main dock and coho release pens. At the Takatz Bay release site, however, SEAK ID 2227 was observed feeding constantly throughout the night of 6 June (ID confirmed at night and in the morning). Humpback whale observations were recorded opportunistically at Hidden Falls and the surrounding survey area, including Takatz release site, for 28 days in May 2014 and June 2014 (Table 3.D-1). Humpback whale observations at release sites did not show a clear diurnal pattern, with whales observed feeding at release sites at nearly any hour of the day and night in either Kasnyku Bay or Takatz Bay.



Table 3.D-1 Humpback whale observations in 2014 in acoustic survey area at Kasnyku Bay. Full effort indicates effort for the entire day, including some night observations. Partial effort means that observers were not present at all times. When observations are listed by the start time of the observation (when the whale was noticed). If the end time is available, it is included. End time is when the whale was last seen because the whale (rather than the observer left the area). The whale ID field lists the identification numbers of whales in the acoustic survey area are not necessarily applicable to all observations that day. CS = Chatham Strait, KB = Kasnyku Bay

Date	Effort	Whale data				Release Data		
		Time(s) observed	Behaviour	ID	Other notable	Species	Site	Biomass (kg)
16-May	Full	No whale observations	-----	-----	-----	Coho	CS	19,157
17-May	Full	00:00; 07:15-08:07; 09:13; 10:00	Dock, net pens, surface lunges	2571	-----		-----	
18-May	Partial	22:30-22:35	Pens	No photos	-----		-----	
19-May	Full	04:45; 05:34; -6:03; 07:24; 07:40; 08:26; 09:41; 10:40; 11:00; 13:49; 19:39; 20:39; 22:10; 23:39	Shoreline, bubbles, dock	2571	-----		-----	
20-May	Full	10:23; 13:36; 16:00; 15:48; 22:10; 22:00	No barrier, no surface lunges	2227	-----	Coho	KB	3,682
21-May	Full	04:20; 05:21; 19:50	Bubbles, dock, net pens	2227; (2571 visual ID)	-----	Chum	KB	8,977
22-May	Full	13:30; 20:56; 23:03; Possibly 2x during the night	Bubbles, dock, net pens	2571	-----	Chum	KB	9,827
23-May	Full	22:22	Dock	2571	-----	Chum	KB	9,041
24-May	Full	No whale observations	-----	-----	-----	Chum	KB	14,342
25-May	Full	12:30-14:30; 20:30-21:00	Shoreline, bubbles, dock	2571	-----	Chum	KB	4,500
26-May	Full	07:30	Dock, surface lunge	(2571 nearby 3 hours later)	-----	Chum	KB	4,547
27-May	Partial	No whale observations	-----	-----	Whale near KB mouth; 2571 outside of KB acoustic area	Coho/ chum	CS/ KB	21,928/ 5,624
28-May	Partial	16:21	-----	No photos	Away from pens; 2571 outside of KB acoustic area		-----	
29-May	Partial	05:40	Dock, inner pens, bubbles	2571	-----		-----	
30-May	Full	20:00	No barrier, No surface lunges	2571	-----		-----	
31-May	None	No whale observations	-----	-----	-----		-----	
1-Jun	Partial	No whale observations	-----	-----	-----		-----	
2-Jun	Partial	No whale observations	-----	-----	~3 whales feeding in Bear Cove on herring in late evening		-----	
3-Jun	Full	10:12	Net pens and dock	2571;2227	-----		-----	
4-Jun	Partial	No whale observations	-----	-----	-----	Chum	KB	6,218
5-Jun	Partial	No whale observations	-----	-----	-----	Chum	KB	7,147
6-Jun	Full	No whale observations	-----	-----	-----	Chum	KB	7,022
7-Jun	Full	No whale observations	-----	-----	Two whales (1834, UNK) feeding on juvenile salmon CS	Chum	KB	7,057

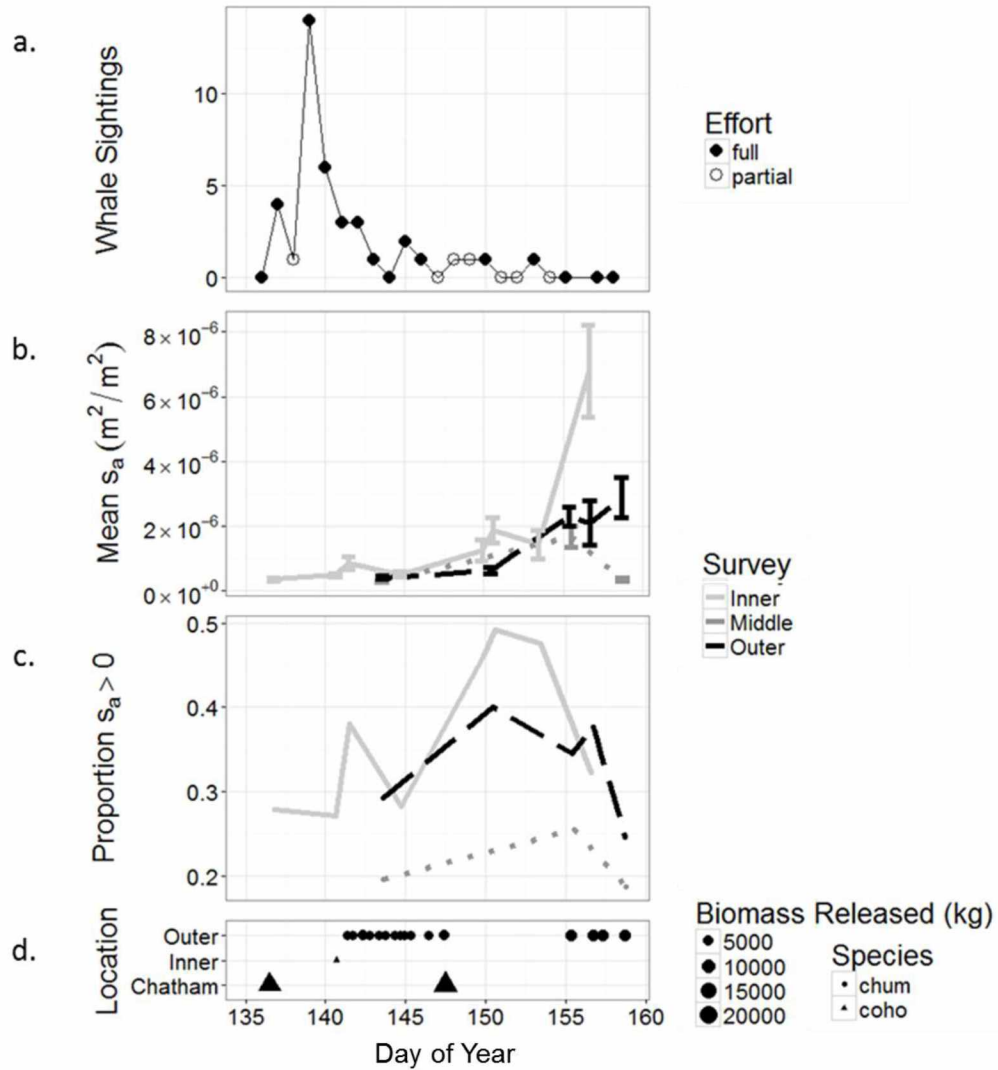


Figure 3.D-2 Timeline of (a) humpback whale sightings where filled circles are a full day of effort and open circles are partial effort; (b) mean  $s_a$  of each acoustic survey; and (c) the proportion of cells in each survey with measured acoustic area backscatter ( $s_a > 0$ ). Acoustic surveys were performed with EK 60 120 kHz transducers on an autonomous surface vessel. Dates are local AKDT. (d) This panel shows the timing, biomass, species, and location of each release.

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## General Conclusion

Humpback whales in Southeast Alaska are feeding on hatchery-released salmon in what appears to be a time of a historically high population, low population growth, and dramatic environmental change. As we enter new climatic and ecological regimes, correlative relationships from historic data are increasingly inadequate as a sole basis for ecological prediction and species management (Cuddington et al. 2013, Kroeker et al. 2017, Morley et al. 2018). This dissertation examines this novel species interaction with consequences for aquaculture and fishery management and has taken important steps toward understanding the scope, characteristics, and impacts of this interaction. It has also developed a mechanistic framework to assess the energetic consequences of humpback whale foraging, which can be applied broadly to make predictions about prey selection and to interpret foraging behaviors, including with respect to novel prey.

Humpback whale foraging at release sites is geographically widespread, but thus far involves few individual humpback whales and specialized behaviors. The findings of chapter 1 demonstrated that humpback whales forage at release sites throughout Chatham Strait, Alaska. Subsequent observations of humpback whales feeding on juvenile salmon by Douglas Island Pink and Chum Inc. (unpublished data) in Lynn Canal and by the Prince William Sound Aquaculture Association (Geoff Clark, personal communication) in southwest Prince William Sound extend the known range of this interaction. Humpback whales are most likely to be observed at release sites during or immediately following the release of salmon. They feed in shallow and exceptionally nearshore areas and frequently use bubble nets. A small number of individual humpback whales are responsible for most observations of whales feeding at release sites.

Although humpback whales feed on four different species of salmon, economic and energetic impacts were species-specific. In chapter 2, we found that humpback whales are most likely to feed on juvenile chum salmon, but that only juvenile coho salmon suffered a detectable decrease in marine survival in years with greater humpback whale predation. The lack of an effect on chum salmon and Chinook was due to low marine survival even in years when whales were not present, suggesting that these species would have been unlikely to survive to harvest in the absence of whales. Considering the frequency of whale predation on coho salmon and the strength of its relationship with marine survival, about 23% of coho salmon revenue may be lost in association with humpback whale predation in Chatham Strait.

In chapter 3, we determine that humpback whales benefit from the distribution of prey in shallow water and low energetic costs of feeding at hatcheries but must overcome diffuse distributions of prey. Feeding on chum salmon is energetically beneficial to whales, but not superlative among regional foraging opportunities. Behaviors that humpback whales use to aggregate juvenile coho salmon to higher densities, notably the creation of bubble nets, appear essential for profitable foraging as these salmon otherwise distribute themselves too diffusely for whales to recuperate the estimated costs of foraging. More generally, we determined that across a range of humpback whale prey species, prey energy density in the water column was the most important factor identified for determining the quality of a prey patch. The role of humpback whale group size while foraging and lunge rate are also important factors that remain particularly poorly understood. Individual prey selection and foraging behavior are subject to changes to the energetic profitability and availability of hatchery and alternative prey resources. The frequency and impact of this interaction in the future will depend the ability of hatchery managers and humpback whales to adapt to each other and the broader changes in their ecosystem.

It is likely that humpback whales that currently feed at release sites will continue to feed there, as long as energetically profitable prey is available. Humpback whales that feed at release sites have demonstrated strong site fidelity within and among years. Regional site fidelity in humpback whales is well-documented (Calambokidis et al. 2008). Local site fidelity on the foraging grounds has received less attention (Hendrix et al. 2012, Pierszalowski et al. 2016) but is likely an important aspect of humpback whale prey selection.

Even if energetically profitable prey remains available at hatcheries, other factors may deter new humpback whales from feeding there in the short term. Some whales may be deterred by the proximity to human activities, navigation hazards, or entanglement risk presented by docks, net pens, and anchor lines. Our results indicate that profitable feeding on some prey species requires specialized learned behaviors (Estes et al. 2003). It is also possible that many humpback whales are still unaware of this potential prey resource, however it is unlikely that this is a major factor. Volkenandt et al. (2015) found a prey-detection radius of about 8 km for humpback whales, and we observed many whales passing near or within this range of the release site but not stopping to feed. If this site was not well known but of high suitability, we would expect foraging to increase as more individuals discover it incidentally over time or through social transmission (Weinrich et al. 1992), yet this does not appear to be the case (Chenoweth et al. 2017). Nonetheless, the methods by which baleen whales locate their prey at different scales is an outstanding question of their foraging ecology (Goldbogen *et al.* 2017). Additionally, density-dependence may be at play, where the relatively small prey patches found at hatchery release sites can only support a small number of individual whales, discouraging new individuals from exploiting hatchery releases.

Despite these potential deterrents, resource limitation could push more humpback whales to feed at release sites in the longer term. Although humpback whales have enjoyed a strong population recovery in Southeast Alaska since the end of industrial whaling (Barlow et al. 2011) recent data indicate the population may be experiencing resource limitation (Neilson et al. 2017, Straley et al. 2017). This limitation could be a natural consequence of their recent population growth or due to the effects of environmental change (Lorenzo & Mantua 2016) on the availability of their prey. Currently, more southerly hatcheries appear less affected by humpback whale predation, possibly because they release their fish earlier in the year when fewer whales are in Southeast Alaska. However, resource limitation could lead to extensions of the feeding season to overlap with those earlier releases (Straley et al. 2017). In addition, if preferred resources become scarce we can expect increased predation on less profitable prey (Estes et al., 2003).

Hatcheries are continuing to adapt to whale depredation but are constrained legally by the Marine Mammal Protection Act and economically by their market. The Marine Mammal Protection Act prohibits harassment of marine mammals, which precludes many direct forms of deterrence. In addition, previous labeling efforts by marine mammal advocates have caused a market reaction against the products of fisheries that are perceived to negatively affect marine mammals (Teisl et al. 2002). Accordingly, hatcheries have focused their efforts on making their fish less susceptible or attractive to whales. One recent initiative is to change the location of release sites. This is promising for several reasons. First, crop rotation has been practiced in terrestrial systems for millennia in part to reduce the effect of pests on crops. Second, humpback whales are known for foraging site fidelity in general (Pierszalowski et al. 2016, Gabriele et al. 2017) and hatchery feeders in particular return to the same site year after year. Third, our

economic analysis found that marine survival of chum salmon is low even in years when humpback whales are not present, suggesting that non-whale predators are playing a larger role in chum salmon marine survival. Moving release sites is likely to deter less mobile predators as well. And, fourth, the Northern Southeast Regional Aquaculture Association recently established a new release site at Crawfish Inlet, south of Sitka, which had very promising returns of three-year-old chum salmon this year (personal communication, Scott Wagner NSRAA 2017).

In addition to adapting to each other, salmon, hatchery managers, and humpback whales are faced with uncertainty caused by changes in climate. The potential impacts of climate change were foreshadowed by ecosystem disruption associated with high offshore water temperatures in 2013 -2015 (Lorenzo & Mantua 2016). Freshwater and ocean conditions play a major role annually in juvenile salmon growth rates, disease during rearing, and early marine survival (Burke 2012, Kohan et al. *in press*). Large-scale climate processes including global climate change, that are expected to increase the severity of ENSO events and regime shifts in the North Pacific will have variable effects on the marine survival of different salmon species and stocks (Mantua et al. 1997, Mantua 2009, Schoen et al. 2017). The effects of climate on populations of salmon prey, predators, competitors, and other prey species for humpback whales could also have indirect effects on humpback whale predation at hatchery release sites. Humpback whales continue to demonstrate their adaptability with innovative foraging techniques (Weinrich et al. 1992, Fleming et al. 2016). For managers adaptability requires a more thorough understanding of the mechanisms of predator-prey interactions particularly where interactions are novel or fall outside the range of historic conditions.



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## Appendix A: IACUC 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

January 17, 2014

To: Jan Straley  
Principal Investigator  
From: University of Alaska Fairbanks IACUC  
Re: [157884-10] Biology of Large Whales in Alaskan Waters

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received:	January 16, 2014
Initial Approval Date:	February 19, 2008
Effective Date:	January 17, 2014
Expiration Date:	February 20, 2015

This action is included on the January 16, 2014 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 detailed in the form 005 "Reporting Concerns".*