

ARTICLE

# The Economic Impacts of Humpback Whale Depredation on Hatchery-Released Juvenile Pacific Salmon in Southeast Alaska

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## Abstract

The goal of this study was to determine whether humpback whale *Megaptera novaeangliae* depredation on hatchery-released juvenile salmon is affecting the economic productivity of hatcheries in Southeast Alaska. From 2010 to 2015, observers monitored five release sites in Chatham Strait, Alaska. Humpback whales were present at the release of 23 of 54 salmon cohorts (defined by release year, species, site, and release strategy). A linear regression model was used to determine whether humpback whale presence at a cohort release affected the proportion of that cohort that survived to harvest. The model included covariates related to management and environmental conditions. The lost fishing revenue for each cohort was determined using the model-predicted marine survival with and without humpback whales and the average commercial value of the adult salmon. Marine survival of Coho Salmon *Oncorhynchus kisutch* was significantly lower for cohorts with humpback whale depredation, resulting in an estimated US\$1 million of lost revenue per year (95% confidence interval = \$747,500–1,205,000) associated with whale depredation (23% of observed ex-vessel fishing revenue from these Coho Salmon cohorts). No significant effect was observed for depredation losses to releases of Chum Salmon *O. keta* or Chinook Salmon *O. tshawytscha*, which tended to have low marine survival even in years of no observed whale depredation, possibly due to compensatory depredation from other sources. Despite Chum Salmon having the highest rates of whale depredation, there is no evidence to suggest that preventing humpback whale depredation alone would be sufficient to increase marine survival and fishing revenue for that species, although it may be necessary in concert with other measures.

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Humpback whales *Megaptera novaeangliae* have recently been documented as depredating juvenile salmon at hatchery release sites, potentially reducing the number of fish that return and causing adverse economic consequences for the fisheries supported by those hatcheries (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.

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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.

In Southeast Alaska, salmon hatcheries are private, nonprofit organizations that supplement the number of juvenile salmon produced in wild runs, thereby increasing the number of adult salmon available for harvest by commercial trollers, seiners, and gillnetters (Heard 2003, 2012). Under state regulation (Alaska Salmon Hatchery and Enhancement Regulations 2019), salmon hatcheries and juvenile salmon release locations are sited to minimize interaction with juvenile wild salmon. Consequently, hatcheries' release sites are typically located on freshwater sources that do not have native salmon. Hatcheries spawn and rear juvenile salmon in artificial freshwater nurseries. Larval and juvenile salmon are typically held through their transition into saltwater (smoltification) and then are released in the marine environment during the spring, 6 or 18 months after hatching. Many of these juvenile salmon succumb to predators, including mammals, fishes, and seabirds, but some successfully migrate offshore and mature in the wild, eventually returning to coastal waters after one or more years at sea. Adult salmon return to their release sites, which are located away from anadromous water sources to minimize straying and interaction with wild salmon. To cover the operational costs of hatcheries, fish processors can buy permits from hatcheries to fish a third of the hatchery-released salmon in specifically designated harvest areas, as determined by the regulatory authority of the Alaska Board of Fisheries. In addition, some hatcheries receive revenue from a self-imposed tax on fishers' commercial landings (currently set at 3% in northern Southeast Alaska). Between 2008 and 2017, commercial salmon harvest in Alaska ranged from 109,000 to 280,000 fish, with hatchery-reared salmon accounting for 16–49% of the total harvest (Stopha 2018). In addition, about 1% of hatchery-reared salmon are caught in sport, personal use, or subsistence fisheries (Stopha 2018). Understanding and minimizing interactions between wild and hatchery stocks remain 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). The hatchery organizations' stakeholders are the licensed commercial fishermen that own limited-entry salmon permits for the region and directly benefit economically from hatchery production by capturing these fish as they return to the hatchery as mature adults. 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 and 971 jobs in 2008 (McDowell Group 2010).

Recent observations of humpback whales feeding near juvenile salmon release sites have coincided with declines in the marine survival of hatchery salmon. Marine survival is the proportion of all released juvenile fish that returned to the release sites as adults, excluding a small percentage that may have strayed into wild streams. Historically, Chum Salmon *Oncorhynchus keta* have been the most lucrative hatchery species in the region, accounting for 90% of the ex-vessel value of salmon harvested in Southeast Alaska (McDowell Group 2010). For the Northern Southeast Regional Aquaculture Association (NSRAA), the marine survival (total harvest) of adult Chum Salmon has averaged about 3% of the number of juveniles released (NSRAA 2016a). These hatchery-reared Chum Salmon are estimated to account for about 75% of the ex-vessel value of NSRAA-produced salmon (McDowell Group 2009). A highly variable but downward trend in marine survival has been apparent from historical Chum Salmon returns to Hidden Falls Hatchery and the adjacent Kasnyku Bay release site since the late 1980s (Figure 1). Because juvenile salmon reared at Hidden Falls but released elsewhere have had more typical marine survival rates, 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 released from NSRAA sites, and NSRAA revenues declined to \$6 million, the lowest level since 2007. This decline is particularly notable because the Hidden Falls Hatchery and the Kasnyku Bay release site had been upheld as a model hatchery program due to the consistently high marine survival (Bachen 1993). Financial losses due to low marine survival are primarily incurred by commercial fishermen, although in years of particularly low survival, the harvest may not be enough to cover the hatchery operating costs, thus threatening the viability of the nonprofit hatcheries themselves.

It is unclear whether humpback whale depredation is limiting marine survival because juvenile salmon face diverse predators and experience high mortality in their first year at sea (Parker 1968; Farley et al. 2007) and because the nature of the interaction between different sources of mortality is unknown. In the worst case, humpback whale predation could be additive or synergistic with other sources of mortality; or it could merely substitute for other predation, with little effect on overall marine survival. The primary objectives of this study were to determine whether humpback whale depredation is affecting the marine survival of hatchery-released juvenile salmon and to quantify any associated losses in revenue.

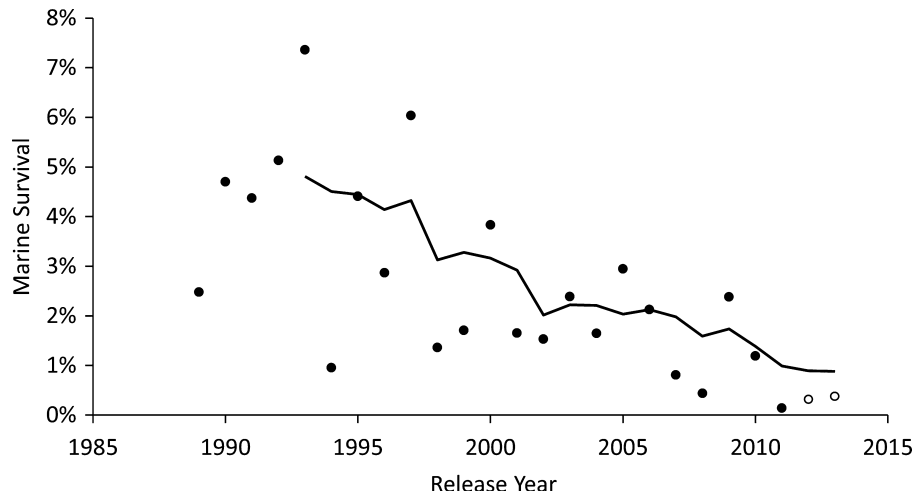


FIGURE 1. Five-year moving average of marine survival for juvenile Chum Salmon smolts raised at Hidden Falls Hatchery and released in Kasnyku Bay and Takatz Bay, Alaska. Open circles represent incomplete cohorts of Chum Salmon whose total marine survival was estimated using methods described in this paper. Data are from the Northern Southeast Regional Aquaculture Association (NSRAA 2016a). Humpback whales were first observed feeding on juvenile salmon at the point of release in 2008.

## METHODS AND MODEL SPECIFICATION

The approach was conceptually simple: partner with aquaculture associations to monitor whale presence at the release of salmon cohorts, analyze the marine survival of those cohorts for evidence of a decrease due to whale depredation, and calculate the market value of those lost fish. Multiple linear regression was used to estimate the effect of humpback whale depredation on the marine survival of juvenile salmon cohorts. Humpback whale depredation information for this analysis came from whale observations by hatchery staff at five sites across 6 years and for four species of salmon: Chum Salmon, Coho Salmon *O. kisutch*, Pink Salmon *O. gorbuscha*, and Chinook Salmon *O. tshawytscha* (Table 1). Cohorts were defined as unique based on year, site, species, and release strategy. Fifty-four salmon cohorts (Table 2) were included as observations in a linear model with marine survival as the response variable. A series of management and environmental covariates was considered for inclusion in the model.

To quantify the degree of humpback whale depredation pressure on a specific cohort, hatchery staff observed releases 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. The NSRAA operates release sites in Kasnyku Bay, Takatz Bay, and Mist Cove; the National Oceanic and Atmospheric Administration (NOAA) operates releases at Little Port Walter; and Armstrong Keta, Inc., operates releases at Port Armstrong (Figure 2). Staff at each site observed the release area for 15 min twice per day during the release

TABLE 1. Summary of the salmon species (i.e., the Species covariate) considered for analysis. Age at release can range by several months depending on environmental factors, latitude, and rearing practices. Time at sea describes the cohorts that return as typical females or alpha males as opposed to nonmarketable precocious males, which may return sooner, in relatively small numbers, and at a smaller size.

Species	Approximate age at release (months)	Time at sea (years)
0-year-old Chinook Salmon	6	2–4
1-year-old Chinook Salmon	18	2–4
Coho Salmon	18	1
Regular Chum Salmon	6	2–5
Late Chum Salmon	6.5	2–5
Pink Salmon	6	1

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 times outside of standardized observation periods). For each cohort, effort day is defined as any day when salmon from that cohort were released as well as the two days following a release. To calculate a humpback whale depredation pressure index (WDPI) for cohort  $i$ , all whales observed during these effort days were summed. 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:

TABLE 2. Summary of salmon cohorts by species and site. Years indicated are the years in which the cohorts were released (as opposed to the brood years or return years). Cohorts indicated with a “(p)” are partial cohorts: a multi-age run that had not completed at the time of analysis or for which the final year’s data were not available. Partial cohorts were included in the data set by using regression of historical data from those sites and the to-date cumulative return to predict the total marine survival.

Site	0-year-old Chinook Salmon	1-year-old Chinook Salmon	Coho Salmon	Regular Chum Salmon	Late Chum Salmon	Pink Salmon	Total cohorts by site
Kasnyku Bay		2011–2013; 2014 (p)	2010–2015	2010–2012; 2013 (p)	2012; 2013 (p)		16
Takatza Bay				2010–2012; 2013 (p)	2012; 2013 (p)		6
Mist Cove			2010–2015				6
Little Port Walter		2010–2012; 2013–2014 (p)					5
Port Armstrong	2010–2012; 2013 (p)	2010–2011; 2012–2013 (p)	2010–2014	2010–2011; 2012 (p)		2010–2014	21
Total cohorts by species	4	13	17	11	4	5	54

$$\text{WDPI}_i = \frac{\sum \text{whales observed}_i}{\text{number of effort days}_i}. \quad (1)$$

Although depredation occurring beyond the first 2 d after a release could also be important—including depredation along the shoreline and out of sight of the hatchery observers—we expected WDPI<sub>i</sub> to be a useful metric because (1) previous research has shown that when a whale is observed at a release site after salmon have been released, observations on subsequent days are more likely (Chenoweth et al. 2017); (2) predation is expected to be most efficient immediately after a release, when juvenile salmon are in highest abundance or most densely aggregated; and (3) previous analysis indicated that the probability of depredation declines with elapsed time after a release (Chenoweth et al. 2017). One unusual observation, in which 10 whales 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 to the release sites as adults, excluding a small percentage that may have strayed into wild streams. As juveniles, all hatchery-released salmon are thermally marked on the otolith, marked with an embedded coded wire tag, or both (Stopha 2018). These markings were used to determine marine survival when the salmon were (1) caught by the common-property fisheries, (2) retained for broodstock at the hatcheries, or (3) captured and sold to fish processors

to recover operational costs of the hatcheries. Aquaculture associations submit annual reports of their activities, including marine survival rates, to the Alaska Department of Fish and Game (Armstrong-Keta 2016; NSRAA 2016a; NOAA, unpublished data).

In two cases, species were subdivided for analysis to reflect distinct rearing strategies that were expected to affect marine survival. Chinook Salmon were released during their first spring (0-year-old fish) at a mean mass of 16 g (SD = 2.5) or during their second spring (1-year-old fish) at a mean mass of 43 g (SD = 20). By releasing 0-year-old Chinook Salmon, operators aimed to reduce rearing costs. Chum Salmon were subdivided into “regular” 2-g (SD = 0.4) or “late” 6-g (SD = 4) categories, with late Chum Salmon being held longer and released later in the same season. The policy of retaining Chum Salmon longer was purposefully adopted to reduce depredation by humpback whales (NSRAA 2011). Figure 1 shows only the returns of regular Chum Salmon for the purpose of continuity with data obtained before the implementation of the late Chum Salmon program.

For cohorts of Chinook Salmon and Chum Salmon that had not yet completed their return, future marine survival was projected. Juvenile Pink Salmon and Coho Salmon mature and return to hatcheries as adults after only 1 year at sea. However, Chinook Salmon can remain at sea for 2–4 years, and although most Chum Salmon adults return after 3 years, they can return after as few as 2 years or as many as 5 years at sea (Armstrong-Keta 2016; NSRAA 2016a). For 11 incomplete cohorts of Chum Salmon and Chinook Salmon, the return to date was used to predict total marine survival by establishing correlations between partial and full cohort returns based



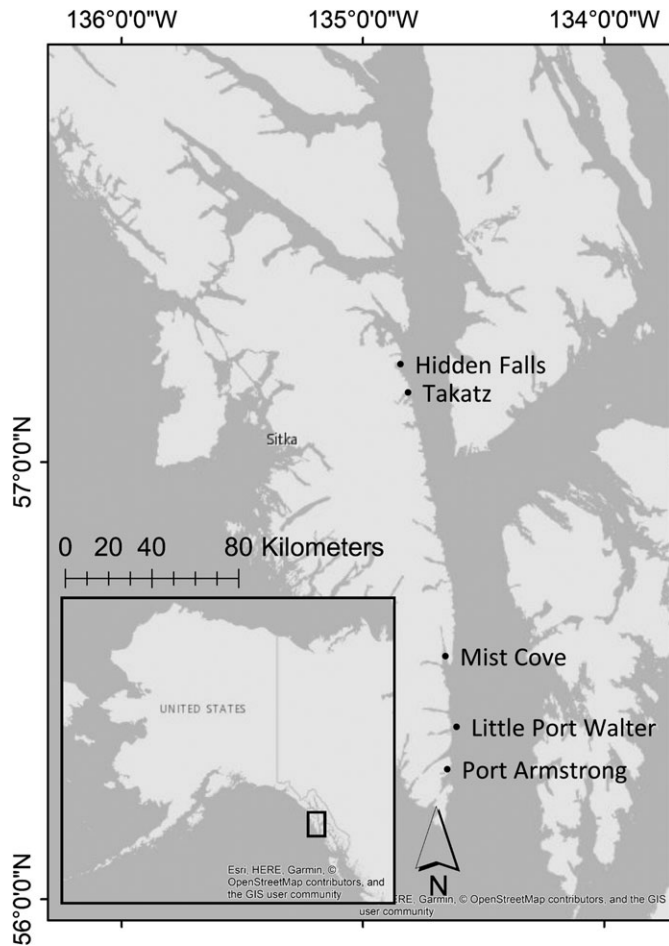


FIGURE 2. Map of the five participating juvenile salmon release sites on the eastern coast of Baranof Island in Southeast Alaska. Hidden Falls, Takatz, and Mist Cove are operated by the Northern Southeast Regional Aquaculture Association (NSRAA); Little Port Water is operated by the National Oceanic and Atmospheric Administration; and Port Armstrong is operated by Armstrong Keta, Inc.

on recent historical data that were specific to each species and release site. This is based on the method used by the NSRAA to generate internal predictions of run strength (NSRAA 2016a). Incomplete cohort marine survival rates were calculated from linear regressions with a minimum  $R^2$  value of 0.72 and a mean  $R^2$  value of 0.88. Among all species and sites, a total of 54 cohorts were included in the analysis, including the projected marine survival for 11 incomplete cohorts (Table 2).

Covariates were considered to account for the influence of environmental conditions and hatchery management decisions on marine survival. Explanatory variables under consideration included the mean individual mass at release (g/juvenile salmon), the total number of individuals released with each cohort, the release site, and the first day of release as a measure of seasonal release timing (Table 3). To account for interannual variability in

environmental conditions, it was necessary to select either year as a factor in the model or specific environmental covariates thought to be important indicators of ocean conditions that vary on an annual scale. Year, as a factor, has the advantage of reflecting differences in productivity caused by variations in a suite of latent environmental factors operating through unobserved processes, but it suffers from a lack of utility as a predictive variable. The advantage of specifying environmental characteristics is that doing so produces a model that is suitable for simulations involving those factors but requires a priori knowledge or assumptions to identify potential key variables. The environmental time series observations considered included spring sea surface temperature (SST; corresponding to the release year), summer SST (first summer at sea), winter SST (first winter at sea), and CPUE of juvenile Chum Salmon during out-migration.

Summer CPUE of juvenile Chum Salmon in Icy Strait, Alaska, was used as an index of early marine survival for all species (Orsi and Fergusson 2015) and as a proxy for environmental conditions during the early marine period, including migration into offshore waters. Chum Salmon have the largest biomass released from hatcheries in Southeast Alaska, and 64% of the total population originates at a hatchery (Orsi and Fergusson 2015). The NOAA's 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, which is thought to be the main out-migration 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 GAK1 in the Gulf of Alaska, south of Resurrection Bay (59°50.7'N, 149°28.0'W; Institute of Marine Science, University of Alaska Fairbanks; <http://www.ims.uaf.edu/gak1/>, data accessed June 2017), and were modeled as a polynomial for each year with station held constant ( $F_{45, 18} = 12.45$ , adjusted  $R^2 = 0.89$ ,  $P < 0.001$ ):

$$SST_{ijk}^{1/3} = \beta_0 + \text{Year}_j(\text{DOY}_i + \text{DOY}_i^2 + \text{DOY}_i^3) + \text{Station}_k + e_i, \quad (2)$$

where  $SST_{ijk}$  is the sea surface temperature on day  $i$  in year  $j$  at station  $k$ ;  $\text{DOY}_i$  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 temperature from March 1 to June 30 because this period corresponds to the release season. Summer SST (Sum.SST) was expressed as the mean modeled SST from June 1 to September 18, corresponding to the ocean conditions during out-migration and the first summer at sea for juvenile

TABLE 3. Candidate model variables. All management variables are specific to cohort, defined by the variables Site, Species, and Year. All environmental variables are specific to year (i.e., all cohorts released in the same year have the same values for all environmental variables).

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

<sup>a</sup>References and data sources: (1) Chenoweth et al. 2017; (2) Northern Southeast Regional Aquaculture Association (NSRAA), Armstrong Keta, Inc., and National Oceanic and Atmospheric Administration; (3) Armstrong-Keta 2016; NSRAA 2016a; (4) Institute of Marine Science, University of Alaska Fairbanks, data from oceanographic station GAK1: <http://www.ims.uaf.edu/gak1/>; and (5) Orsi and Ferguson 2015.

salmon. Winter SST (Win.SST) was characterized as the mean modeled SST from January 1 to March 31 of the year following the release year and reflects the minimum temperatures from the first winter at sea.

A preliminary analysis was used to identify the best model for determining the impact of whale depredation on marine survival. Model selection proceeded iteratively since the number of candidate covariates and relationships among them meant that not all candidate covariates could be included in a full model. For model selection, Akaike's information criterion bias-corrected for small sample sizes (AIC<sub>c</sub>) was used (Burnham et al. 2011). We used *F*-statistics and *P*-values to characterize model fit and as measures of confidence in coefficient estimates. A comparison of alternative models of particular interest is presented in Table 4. The preferred model explained marine survival for the *i*th cohort of salmon species *j* (MarSurv<sub>*ij*</sub>) as a function of the interaction of WDPI<sub>*i*</sub> and a binary variable (Coho Salmon) that indicated whether or not the species was Coho Salmon; a binary variable (MistCove) that differentiated Mist Cove from all other release sites; Species<sub>*j*</sub>; CPUE<sub>*i*</sub>; Sum.SST<sub>*i*</sub>; and Win.SST<sub>*i*</sub>. The interaction between Coho Salmon and WDPI<sub>*i*</sub> was included because the influence of WDPI<sub>*i*</sub> 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 (Box and Cox 1964) was used to identify a transformation of ¼ to ensure

normality in the residuals of the preferred model:

$$\text{MarSurv}_{ij}^{1/4} = \beta_0 + (\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species}_j + \beta_1(\text{CPUE}_i) + \beta_2(\text{Sum.SST}_i) + \beta_3(\text{Win.SST}_i) + e_i. \quad (3)$$

This model accounted for 86% ( $F_{11, 42} = 30.8$ ,  $P < 0.001$ ) of the observed variation in marine survival. Coefficient estimates, SEs, and *P*-values are reported in Table 5.

This marine survival model allowed us to determine the expected marine survival for a depredated cohort if whales had not been present—the key variable in determining lost revenue (LR). Lost revenue from these cohorts was estimated as

$$\text{LR}_{jk} = \left( \sum_{m=k+1}^{2016} \text{PropRet}_{jm} \times P_{jm} \times W_{jm} \right) \times \Delta \text{MarSurv}_{jk} \times N_{jk}, \quad (4)$$

where the lost revenue (LR<sub>*jk*</sub>) of catches from a cohort of species *j* released in year *k* equals the sum product of the proportion returning (PropRet<sub>*jm*</sub>) in each subsequent year *m* (Armstrong-Keta 2016; NSRAA 2016a; NOAA, unpublished data), the inflation-adjusted average ex-vessel price (*P*<sub>*jm*</sub>) for species *j* in return year *m*, the average weight

TABLE 4. Candidate models describing the marine survival of juvenile salmon cohorts released from Southeast Alaska salmon hatcheries. The response variable for all models is marine survival ( $\text{MarSurv}^{1/4}$ ). Model parameters are defined in Methods and in Table 3 ( $\text{Adj } R^2$  = coefficient of determination adjusted for the number of parameters;  $K$  = number of estimated parameters for each model;  $\text{AIC}_c$  = Akaike's information criterion bias-corrected for small sample size;  $\Delta\text{AIC}_c = \text{AIC}_c$  for each model minus the  $\text{AIC}_c$  for the best model). Models include the best model (model 1) and the best model plus each of the rejected covariates: Mass (model 2); Release (model 3); DOY (model 7); and Spr.SST (model 9), which replaced CPUE, as they both are proxies for spring conditions. Also included are the best model without the least significant covariate (Win.SST; model 5), a model without the predictor of interest ( $\text{WDPI}_i$ ; model 6), and a model in which Year as a factor replaced all annual-scale environmental covariates (model 4). Other models include a redefinition of Species without subdividing by release strategy (noted here as Species\*; models 2 and 8) and a null model (model 10).

Model	Parameters	Adj $R^2$	$K$	$\text{AIC}_c$	$\Delta\text{AIC}_c$
1	$(\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species} + \text{CPUE} + \text{Sum.SST} + \text{Win.SST}$	0.86	12	-155	0
2	$(\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species}^* + \text{CPUE} + \text{Sum.SST} + \text{Win.SST} + \text{Mass}$	0.85	11	-154	1
3	$(\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species} + \text{CPUE} + \text{Sum.SST} + \text{Win.SST} + \text{Release}$	0.86	13	-153	2
4	$(\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species} + \text{Year}$	0.86	14	-152	3
5	$(\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species} + \text{CPUE} + \text{Sum.SST}$	0.84	10	-151	4
6	$\text{MistCove} + \text{Species} + \text{CPUE} + \text{Sum.SST} + \text{Win.SST}$	0.83	10	-149	6
7	$(\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species} + \text{CPUE} + \text{Sum.SST} + \text{Win.SST} + \text{DOY}$	0.84	13	-149	6
8	$(\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species}^* + \text{CPUE} + \text{Sum.SST} + \text{Win.SST}$	0.82	10	-145	10
9	$(\text{WDPI}_i \times \text{Coho Salmon}) + \text{MistCove} + \text{Species} + \text{Spr.SST} + \text{Sum.SST} + \text{Win.SST}$	0.78	11	-132	23
10	(Intercept only)		1	-67	88

TABLE 5. Parameter estimates and significance values for equation (2), with marine survival ( $\text{MarSurv}^{1/4}$ ) as the response variable. Parameters are defined in Methods and in Table 3.

Parameter	Estimate	SE	$P$ -value
Intercept (0-year-old Chinook Salmon)	-0.04	0.08	0.6
Coho Salmon	0.34	0.03	<0.001
1-year-old Chinook Salmon	0.10	0.03	<0.001
Late Chum Salmon	0.13	0.03	<0.001
Pink Salmon	0.17	0.03	<0.001
Regular Chum Salmon	0.09	0.03	0.003
MistCove	0.08	0.02	0.001
CPUE	0.03	0.01	<0.001
Sum.SST	-0.03	0.005	<0.001
Win.SST	-0.02	0.01	0.01
$\text{WDPI}_i \times \text{Coho Salmon}$	-0.17	0.05	0.004
$\text{WDPI}_i$	-0.012	0.02	0.95

( $W_{jm}$ ) of returning individuals of species  $j$  in year  $m$ , the total number of salmon released from that cohort ( $N_{jk}$ ), and the total marine survival of that cohort ( $\Delta\text{MarSurv}_{jk}$ ; Armstrong-Keta 2016; NSRAA 2016a; NOAA, unpublished data). The values of  $\Delta\text{MarSurv}$  per cohort were estimated from the difference between modeled marine

survival under observed  $\text{WDPI}_i$  and modeled marine survival under a hypothetical scenario of  $\text{WDPI}_i = 0$ , with all other covariates representing observed conditions. Average ex-vessel prices per pound and adult weight ( $W$ ) 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 using a Consumer Price Index deflation factor to ensure comparability across years. The  $P_{jm}$  is treated as exogenous to the influence of whale depredation because the price of salmon is determined by an interplay of global supply and demand, in which small variations in salmon production from Southeast Alaska hatcheries play a minor role (Herrmann 1993; Asche et al. 1999; Valderrama and Anderson 2010). Where cohorts were incomplete, marine survival was the predicted value of the total return, and price and weight were calculated based on the completed return years.

## RESULTS

Salmon cohorts in this study demonstrated high variability in whale depredation pressure, with values of  $\text{WDPI}_i$  ranging from 0 to 1.5 whale observations per day. There was also a contrast in  $\text{WDPI}_i$  among different sites and different species. Cohorts of each species at every site

included one or more that had a  $WDPI_i$  of 0 and one or more that had nonzero  $WDPI_i$  ( $WDPI_i > 0$ ). However, nonzero  $WDPI_i$  was not included in the analysis for Pink Salmon. This species was only released from Port Armstrong and first experienced nonzero  $WDPI_i$  in 2015, a year for which return data were not yet available for analysis. Regular Chum Salmon experienced the highest level of humpback whale depredation pressure (Table 6).

The Coho Salmon was the only species for which estimated reductions in marine survival due to  $WDPI_i$  were statistically significant (Table 5; Figure 3). The relationship between  $WDPI_i$  and Chum Salmon or Chinook Salmon marine survival was negative but not statistically significant. All of the Pink Salmon releases in this data set had a  $WDPI_i$  of 0, so the effect of whale depredation could not be tested (Table 5; Figure 3). Coho Salmon released from Mist Cove had higher marine survival than Coho Salmon released from Kasnyku Bay and Port Armstrong, the other release sites for that species. The predictor CPUE (i.e., juvenile Chum Salmon CPUE in NOAA's Icy Strait out-migration survey) had a positive relationship with marine survival, while the marine survival declined with increasing Sum.SST and Win.SST.

Lost revenues for each cohort are shown in Figure 4. Modeled LR to hatcheries and Coho Salmon fisheries totaled \$3,890,000 (95% confidence interval = \$2,990,000–4,820,000), or approximately \$1 million per year, over the 4 years for which all cohort returns were measured or projected based on partial returns. Lost revenues were determined by comparing modeled marine survival for the observed conditions for each cohort against a hypothetical scenario in which no whale depredation was observed ( $WDPI_i = 0$ ). This LR is about 23% of the \$16,578,000 in revenue generated by Coho Salmon over this period.

In addition to summarizing the results for observed cohorts, the model was used to explore hypothetical release scenarios by crossing the range of observed values for release site, Sum.SST, and  $WDPI_i$  (Figure 5). The absolute

effect of humpback whales on numbers of returning salmon and value depended on the values of the other release conditions. Whales had the largest adverse effect on marine survival when conditions such as release site and Sum.SST were favorable for salmon marine survival (Figure 5). The model predicted that Coho Salmon marine survival under favorable conditions of Sum.SST and release site but with a hypothetical  $WDPI_i$  value of 1 would be roughly equivalent to marine survival with a  $WDPI_i$  of 0 under unfavorable site and Sum.SST conditions.

## DISCUSSION

Humpback whale depredation on hatchery releases of Coho Salmon is estimated to reduce fisheries revenues by approximately \$1 million per year in fisheries that are dependent on Coho Salmon from the Hidden Falls, Mist Cove, and Port Armstrong release sites. While humpback whales were also observed to depredate on hatchery releases of Chum Salmon and Chinook Salmon, estimates of the associated reductions in fisheries revenues were not statistically significant. Significant losses associated with humpback whale depredation are currently restricted to Coho Salmon, perhaps because they spend only 1 year at sea, have the highest marine survival, and have the greatest absolute variability in marine survival. For other species, marine survival was unexpectedly low during this period—only about 1% or less, even for cohorts with a  $WDPI$  of 0; therefore, detecting further declines due to whale depredation was unlikely.

The observed reduction in marine survival could be caused by a combination of consumptive and nonconsumptive mortality. As an example of nonconsumptive mortality, the presence of humpback whales in a release area may interfere with the foraging efficiency or energetics of juvenile salmon (Preisser et al. 2005). Moreover, due to their bulk lunge filter-feeding style of predation, humpback whales are less selective than other predators at targeting specific individuals of low fitness. Consequently,

TABLE 6. Marine survival and whale depredation pressure index ( $WDPI_i$ ) for each species of salmon at five sites (MC = Mist Cove; KB = Kasnyku Bay; PA = Port Armstrong; TB = Takatz Bay; LPW = Little Port Walter), 2010–2015.

Species	<i>n</i>	Marine survival (%; mean ± SD)	$WDPI_i$ (mean ± SD)	Sites
Coho Salmon at MC	6	7.6 ± 3.2	0.22 ± 0.25	MC
Coho Salmon at sites other than MC	11	4.8 ± 3.4	0.22 ± 0.24	KB, PA
Pink Salmon	5	1.4 ± 1.0	0.0	PA
Late Chum Salmon	4	0.7 ± 0.2	0.08 ± 0.17	KB, TB
1-year-old Chinook Salmon	13	0.5 ± 0.4	0.15 ± 0.30	KB, PA, LPW
Regular Chum Salmon	11	0.4 ± 0.5	0.50 ± 0.55	KB, TB, PA
0-year-old Chinook Salmon	4	0.1 ± 0.1	0.33 ± 0.47	PA



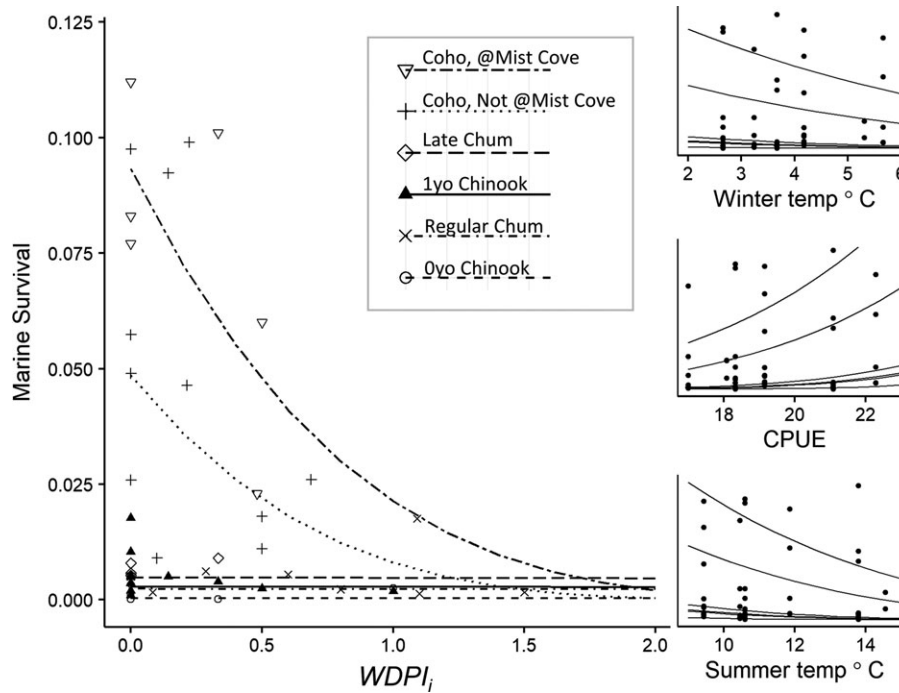


FIGURE 3. Fitted relationships between marine survival of hatchery salmon ( $y$ -axis of all subplots) and the whale depredation pressure index ( $WDPI_i$ ) by species (subdivided by release strategy) and covariates (equation 3). Coho Salmon are subdivided based on site of release (at Mist Cove or not at Mist Cove); Chum Salmon are subdivided based on the seasonal timing of their release (regular or late); and Chinook Salmon are subdivided based on their age at release (0 or 1 year old [yo]). Lines indicate fitted values for marine survival across a range of three different covariates (winter temperature [temp], CPUE, and summer temperature) when the others were 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. For ease of interpretation, Pink Salmon are not included in this figure since they were not observed to experience whale depredation.

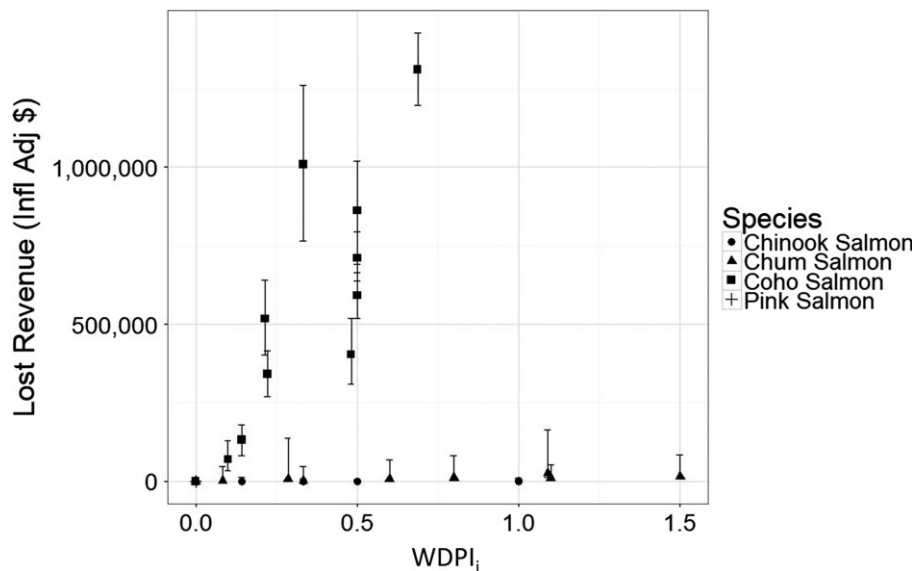


FIGURE 4. Lost revenue (inflation adjusted) at five release sites attributed to the whale depredation pressure index ( $WDPI_i$ ) by hatchery release cohort. Lost revenue is defined as the difference between the predicted value for marine survival of each cohort under observed values for the  $WDPI_i$  and the predicted value if all covariates remained the same but the  $WDPI_i$  was set to zero over the same period. Revenues are derived from marine survival 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 return year weighted by the proportion of the total return that occurred in that year (equation 4). All cohorts of Pink Salmon are located at (0,0).

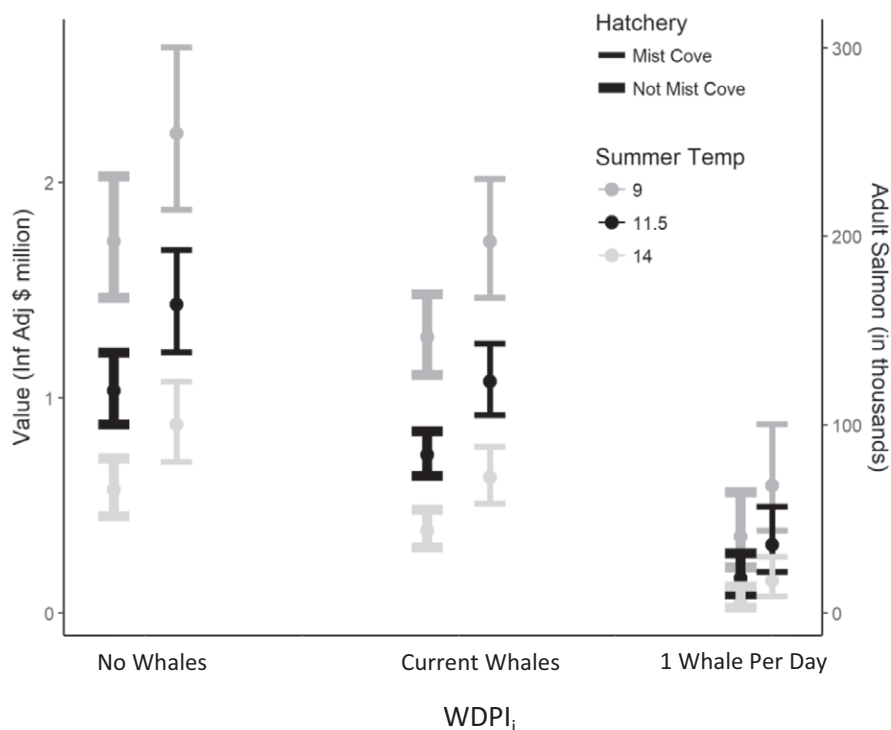


FIGURE 5. Effects of site, temperature, and whale depredation pressure index (WDPI<sub>i</sub>) on the total value (inflation adjusted) of Coho Salmon cohorts. Value of Coho Salmon returns is presented under different whale depredation scenarios, including no whales (WDPI<sub>i</sub> = 0), the mean for cohorts in the study (“current whales”), and 1 whale observed for each day (WDPI<sub>i</sub> = 1). Observation days included all release days for a cohort and the 2 d after each release. Winter temperature was set at 4.1°C, the mean for the 6-year data set. Error bars are SEs calculated from the model (equation 3) for estimated marine survival. Marine survival was converted to adult salmon numbers and value by using equation (4). 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.

humpback whales may be more likely than other predators to feed on salmon that would otherwise have had a relatively strong chance of surviving.

For Chum Salmon or Chinook Salmon cohorts, the lack of a significant reduction in marine survival associated with humpback whale predation may be a result of compensatory predation by other predators. Humpback whales are among the first in a long and diverse series of predators that hatchery salmon must negotiate, beginning at the release site, continuing along the out-migration corridor to offshore waters, and upon their return to coastal waters where they are harvested (Petersen and DeAngelis 2000). The effect of humpback whale predation on juvenile salmon appears to be greatest where conditions indicate that 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, an effect of whale depredation was detected in Coho Salmon, which typically have much higher return rates than other salmon species. Taking measures to reduce whale depredation at the time of release might be particularly effective at Mist Cove or during years of favorable environmental conditions, when nonwhale mortality is expected to be relatively low.

However, some options for mitigating depredation from whales may increase the exposure of juvenile salmon to other predators. Traditionally, hatcheries release their fish en masse to overwhelm common local predators, such as Dolly Varden *Salvelinus malma* and other piscivorous fishes, North American river otters *Lontra canadensis*, mink, harbor seals *Phoca vitulina*, and gulls. That strategy is supported by studies in freshwater, where juvenile salmon have been shown to survive better when migrating in large numbers, satiating place-based predators (Furey et al. 2016). However, 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). Ims (1990) predicted that for a generalist predator capable of prey switching, such as a humpback whale, large releases that are designed to overwhelm predators may increase total predation, an outcome that is exacerbated by the high satiation threshold for these large animals (Klumov 1963; Witteveen et al. 2006). Therefore, some sites have attempted to mitigate humpback whale depredation through a gradual release (known colloquially as a “trickle release”) that minimizes the biomass of salmon entering the release area at a single time (NSRAA 2011; Reifentstahl 2012). However,

although a trickle release strategy may reduce a humpback whale's foraging efficiency, it increases the risk of predation by other predators.

The results of this study indicate that mitigating humpback whale depredation at release sites would not be sufficient to increase marine survival of Chum Salmon and Chinook Salmon, although it may be necessary in concert with other measures. It is possible that humpback whales are consuming a large number of juvenile 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 due to the influence of adverse environmental conditions. Whale depredation of juvenile Chum Salmon remains a concern, as whales were most commonly sighted after releases of juvenile Chum Salmon cohorts. The concern is exacerbated by the fact that Chum Salmon have historically generated the most revenue for the private, nonprofit salmon hatcheries (McDowell Group 2010).

The relatively high marine survival and less-frequent observations of whale depredation for late-release Chum Salmon compared to the regular Chum Salmon are encouraging (NSRAA 2015). Moreover, these gains in marine survival for late-release Chum Salmon 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 (Chip Blair, NSRAA, personal communication). However, it is unclear whether the improved marine survival of late Chum Salmon is due to a reduction in humpback whale depredation or because 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, the projections of returns for incomplete cohorts in this study were based on the age composition of regular Chum Salmon. Since early data indicate that late Chum Salmon may tend to return at a younger age, these projections may overestimate the ultimate marine survival of the partial cohorts (NSRAA 2015).

The opportunity to feed on hatchery-released juvenile salmon may increase the populations of nonwhale predators near the release sites over time, as sometimes occurs when other types of anthropogenically sourced food resources enter the environment (Boarman et al. 2006; Oro et al. 2013; Heath et al. 2014). However, they are probably not significantly impacting the humpback whale population, due to the low number of whales that feed there (Chenoweth et al. 2017). Salmon reared at Hidden Falls but 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 the poor returns at Kasnyku Bay and Takatz Bay. To avoid these local conditions, the NSRAA is expanding production to more facilities and transporting salmon to other sites prior to release—a strategy that is analogous to pest control through crop rotation (NSRAA 2016b, 2017). Returns of 3- and 4-year-old Chum Salmon to one of these sites in July 2018 exceeded expectations, indicating anomalously strong marine survival (a minimum of 5.1% marine survival for the 2014 release cohort after only 3- and 4-year-old fish had returned; and a minimum of 9.1% marine survival for the 2015 release cohort after only 3-year-old fish had returned;

TABLE 7. Hatchery production costs (US\$) by salmon species and site for cohorts released before and after the 2008 observation of targeted humpback whale predation. Costs are based on unpublished data from the Northern Southeast Regional Aquaculture Association (available online at: [https://www.nsr\\_aa.org/\\_pdfs/2018\\_Spring\\_Board\\_Mtg/NSRAA\\_Board\\_Book\\_Spring2018.pdf](https://www.nsr_aa.org/_pdfs/2018_Spring_Board_Mtg/NSRAA_Board_Book_Spring2018.pdf)). Cost per smolt was calculated through the 2014 release season for Chum Salmon and through the 2015 release season for Coho Salmon. Smolt and adult costs were determined by dividing the total hatchery budget by the total production in terms of biomass and then multiplying by the average weight of an individual of each species.

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

NSRAA, unpublished data [summarized at: <https://www.nsraa.org/?p=3849>].

Avoiding whale depredation appears to be increasing rearing costs. In the 8 years (2008–2015) since humpback whales were first reported as 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 (NSRAA, unpublished data [available online at: [https://www.nsraa.org/\\_pdfs/2018\\_Spring\\_Board\\_Mtg/NSRAA\\_Board\\_Book\\_Spring2018.pdf](https://www.nsraa.org/_pdfs/2018_Spring_Board_Mtg/NSRAA_Board_Book_Spring2018.pdf)]; Table 7). While substantial increases in the cost per adult could be partially attributed to low marine survival, there were also smaller increases in the cost per smolt released, indicating an increase in rearing costs. The Mist Cove Coho Salmon program is the only one for which mean costs of production were less than the mean market value of the catch for cohorts released after 2007, although this was the case for some individual cohorts of each program.

This study also points to environmental conditions affecting the marine survival of juvenile salmon that are outside of the control of managers. Juvenile salmon CPUE in Icy Strait, an important out-migration 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 being 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 (1) 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 (2) 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, that could affect salmon cohort strength in the years to come (Shanley et al. 2015).

Whale depredation on released juvenile salmon is not addressed in U.S. Department of Agriculture (USDA) programs intended to cover disasters and depredations that affect agriculture, including aquaculture (Agricultural Act of 2014). Through the USDA Livestock Indemnity Program, livestock ranchers can be compensated up to 75% of the cost of animals lost due to depredation by wild predators, but this benefit does not extend to aquaculture losses. Fishing and aquaculture losses can be covered under the USDA 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 USDA 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 was 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; Rojas-Bracho and Reeves 2013; Roman et al. 2013). In some areas where marine mammal populations are growing, they do not appear to be limiting fishery productivity (Corkeron 2009), but hatchery release sites are among the places where they do pose quantifiable management challenges (Larson et al. 2013; Peterson et al. 2013, 2014).

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