

Exxon Valdez Oil Spill
Long-Term Monitoring Program (Gulf Watch Alaska) Final Report

Long-term Monitoring of Humpback Whale Predation on Pacific Herring in
Prince William Sound

Exxon Valdez Oil Spill Trustee Council Project 21120114-O
Final Report

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Study History: In 2005, a group of scientific investigators collaborated to integrate information about the Pacific herring (*Clupea pallasii*) population in Prince William Sound and identify factors contributing to their lack of recovery (*Exxon Valdez* Oil Spill Trustee Council project 050794); top-down control was identified as likely having greater influence on Prince William Sound herring than other herring stocks in Alaska. The group stated “that lingering oil exposure from the *Exxon Valdez* oil spill does not play a role in limiting the recovery of herring.” The group further noted that “of the two top-down forces, disease and predation, recent evidence suggests that disease continues to episodically affect the population, but there were insufficient data to assess the role of predators in limiting recovery”. They concluded that herring population assessment modeling requires better quantification of the significance of predation. For the winters of 2007-2008 and 2008-2009, project 100804 evaluated humpback whale (*Megaptera novaeangliae*) predation rates on herring in Prince William Sound and estimated whales consume between 27%–77% and 21%–63%, respectively, of the pre-spawning adult herring biomass. From 2012-2014, mark–recapture models estimated a humpback whale population of 461 individuals (95% Confidence Interval 402–547) utilizing Prince William Sound. In 2012-2014, increased whale predation of euphausiids (*Thysanoessa* sp. and *Euphausia pacifica*) may have buffered herring populations from whale predation. Projects 10100804 and 16120114-N yielded several publications relating to interactions between cetaceans and herring (Ballachey et al. 2014, Boswell et al. 2016, Moran et al. 2018a, Moran et al. 2018b, Straley et al. 2018, Arimitsu et al. 2021, Suryan et al. 2021). This study continues the assessment of humpback whale predation on Pacific herring in Prince William Sound.

Abstract: Humpback whale (*Megaptera novaeangliae*) numbers have failed to recover in Prince William Sound, Alaska following a steep decline during the 2014-2016 northeast Pacific marine heatwave. Humpback whales in Prince William Sound feed primarily on Pacific herring (*Clupea pallasii*), especially when herring aggregate in large shoals during the spring, fall, and winter. Herring and whales both declined following the Pacific marine heatwave (2014-2016). However, in 2020 and 2021 there was some recovery in the herring population, but no corresponding increase in humpback whale numbers. Prior to the Pacific marine heatwave, encounter rates on standardized fall surveys (whales seen/nautical mile traveled) averaged 0.22 ± 0.13 standard deviation. In the years following the Pacific marine heatwave (2017-2021), fall encounter rates dropped ten-fold to an average of 0.03 ± 0.02 standard deviation. Whale abundance estimates from mark-recapture models paralleled the declines seen in the encounter rates, falling from 264 ± 22 in 2014 to an estimated 108 ± 28 standard error whales in 2021. We

estimated whales consumed between 3% and 13% of the annual spawning herring biomass in 2021. The decline in the number of whales following the Pacific marine heatwave, either through mortality or emigration, apparently has removed some of the predation pressure on herring, potentially aiding the modest recovery of herring in Prince William Sound.

Key words: Abundance, Alaska, *Clupea pallasii*, humpback whales, mark-recapture, *Megaptera novaeangliae*, Pacific herring, predation, Prince William Sound.

Project Data: Data collected for this project included the following:

- Photographs (jpg format) of humpback whale flukes, biopsies environment, prey, and sampling effort associated with fluke photographs. Custodian - Janice M. Straley University of Alaska Southeast, 1332 Seward Ave, Sitka, Alaska 99835; work phone: (907) 747-7779.
- Lengths, weights, and chemical analysis of herring and other prey species were also collected. Herring data are stored in an Access database. Custodian - Johanna J. Page, Auke Bay Laboratories, National Marine Fisheries Service, 17109 Point Lena Road, Juneau, AK 99801; work phone: (907) 789-6612, fax: (907) 789-6094.
- CTD and porpoise data. Custodian – John R. Moran, Auke Bay Laboratories, National Marine Fisheries Service, 17109 Point Lena Road, Juneau, AK 99801; work phone: (907) 789-6014, fax: (907) 789-6094.

These data are archived by the Gulf Watch Alaska's *Exxon Valdez* Oil Spill Trustee Council. Data is publicly available at: <http://portal.aos.org/gulf-of-alaska.php#metadata/54adceab-74cb-4419-b02c-bacb6d2acb8b/project/files>.

There are no limitations on the use of the data, however, it is requested that the authors be cited for any subsequent publications that reference this dataset. Data users should pay careful attention to the contents of the metadata file associated with these data to evaluate data set limitations or intended use.

The data custodian is Carol Janzen, Director of Operations and Development, Alaska Ocean Observing System, 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703.
janzen@aos.org.

Data are archived by Axiom Data Science, a Tetra Tech Company, 1016 W. 6th Ave., Anchorage, AK 99501.

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Long-term Monitoring of Humpback Whale Predation on Pacific Herring in Prince William Sound

EXECUTIVE SUMMARY

In this report we describe the relationship between humpback whales (*Megaptera novaeangliae*) and Pacific herring (*Clupea pallasii*) in Prince William Sound (PWS) from 2017-2021. Nine surveys covering 3,672 nautical miles were completed in collaboration with the Integrated Predator-Prey Survey team (Humpback Whales Project 21120114-O, Marine Birds Project 21120114-E, and Forage Fish Project 21120114-C). However, when warranted, we include data from our previous surveys. This project continues the long-term monitoring of humpback whale predation on Pacific herring which began with data from Restoration project 100804, collected during the fall/winter months of 2007-2008 and 2008-2009 and continued with project 16120114-N from 2011-2015 as well as opportunistic observations made by other researchers. The *Exxon Valdez* Oil Spill Trustee Council-funded Prince William Sound Herring Synthesis (Restoration project 050794) associated the failed recovery of PWS herring with top-down effects such as predation and disease. Evidence of disease as a significant factor is episodic, suggesting that there is a potential for population recovery. In contrast, predation would be continuous, if not increasing, as humpback whale populations in the North Pacific, including PWS, recover post-whaling. However, following the Pacific marine heatwave (PMH) in 2014-2016, whale and herring numbers declined dramatically in PWS. As of 2021, there is no sign of recovery for whales. In contrast, herring populations are showing signs of recovery, suggesting that whale predation post-heatwave is less of an issue in limiting herring recovery in PWS.

The typical pattern of whale movement into PWS begins in early fall as herring migrate through Montague Strait. Whale numbers increase during the fall and early winter as they accompany herring to overwintering areas in bays and fjords. In mid to late winter, whale numbers drop off dramatically with the annual migration to the Hawaiian breeding grounds. In the spring whales return to PWS to target dense aggregations of pre-spawning herring. After spawning, herring and whales disperse, resulting in lower whale numbers during the summer months. In December of 2014 there was an exception to this pattern, whales and herring were largely absent at their traditional overwintering grounds. During the following spawning event (April 2015), no large shoals of herring were seen and whales were feeding on small, fast moving, schools of herring. This pattern continued through 2021. Using encounter rates (number of whales seen/nautical miles traveled), we did not detect a significant inter-annual increase or decrease in the number of individual whales encountered within PWS from September 2007 to April 2015. However, following the PMH, 2017–2021, encounter rates within PWS during fall surveys dropped from a pre-PMH average of 0.22 ± 0.13 SD to 0.03 ± 0.02 SD post-PMH. This decline may be linked to changes in prey associated with above average water temperature in the Gulf of Alaska. Mark-recapture models showed similar declines in humpback whale abundance.

Their high energy density, large biomass, and predictable migration patterns make adult herring the most important forage species for humpback whales in PWS. Visual observations, prey sampling, and stable isotope analysis were in agreement; humpback whales foraging within PWS are primarily focus on herring, more so than humpback whales in the Gulf of Alaska. As a result, the trophic level of humpback whales sampled in PWS is higher than humpback whales in the Gulf of Alaska. As herring populations declined following the PMH, we expected a corresponding decline in the number of whales using PWS. However, the recent increase in herring numbers is not reflected in whale abundance.

PWS whale abundance declined following the PMH. Prior to the PMH, there was an increasing trend in humpback whale abundance in PWS that paralleled the trend seen across the North Pacific. For this reporting period (2017-2021), we estimate the percentage of the spawning biomass consumed by whales for a 30-day period in the spring and 90-day period in the fall when predation is most intense. Spring consumption estimates ranged from a low of 1% - 4% in 2021 to a high of 10% - 34% in 2017. During the fall months we estimated a low of 2% - 9% in 2021 to a high of 7% - 28% in 2017. It should be noted that humpback whales also feed on juvenile herring which are not included in the Bayesian age structured assessment estimates, thus these results may be biased high depending on the proportion of juvenile herring consumed.

Humpback whale predation on herring is supported by stable isotope analyses and field observation, indicating PWS whales are primarily piscivores. In addition, humpback whales exhibit a high degree of fidelity to their foraging grounds. If the number of whales foraging in PWS is decreasing while the herring populations are increasing, and whales preferentially forage on herring, then a perturbation to whale populations (i.e., the PMH) may have released some of the predation pressure on herring. The failure of humpback whale recovery in PWS after the PMH may have shifted the ecosystem dynamics to favor herring recovery, while leaving unanswered questions as to why whale numbers remain depressed.

Our monitoring efforts have provided information to the National Marine Fisheries Service regarding reclassification of humpback whales under the Endangered Species Act; Designating Critical Habitat for the Central America, Mexico, and Western North Pacific Distinct Population Segments of Humpback Whales; Recovery Status Review for the Central America, Mexico, and Western North Pacific Distinct Population Segments of Humpback Whales (*Megaptera novaeangliae*); Post-Delisting Monitoring of Nine Distinct Population Segments of Humpback Whales and Notice of Intent To Prepare a Recovery Plan for the Central America, Mexico, and Western North Pacific Distinct Population Segments of Humpback Whales; Biologically Important Areas II for Cetaceans in US Waters – Gulf of Alaska Region; Ecosystems Considerations Chapter for the North Pacific Fishery Management Councils Stock Assessment Reports, and numerous consultations for estimating “takes” under the Marine Mammal Protection Act.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are important marine predators that have the potential to control the productivity of forage populations. Growing humpback whale populations increase this potential. As of 2011, the humpback whale population in the North Pacific Ocean was growing at about 5% per year and was estimated to be in excess of 20,000 individuals (Witteveen 2008), which prompted concern that whales may be competing for fishery production directly by consuming commercially valuable species or indirectly by consuming prey of harvested species (Gerber et al. 2009, Clapham et al. 2007, Morishita 2006, Pearson et al. 2012). In the Gulf of Alaska, humpback whales prey on Pacific herring (*Clupea pallasii*), capelin (*Mallotus catervarius*), eulachon (*Thaleichthys pacificus*), juvenile walleye pollock (*Gadus chalcogrammus*), and Pacific sand lance (*Ammodytes personatus*) (Witteveen 2008) in addition to euphausiids. Forage fish species made up one third of humpback whale diets near Kodiak Island, Alaska (Witteveen 2008) and isotopic analysis of humpback whale tissues indicates whales selectively consume these forage fish. These same isotopic data indicate that some whale subunits selectively consume forage fish to an even greater extent than those near Kodiak Island (Witteveen et al. 2006). Pacific herring are commercially exploited in Alaskan waters with an ex-vessel value of approximately \$4.4 – \$9.3 million annually for the years 2017–2021 (ADF&G 2022), most of which supports the economies of small coastal communities. Humpback whales prey upon many of these harvested herring populations. Their large size, relatively high metabolic rates and increased population have warranted concern that humpback whales could be removing a significant amount of biomass from these locally harvested fish populations.

The degree of top-down control that humpback whales exert on local forage fish populations is likely to vary across their range. Humpback whales demonstrate fidelity to foraging areas (Baker et al. 2013) and show individual preferences for a particular prey type. By returning each year and focusing their foraging in specific locations whales could exert top-down control on some local prey populations. However, the extent of control depends on the size of the prey population (Bax 1988). Impacts of humpback whale foraging on local populations would be particularly acute when humpback whales exploit forage fish that congregate in predictable locations, as is the case for overwintering herring (Gende and Sigler 2006, Sigler and Csepp 2007, Sigler et al. 2017). Humpback whales have been observed foraging on large, dense, overwintering shoals of herring in southeastern Alaska and PWS (Boswell et al. 2016, Straley et al. 2018). The relationship between whales and their prey is further complicated by several years of anomalously warm water (Di Lorenzo and Mantua 2016) that may be adding additional stress to the North Pacific ecosystem.

In addition to estimating abundance, seasonal and inter-annual trend and diet, we continue to address the significance of whale predation on herring by relating the potential herring biomass removed by whales in Prince William Sound (PWS) to estimates of herring abundance. To

estimate the herring biomass removed, we combined abundance estimates and observed diets with published data on whale size and metabolic demands. We used a bootstrap approach to vary parameter values for the models to provide low- and high-end estimates that bracketed the range of all potential population estimates.

OBJECTIVES

1. Estimate trends in humpback whale abundance, diet, and distribution.
2. Evaluate prey quality and trophic position through analysis (using bomb calorimetry and stable isotopes).
3. Estimate the impact of humpback whale predation on herring.

METHODS

Study Area

We monitored humpback whale abundance and attendance patterns within PWS (60° 35' N, 147° 10' W), an area of relatively protected waters in the northern Gulf of Alaska, characterized by complex coastlines of glacial fjords and islands. Effort exerted toward identifying whales in the field was quantified as the number of hours spent searching and the distance covered over water while searching. Depending on weather, surveys were conducted in a clockwise or counterclockwise circuit around PWS. Collaboration with other *Exxon Valdez* Oil Spill Trustee Council-funded projects, and traditional local knowledge were employed to ensure aggregations of whales were not overlooked during our surveys.

Estimating trends in humpback whale abundance, diet, and distribution (Objective 1)

Abundance trends

Whale attendance records were used to estimate whale abundance by cataloging individuals present and through mark-recapture analysis. We used the unique marking patterns on whale flukes to identify individual whales and maintained photographic records for each individual (Katona et al. 1979). Table 1 summarizes our sampling effort for each survey during this reporting period.

We used Nikon D-700, D-800, and D-850 cameras with 80-200 mm or 300 mm lenses to capture digital images of the ventral side of humpback whale flukes and identify individuals (Katona et al. 1979). For the mark-recapture analysis, all photographs were ranked as good, fair, poor, and insufficient quality (Straley et al. 2009). Photographs deemed poor or of insufficient quality were excluded from the mark-recapture analysis to avoid potential bias from matching errors. Further, photographs of humpback whale calves also were excluded because the sighting probability for a

calf co-occurs with their mothers and therefore is not independent and because the resighting probability later drops as calf flukes tend to change more than adult flukes.

The R Rcapture (Rivest et al. 2022) package and Jolly-Seber-Cormack Estimator allow us to estimate humpback whale survival, emigration, and abundance within PWS. The goal is to model the encounter histories for the humpback whales as a function of year (resighting probability in a given year) and account for individual heterogeneity in resighting effect due to either poor fluke quality, individual behavior, and survey effort. Sighting histories from our previously funded efforts in PWS were included in this analysis. In addition, we conducted a closed population estimate based on the Chapmanized Petersen estimator (Chapman and Junge 1956) to contrast these estimates with the population estimate under the assumption of no migration between the years. This method has been used in the previous studies and repeating it here allowed us to assess the open population assumption violations if the two estimates were to vary drastically.

Table 1. A summary of humpback whale survey effort in Prince William Sound, Alaska for this reporting period (2017-2021).

Survey	Season	Effort (days)	Whale Photo ID
September 2017	Fall	8	8
December 2017	Winter	4	7
March 2018	Early spring	6	16
September 2018	Fall	9	14
April 2019	Spring	5	4
September 2019	Fall	8	9
September 2020	Fall	6	11
April 2021	Spring	6	6
September 2021	Fall	9	8

Humpback whale diet

A combination of techniques was used to identify prey when whales were located, including direct observations of prey being consumed, collection of remains after feeding, and visual interpretation of the prey fields observed on a dual 50/200kHz frequency echo sounder. Prey distinctly visible on the 50kHz frequency were presumed to be fish. Prey visible only on the 200kHz frequency were presumed to be smaller and categorized as zooplankton. Prey identity was confirmed by collections using herring jigs, zooplankton tows, cast nets and skim nets (used to clean swimming pools). Samples included fish, scales, and zooplankton at and below the water surface near feeding whales. Prey identification was recorded as certain, probable, or undetermined. Only cases where the identification was certain or probable were used to assign specific prey.

We combined prey observations from the post Pacific marine heatwave (PMH) period (2017-2021) due to small sample size, which was the result of low whale numbers during those years. Spring and fall were treated separately.

Distribution

Location, date, time of day, group size, demographics and environmental data were recorded for all cetaceans encountered. These data were plotted using ArcGIS to describe the seasonal distribution of humpback whales within PWS.

Evaluate prey quality and trophic position through chemical analysis (using bomb calorimetry and stable isotopes) (Objective 2)

Biopsies of humpback whale skin and whole prey species were collected for bulk stable carbon and nitrogen isotopic analysis to independently estimate whale diets based on trophic level. In addition, direct observation of diets provides only a “point-in-time” estimate and does not provide dietary information on periods when whales are not being observed. Stable isotope analysis provides a time-integrated measure of whale diet. In addition, trophic position is estimable from stable isotope analysis. For example, if whales in PWS consume large amounts of herring they should occupy a higher trophic position than herring (i.e., higher $\delta^{15}\text{N}$ values). Biopsies were collected using a crossbow bolt with a coring tip. Samples were recovered immediately, labeled, and frozen. Prey samples were collected by jigging, trawls and cast nets. At the end of the survey the biopsy and prey samples were transported to the National Oceanic and Atmospheric Administration (NOAA) Auke Bay Laboratories in Juneau, Alaska and stored at -80°C until they are processed. Isotopic analysis was conducted by using a Thermo Delta V gas chromatograph/isotope ratio mass spectrometer. Pilot analyses showed that lipid content in tissues influenced $\delta^{13}\text{C}$ values; therefore, whale and prey tissues were lipid-extracted prior to quantification of stable isotope ratios. Stable isotope values (expressed in δ notation) were generated for samples using the methods described in Seymour et al. (2014). The isotope ratio mass spectrometer is calibrated using certified standards from the International Atomic Energy Agency and the US Geological Survey; these quality control standards were interspersed throughout the analytical run. If the quality assurance standard results differed from certified values by more than the known standard deviation of the reference material, the sample was re-analyzed until results of quality assurance standards were within the expected tolerances.

We measured the energy content of humpback whale prey from each survey to evaluate changes in prey quality over time. Energy content was measured using calorimetric methods as outlined by Siddon et al. (2013). Samples of prey were weighed and dried, and the homogenized tissue was pressed into pellets. The pellets were combusted in a Parr Instrument 6725 Semi-micro Bomb Calorimeter to measure the energy released. Quality assurance procedures include the use of duplicate samples to evaluate precision, reference materials to evaluate accuracy and blanks (benzoic acid) to evaluate cleanliness. Pre-determined limits for variation observed in quality

assurance samples were set, where precision estimates from duplicate tissue and reference samples must not vary by more 15% coefficient of variation (CV).

Estimating the impact of humpback whale predation on herring (Objective 3)

The large size of humpback whales prevents direct measurement of ingestion rates; therefore, we utilized multiple sources of published values for estimated daily consumptions (Reilly et al. 2004, Witteveen et al. 2006, Roman and McCarthy 2010) and applied a parametric bootstrap (Tibshirani and Efron 1993) approach to estimate the expected median and range of herring consumption by whales. The model was run separately for spring and fall due to difference in diet and abundance. The other parameters were drawn from distributions of diet, seasonal abundance, and daily consumption rates. To account for uncertainty in whale abundance estimates, at each bootstrap iteration, the number of whales was drawn from a Poisson distribution with shape parameter (λ) being the estimated whale abundance in a given year/season (Table 2). The proportion of herring in the diet for each year was used for the low-end estimates. Because of uncertainty in distinguishing herring from other fish, the high-end estimates treated unidentified fish as herring. Therefore, the total seasonal consumption of herring by year in season s and year y is denoted by $C_{s,y}$ and the median and 95% CI are drawn from 1,000 bootstrap iterations calculated as follows:

$$\hat{C}_{s,y}^{(b)} = N_{s,y}^{(b)} \pi_{s,y}^{(b)} F^{(b)} D_s$$

$\hat{C}_{s,y}^{(b)}$ is the b^{th} bootstrap iteration of the estimated total seasonal consumption of herring by whales in season s and year y .

$N_{s,y}^{(b)} \sim \text{Poisson}(\hat{\lambda}_{s,y})$ is the whale abundance drawn from a Poisson distribution, where $\hat{\lambda}_{s,y}$ is the total estimated whale abundance from the mark-recapture Jolly-Seber population estimates in season s and year y .

$\pi_{s,y}^{(b)} \sim \text{Uniform}[Herr_{min,s,y}, Herr_{max,s,y}]$ is the observed proportion of herring consumed by whales in year y and season s , where $Herr_{max}$ includes unidentified forage fish. However, in the years lacking these observations, the bootstrapping procedure included random year's observation ($Herr_{min}, Herr_{max}$) at each iteration. These observations were only available in years: 2007-2008, 2011-2014, and 2017-2021 in the fall season; and 2013-2021 in the spring season. Therefore, in the years where these observations were not available, we selected at random $Herr_{min,s}, Herr_{max,s}$ values from the observed years in the respective seasons.

$F^{(b)} \sim \text{Uniform}(\hat{F}_{min}, \hat{F}_{max})$ is the minimum and maximum estimated daily food consumption requirements of an average whale based on published values.

$D_s \in [30, 90]$ is the number of days whale feed on herring in the spring and fall respectively. We used 30 and 90 days of feeding duration for spring and fall respectively, to reflect the minimum

number of observed feeding days. Therefore, the total herring biomass removed by whales is biased low. We did this to ensure that our estimates reflected a known directional bias since we did not know the expected variation in the seasonal consumption duration.

The bootstrap procedure was carried out for 1,000 replications and the respective quantiles (2.5%, 50%, and 97.5%) calculated.

Table 2. Seasonal break down for mark-recapture estimates, foraging days for the consumption model and whale and herring behavior in Prince William Sound, Alaska.

Season	Mark-recap. period	Characteristics of season
Spring	Feb–Jun	Return from breeding grounds, herring spawning.
Summer	Jul –Aug	Whale numbers drop in PWS as herring disperse.
Fall	Sep–Jan	Whales return to PWS with migrating herring.

We estimated the potential biomass removed for each year using different modeling scenarios because of the uncertainty in daily metabolic needs diet composition, and the numbers of whale present. The different scenarios represent the range of plausible abundance estimates for whales within PWS. Dividing the total biomass consumed under a given scenario by seasonal estimates of herring abundance from a Bayesian age structured assessment (BASA) model gives a measure of the intensity of humpback whale predation (Joshua Zahner, pers. comm., School of Aquatic and Fisheries Sciences University of Washington).

Whale recapture rates were extremely low following the PMH and consequently abundance estimates were highly variable. The removal of herring by whales was taken from the median spawning biomass estimate from the BASA model. The proportion of herring in the diet for each year was used for the low-end estimates. Because of uncertainty in distinguishing herring from other fish, the high-end estimates treated unidentified fish as herring. Daily consumption rates for humpback whales were taken from the literature (Reilly et al. 2004, Witteveen et al. 2006, Roman and McCarthy 2010).

RESULTS

Estimating trends in humpback whale abundance, diet, and distribution (Objective 1)

Abundance trends

Humpback whale numbers have failed to rebound in PWS following a decline associated with the 2014-2016 PMH in the Gulf of Alaska. Encounter rates for humpback whales during the fall survey were lower than the preceding years (Table 3). The reduction of humpback whales is possibly related to a decline in the biomass of herring in PWS or lingering population effects from the PMH.

By using the unique markings on the flukes from our surveys and opportunistically collected photographs, we identified 403 individual whales that used the waters of PWS from November of 2006 through Sept of 2021. Because it is unlikely that we photographed all of the whales within PWS, this number should be considered a minimum estimate of abundance for the time period. The total number of whales that have ever inhabited PWS during this time period as estimated by the Jolly-Seber-Cormack mark-recapture model is 428, excluding calves. Annual estimates of whale abundance in PWS from both the Chapmanized Petersen (closed) and Jolly-Seber-Cormack (open) estimators are summarized in Table 4.

Table 3. Encounter rates of humpback whales in Prince William Sound during fall surveys. Gulf Watch Alaska sampling began in 2012, no surveys were conducted in 2015-16, but resumed in 2017 and will continue annually as funding allows.

Month/year	Counts of whales	Nautical miles (NM) surveyed	Encounter rate Whales/NM
Sep 2008	71	412	0.17
Oct 2011	62	441	0.14
Sep 2012	81	444	0.18
Sep 2013	113	355	0.32
Sep 2014	181	427	0.42
Sep 2017	13	543	0.02
Sep 2018	23	541	0.04
Sep 2019	32	573	0.06
Sep 2020	17	337	0.05
Sep 2021	23	530	0.04

Annual humpback whale abundance estimates and standard errors derived from Chapmanized Petersen (closed) and Jolly-Seber-Cormack (open) estimators for Prince William Sound. Calves were excluded.

Table 4. Annual humpback whale abundance estimates and standard errors derived from Chapmanized Petersen (closed) and Jolly-Seber-Cormack (open) estimators for Prince William Sound. Calves were excluded.

Year	Closed pop. estimator		Open pop. estimator	
	Abundance	SE	Abundance	SE
2007	146	115	135	11
2008	230	175	200	13
2011	213	204	170	15
2012	268	1227	230	17
2013	223	493	178	15
2014	253	877	264	22
2015	205	1324	160	41
2017	155	3432	104	21
2018	81	620	103	29
2019	61	261	108	28
2020	43	158	108	28
2021	42	231	108	28

Humpback whale diet

Humpback whales in PWS continue to primarily feed on Pacific herring (Fig. 1). Whales foraging during the spring from 2018-2021, focused on spawning herring, 76% of the time. We were unable to determine what whales were feeding on for 24% of our observations. Fall foraging observations for 2017-2021 were more diverse, but more uncertain. Herring were the most observed prey type (32%), followed by euphausiids (13%), and unidentified forage fish (2%). For 52% of foraging whales, we were unable to identify the prey type. Fig. 2 illustrates these results and compares them to previous years.

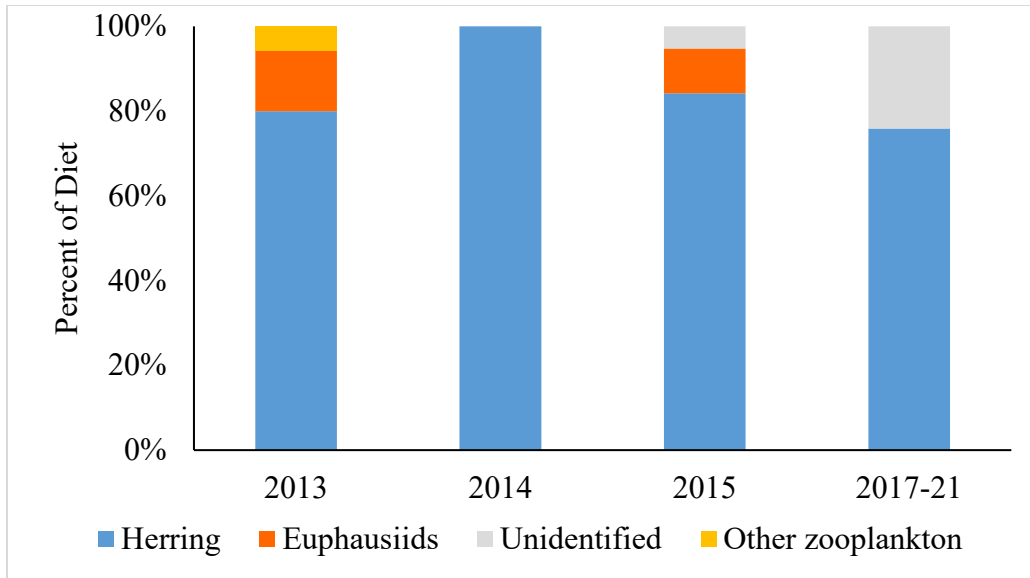


Figure 1. Observed prey during spring by year for humpback whales in Prince William Sound, Alaska. Observations from 2017-2021 were pooled due to small sample sizes.

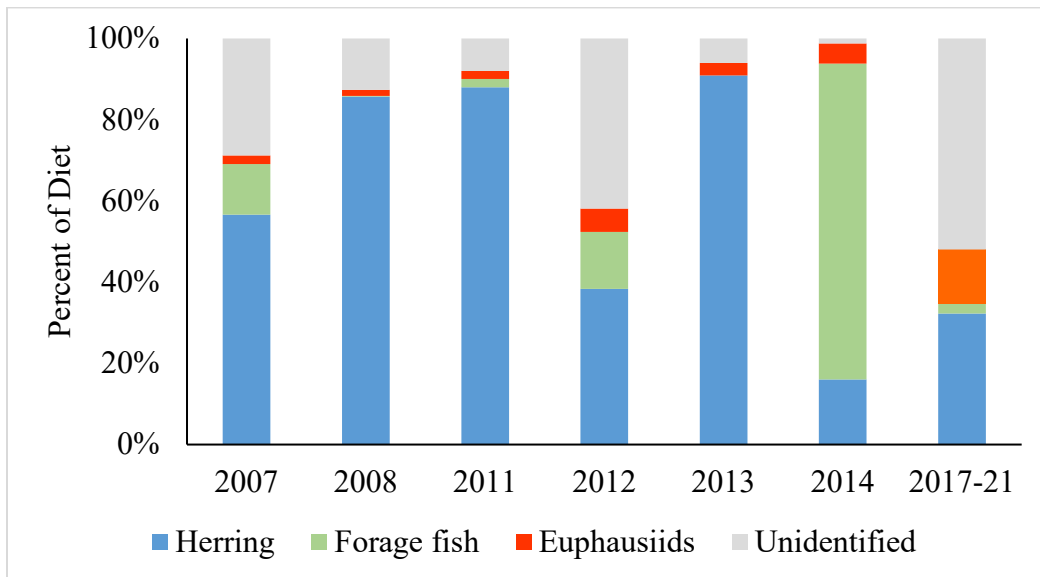


Figure 2. Observed prey during fall by year for humpback whales in Prince William Sound, Alaska. Observations from 2017-2021 were pooled due to small sample sizes. Forage fish may include herring.

Distribution

Humpback whales in PWS favored the eastern region during the spring and the southwestern region during the fall (Fig. 3). The distribution pattern was similar to earlier years, although abundance was lower (Fig. 4)

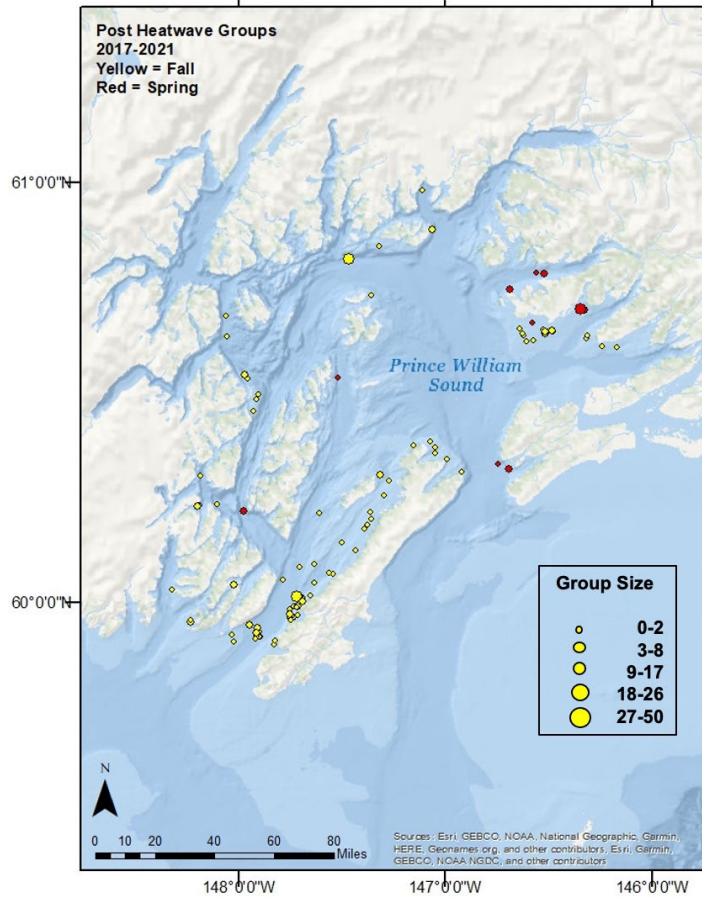


Figure 3. The distribution of humpback whales in Prince William Sound, Alaska (2017–2021). Red circles indicate spring surveys and yellow circles indicate fall surveys.

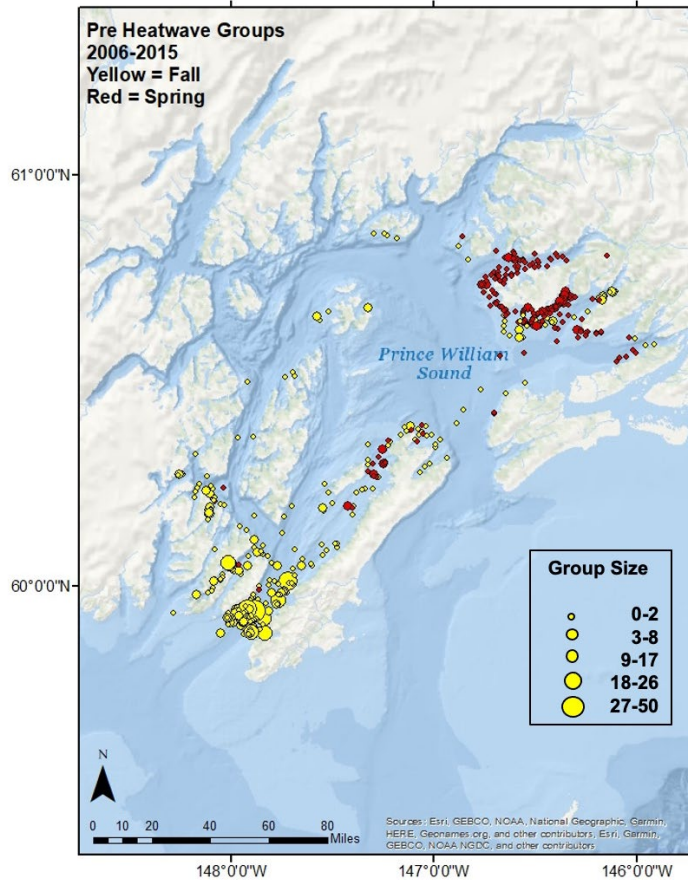


Figure 4. The distribution of humpback whales in Prince William Sound, Alaska before the Pacific marine heatwave (2006–2015). Red circles indicate spring surveys and yellow circles indicate fall surveys.

Evaluate prey quality and trophic position through chemical analysis (using bomb calorimetry and stable isotopes (Objective 2)

Prey quality

Fall adult herring are the most energy dense prey consistently available to humpback whales in PWS (Figs. 5 - 7). Their abundance, schooling behavior, and predictability enhance their status as the preferred prey. Spawning herring, although not as energy rich as fall herring (Fig. 7), provide a critical resource for whales following fasting and migration from the breeding grounds.

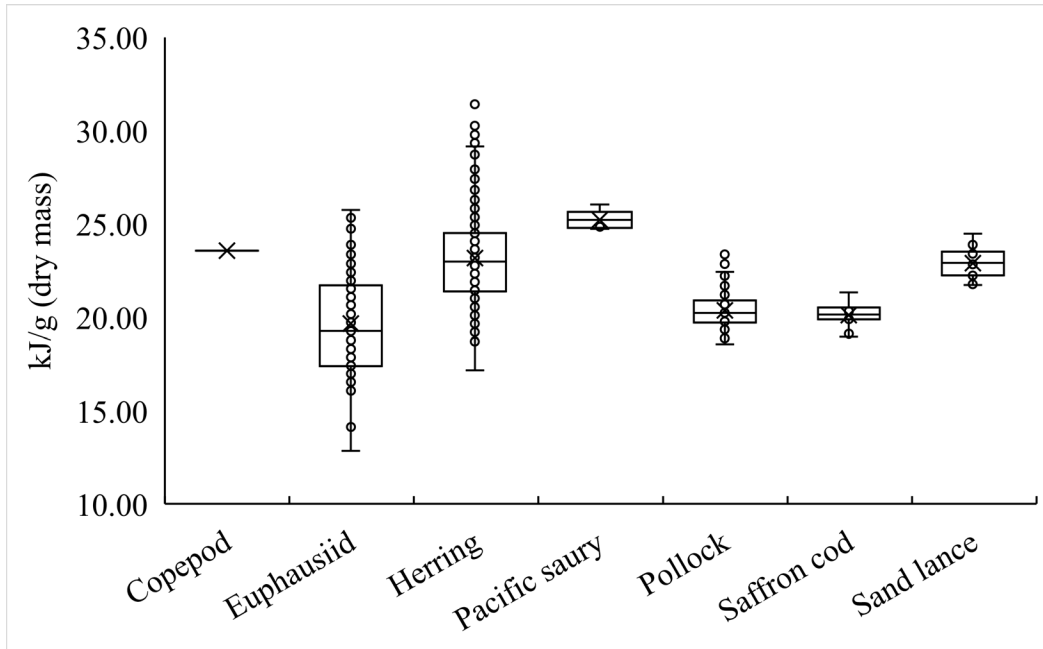


Figure 5. Average energy density (kJ/g of dry mass) of available humpback whale prey in Prince William Sound, Alaska. Quartiles, mean, and outliers displayed.

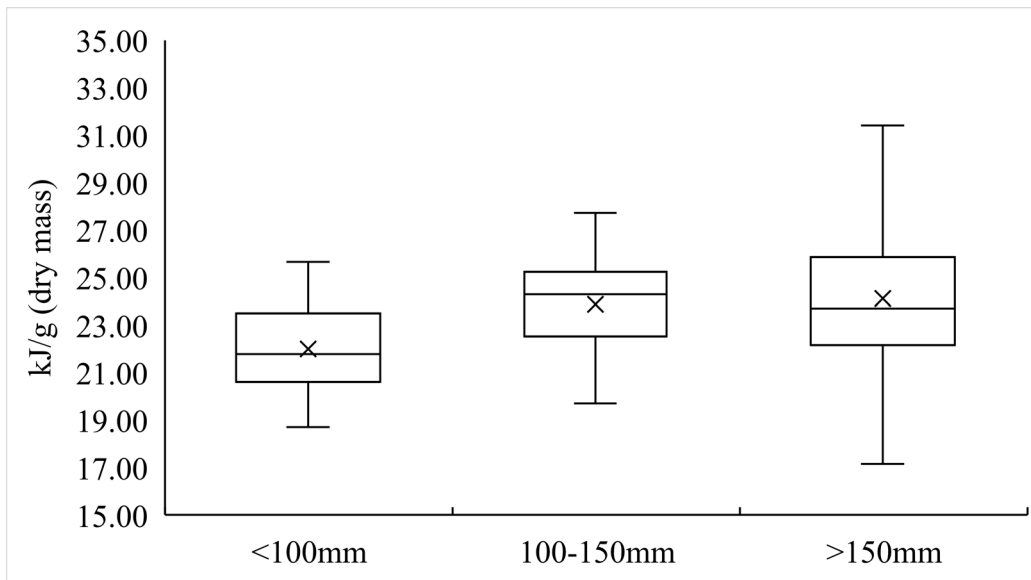


Figure 6. A comparison of the average energy density (kJ/g of dry mass) of Pacific herring by length in Prince William Sound, Alaska. Herring over 100 mm were significantly different than those under 100mm. Quartiles, mean (X), and outliers are displayed.

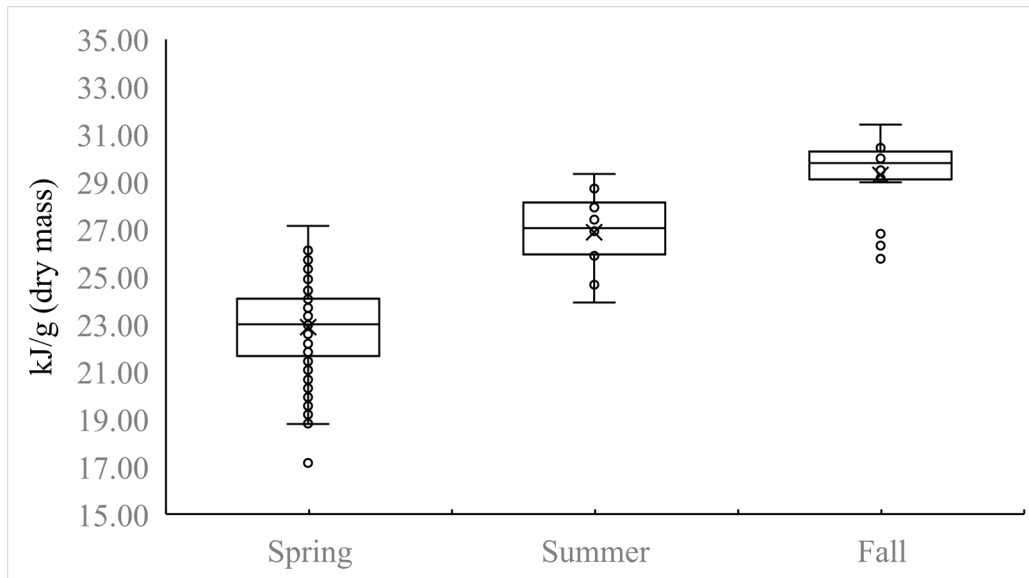


Figure 7. A comparison of the average energy density (kJ/g of dry mass) of Pacific herring by Season in Prince William Sound, Alaska. The three seasons were significantly different. Quartiles, mean (X), and outliers are displayed.

Humpback whales also prey upon euphausiids in PWS. We did not detect a difference in energy density in the two dominant species: *E. pacifica*, and *T. spinifera*. *T. inermis*, a rarely sampled species, had a similar energy density. Only one sample of *T. longipes* was measured (Fig. 8).

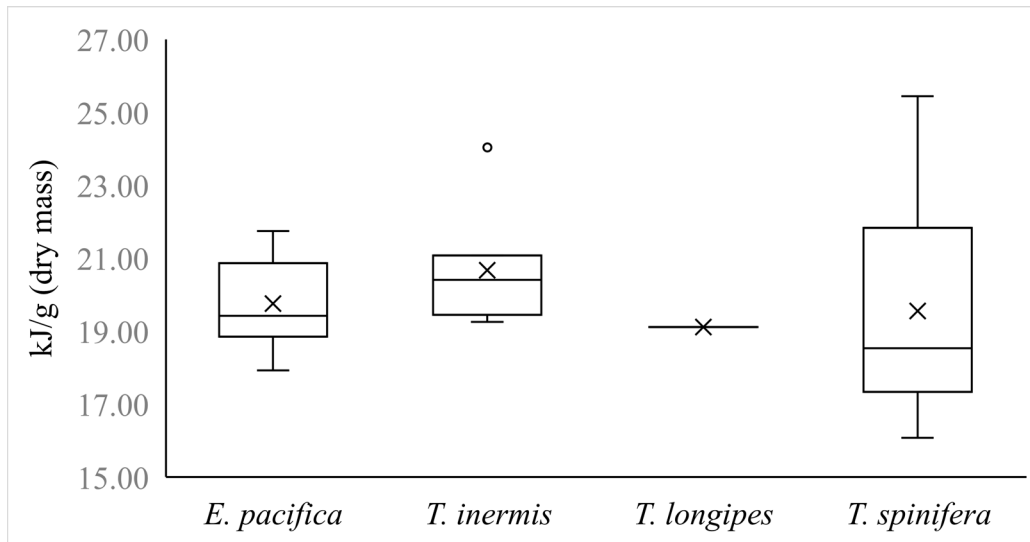


Figure 8. A comparison of the average energy density (kJ/g of dry mass) of euphausiids species in Prince William Sound, Alaska. No significant differences between species. Quartiles, mean (X), and outliers are displayed.

Trophic position

The relative trophic levels of whales in PWS as inferred from stable isotope analysis were in agreement with observed diets (Fig. 9.). There is overlap in the trophic position of the primary prey items. Humpback whale $\delta^{15}\text{N}$ values averaged 13.56‰ (SD = 0.70‰), slightly less than one trophic level above herring, which had $\delta^{15}\text{N}$ values averaging 12.35‰ (SD = 0.73‰), suggesting a diet of herring with some euphausiids. Interestingly, the two dominant euphausiids species in our samples differed trophically, *T. spinifera* had significantly higher $\delta^{15}\text{N}$ values than *E. pacifica* (Fig. 9).

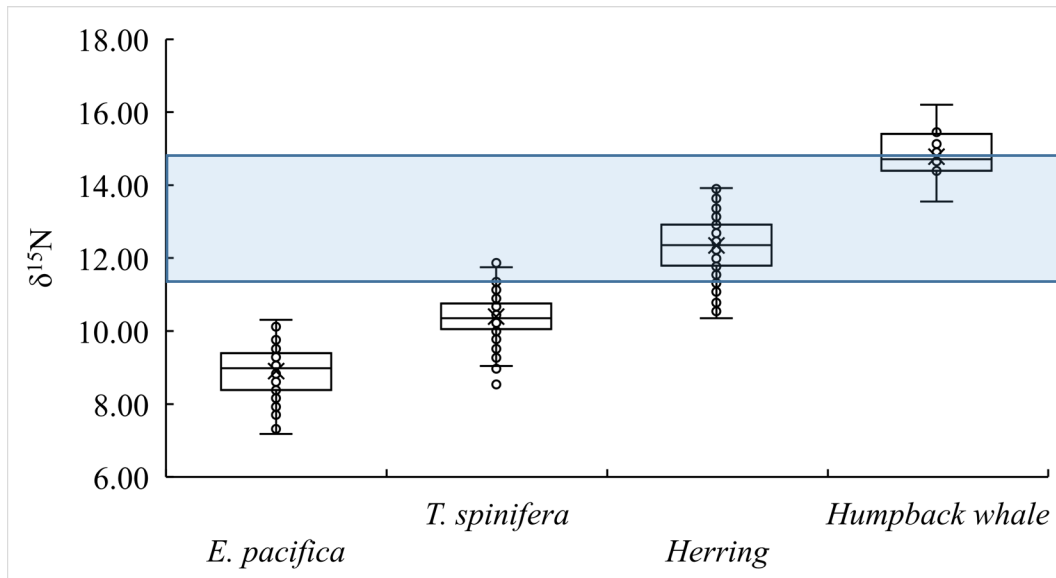


Figure 9. The relative trophic position of humpback whales, Pacific herring and the most abundant euphausiids in Prince William Sound, Alaska. The shaded area approximates one trophic level. Quartiles, mean (X), and outliers are displayed.

Estimating the impact of humpback whale predation on herring (Objective 3)

The proportion of herring biomass consumed by humpback whales decreased during this study period (2017-2021) relative to the pre-PMH period (2007-2014) when using whale abundance estimated from the Jolly-Seber-Cormack open population model (Tables 5 and 6). These patterns also hold true when using whale abundance estimates based on count data (Tables 7 and 8).

Table 5. The percentage of herring from the Bayesian age structured assessment (BASA) biomass estimate consumed by whales (estimated from the Jolly-Seber-Cormack model) during the spring spawning period. Note: Juvenile herring are consumed by whales but not included in the BASA biomass estimate.

Year	Whale abundance	SE	% of herring biomass consumed		
			Low	Mid	High
2007	98	59.40	0.2%	3.5%	8.9%
2008	71	70.26	0.1%	2.2%	5.2%
2011	80	71.73	0.2%	3.2%	8.1%
2012	119	21.96	0.4%	5.6%	13.7%
2014	105	22.45	6.6%	12.2%	22.5%
2015	25	0.00	1.6%	3.5%	7.4%
2017	107	40.02	9.5%	18.2%	33.7%
2019	43	31.69	1.3%	3.1%	6.5%
2021	43	31.69	0.8%	1.9%	4.2%

Table 6. The percentage of herring from the Bayesian age structured assessment (BASA) biomass estimate consumed by whales (estimated from the Jolly-Seber-Cormack model) during the fall. Note: Juvenile herring are consumed by whales but not included in the BASA biomass estimate.

Year	Whale abundance	SE	% of herring biomass consumed		
			Low	Mid	High
2007	132	12.04	7.1%	14.1%	25.7%
2008	201	13.57	13.5%	24.5%	41.8%
2011	165	14.53	15.7%	28.5%	50.7%
2012	173	16.76	8.8%	16.8%	30.8%
2013	159	17.06	21.2%	38.4%	67.0%
2014	167	34.19	6.7%	29.2%	78.6%
2017	65	12.57	7.1%	14.6%	28.0%
2018	73	10.55	7.0%	14.5%	27.7%
2019	73	10.55	3.3%	7.0%	14.0%
2020	73	10.55	2.4%	5.1%	10.5%
2021	74	12.06	1.9%	4.3%	9.2%

Table 7. The percentage of herring from the Bayesian age structured assessment (BASA) model biomass estimate consumed by whales (based on counts) during the spring spawning period. Note: Juvenile herring are consumed by whales but not included in the BASA biomass estimate.

Year	Counts of whales	% biomass consumed
2012	24	1.6%
2013	57	4.7%
2014	133	14.1%
2015	94	14.4%
2018	11	2.0%
2019	11	0.9%
2021	10	0.5%

Table 8. The percentage of herring from the Bayesian age structured assessment (BASA) biomass estimate consumed by whales (based on counts) during the fall. Note: Juvenile herring are consumed by whales but not included in the BASA biomass estimate.

Year	Counts of whales	% biomass consumed
2008	71	7.1%
2011	62	8.6%
2012	81	12.7%
2013	113	21.6%
2014	181	44.7%
2017	13	6.1%
2018	23	9.6%
2019	32	6.4%
2020	17	2.5%
2021	23	2.8%

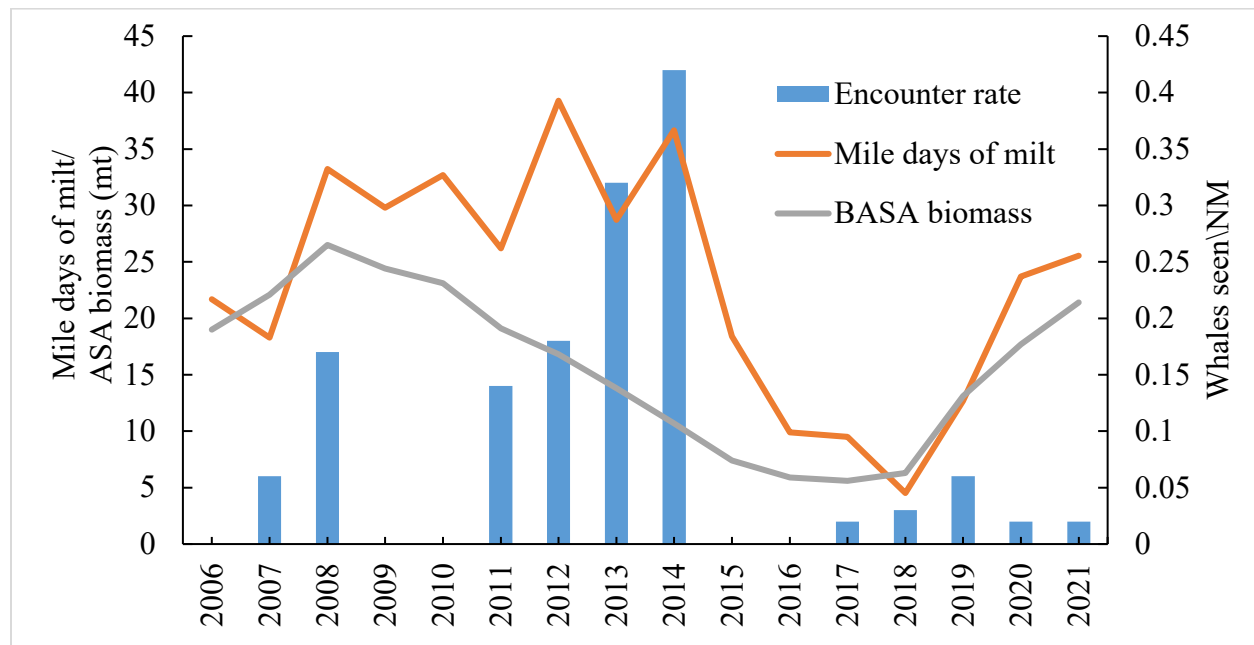


Figure 10. The mile-days of milt (cumulative miles of herring spawn) as reported by Alaska Department of Fish and Game surveys conducted by S. Haught and S. Moffitt and the Herring Research and Monitoring program, herring biomass from the Bayesian age structured assessment model and humpback whale encounter rates from fall surveys in Prince William Sound, Alaska.

DISCUSSION

Estimating trends in humpback whale abundance, diet, and distribution (Objective 1)

Abundance trends

Humpback whale numbers have declined dramatically in PWS following the PMH. This trend stands in stark contrast to our observations prior to the PMH, which showed a steady increase in whale numbers. Estimating the number of whales within PWS presents some challenges. Humpback whales show high fidelity to their breeding and feeding grounds and have relatively low reproductive/mortality rates suggesting a closed population estimator would be appropriate. However, mortality and migration likely increased following the PMH, which would dictate an open population estimator. For both mark-recapture models, open and closed, the small number of whales marked during the post-PMH years and gaps in effort (years we were not funded to survey) increased the uncertainty in our abundance estimates. Both estimators provided similar abundance trends over time and declines post-PMH, despite having differences in estimated abundance values. Despite being subject to environmental conditions, encounter rates during fall surveys also indicate a sharp decline in whales following the PMH.

The number of whales identified individually by their flukes give us a minimum count of whales. Unfortunately, not all whales show their flukes when diving and it is unlikely that we encountered every whale during our surveys. We do have agreement between the open population abundance estimate, 428 individuals, and the total number of individual whales identified by their flukes, 403 individuals. The number of unique identifications does include calves, which are not included in the abundance estimate.

Encounter rates include all whales seen on a survey, not just those photographed. Fall surveys are consistent in the area searched that allows for relative comparisons between years to establish trends. Although many factors influence counts of whales (e.g., weather, effort, recounting whales), the encounter rate trends are consistent with the models and individual identifications.

Our population estimates from the mark-recapture model and photographic identification represent the number of whales that spend some portion of their time within PWS. The number of humpback whales in PWS at any given time is influenced by many factors. The primary driver being the annual migration between high latitudes for feeding and low latitudes for reproduction. During migration and while in Hawaiian waters very little feeding takes place, humpback whales rely on blubber reserves accumulated on the feeding grounds in Alaska. The peak of breeding activities for PWS humpbacks generally occurs in February and March in Hawaiian waters and a round trip migration takes approximately 60 days. The migration to the breeding ground is staggered, with some whales leaving and returning early, while others leave and return later in the season. These movements may inflate whale abundance when determining how many whales are foraging in PWS at any given time (i.e., the abundance estimates reflect the total number of humpback whales using PWS in a season).

Humpback whale diet

Pacific herring continue to dominate humpback whale diets in PWS. Fewer whales post-PMH in this study period resulted in small sample sizes for diet analysis, therefore, we opted to pool foraging observations across years (2017-2021) for spring and fall. As in past years, spring was dominated by whales targeting spawning herring. However, following the PMH, spawning herring schools were more mobile and ephemeral relative to earlier years. Whales “chased” smaller, fast moving, schools of herring. Prior to the PMH, large shoals of herring would stage in deeper water before spawning and whales would forage in the same area for hours to days.

Determining prey during the fall survey proved to be more difficult than in previous years. Following the marine heatwave, we saw whales targeting small schools of juvenile herring, usually less than 0.5 m in diameter, a lower quality prey that may incur higher foraging cost when compared to large shoals of adult herring (Fig. 5). These shallow, small schools are hard to detect acoustically and difficult to capture which result in their frequent classification as unidentified forage fish, which increased the uncertainty of the results of our consumption models. Euphausiids were also seen in fall diets, which may have resulted in an increase in their abundance or prey switching by whales due to a lack of herring.

Distribution

There were no obvious changes in the seasonal distribution of whales in PWS following the PMH (Fig. 3) when compared to the pre-heatwave distribution (Fig. 4). Whales continue to focus on spawning herring in the eastern PWS and the north end of Montague Island in the spring. Fall observations continue to be concentrated around Montague Entrance, however, areas such as Whale Bay and Sawmill Bay have become less important.

Evaluate prey quality and trophic position through chemical analysis (using bomb calorimetry and stable isotopes (Objective 2)

Their high energy density, large biomass and predictable migration patterns make adult herring the most important forage species for humpback whales in PWS, particularly in the fall when herring are at their peak energy density. We consistently observed humpback whales feeding on adult herring during the spring and fall, however, following the PMH, humpback whales more often targeted small schools of juvenile herring. Often whales would cue on foraging flocks of birds consuming most of the fish and ending the feed bout for the birds. This method of foraging appears to be more costly than pre-PMH foraging on adult herring as it involves longer search times and active surface lunges on small schools of juvenile herring, which are less energy dense than adult herring.

Observational data was in agreement with the stable isotope analysis indicating that PWS humpback whales are feeding at a higher trophic level than other humpbacks in the Gulf of Alaska which consume more euphausiids (Szabo 2015, Wright et al. 2015, Witteveen and

Wynne 2016, Moran et al. 2018, Straley et al. 2018). Higher trophic levels are indicative of a more piscivorous (e.g., foraging exclusively on herring) diet.

Estimating the impact of humpback whale predation on herring (Objective 3)

Predation rates by whales on herring are down and herring populations within PWS are recovering to pre-PMH levels. The estimated biomass of herring removed by humpback whales was strongly influenced by the number of whales within PWS. Our population estimates from the mark-recapture analysis may overestimate the number of whales feeding on herring within the boundaries of PWS at any given time, especially in the post-PMH years. We therefore presented two approaches in an attempt to account for uncertainty in our model. Uncertainty in the prey composition, days foraging, and daily consumption rates increase the range of estimated consumption by whales. Our simplified model attempts to provide a straightforward estimate of consumption relying on observations when uncertainty in the abundance estimate was low due to low recapture rates, and while values may differ slightly, the temporal trends are strongly evident in both.

We know that whales also feed on juvenile herring which are not included in the BASA biomass estimates. In the post-PMH years it became increasingly difficult to determine the age of herring preyed on by whales. Prior to the PMH we typically saw whales feeding on large shoals of relatively stationary adult herring. Small mobile schools observed after the PMH proved harder to identify. Whale feeding on juvenile herring results in overestimates in both consumption models (the BASA estimate does not include juvenile herring, yet they contribute to the whale's energy requirements). Given that the consumption estimates vary, it is clear that predation pressure on herring by whales in PWS has been greatly reduced following the PMH.

In the past we found a correlation between humpback whale abundance, herring biomass, and mile-days of milt (the cumulative miles of milt, spawn, observed over the survey season; Fig. 10). However, 2019, 2020, and 2021 proved to be an exception. Whale numbers did not increase with the increase in abundance with the herring. The decline in whale abundance was not unique to PWS. Similar trends were seen in Hawai'i and Glacier Bay, Alaska following the PMH (Frankel et al. 2022, Gabriele et al. 2022), however, recovery in PWS has been delayed. We are uncertain as to why humpback whales have failed to return to PWS following the PMH, but their absence may provide some reprieve from predation pressure on local herring stocks.

CONCLUSIONS

Humpback whale numbers have failed to recover in PWS following a steep decline during the 2014-2016 PMH. Humpback whales in PWS feed primarily on Pacific herring, especially when herring aggregate in large shoals during the spring, fall, and winter. Typically, humpback whale numbers and distribution within PWS correlate to herring biomass. Initially both herring and whales declined following the PMH. However, in 2019-2021 there was consistent recovery in

the herring population, but no corresponding increase in humpback whale numbers. With the recent increase in herring populations to pre-PMH levels, it is unlikely that a change in herring behavior or a reduction in the caloric value of prey has made PWS a less profitable location for whales to forage. At this time, it seems more plausible that a portion of the PWS humpback whale population may not have survived the prey shortages associated with the PMH. Determining the fate of the missing PWS whales and the mechanisms behind their decline is critical to understand how this population responds to future predicted marine heatwaves associated with global climate change. Meanwhile, PWS herring seem to be released from some humpback whale predation pressure and are increasing in abundance.

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