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 16120114-N
Final Report

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Study History: In 2005, a group of scientific investigators collaborated to integrate information about the Pacific herring (*Clupea pallassi*) population in Prince William Sound and identify factors contributing to its lack of recovery (*Exxon Valdez* Oil Spill Trustee Council project 050794); top-down control was identified as probably having more influence in Prince William Sound than on other herring stocks in Alaska. The group concluded that lingering oil exposure from the *Exxon Valde*z oil spill does not play a role in limiting the recovery of herring. Of the two top-down forces, disease and predation, there was recent evidence that disease continues to have episodic events affecting the population, but there were insufficient data to assess the role of predators in limiting recovery. Future herring population assessment modeling requires better quantification on 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 between 27%–77% and 21%-63%, respectively, of the pre-spawning adult herring biomass to be consumed by whales. Project 100804 yielded several publications relating to interactions between cetaceans and herring (Ballachey et al. 2015, Boswell et al. 2016, Moran et al. 2018a, Moran et al. 2018b, Straley et al. 2017). This study continues the assessment of humpback whale predation on Pacific herring in Prince William Sound. Results are published in Moran et al. (2018a) and Straley et al. (2018) and presented as Appendices in this report.

Abstract: Humpback whale (*Megaptera novaeangliae*) predation continues to be a significant source of mortality on Pacific herring (*Clupea pallasii)* in Prince William Sound. Using mark–recapture models we estimated a population of 461 (95% C.I. 402–547) humpback whales that forage in Prince William Sound during at least part of the year. The seasonal movement of these whales into the Sound is largely driven by the movements of adult herring. Whale numbers increase in the spring with the spawn, decline during the summer, then peak in the fall and winter as herring move into the Sound to overwinter. Our lowest estimate of consumption represents 12%-34% of the pre-spawning adult biomass of herring being removed by whales. In 2012-2014, an increase in krill consumption (*Thysanoessa* sp.) may have buffered herring populations from whale predation. In December of 2014, we did not locate any overwintering shoals of herring. During the following spawning event, in the spring of 2015, whales were seen feeding on small scattered schools of herring, while the large spawning schools typically targeted were absent. We do not know if these behavioral shifts are a temporary anomaly associated with unusual oceanographic events, or a new paradigm for humpback whale herring interactions within 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 photographs (jpg) of humpback whale flukes, environment, prey, and effort associate with fluke photographs.

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Herring lengths, weights, and chemical analysis of herring and other prey species were also collected. Herring related data are stored in an Access database.

Custodian - Johanna J. Vollenweider, Auke Bay Laboratories, National Marine Fisheries Service, 17109 Point Lena Road, Juneau, AK 99801, (work phone: (907) 789-6612, 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.aoos.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. It is strongly recommended that careful attention be paid to the contents of the metadata file associated with these data to evaluate data set limitations or intended use.

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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 22 surveys covering 7627 nautical miles. To produce a more comprehensive time series, we have included data from Restoration project 100804, collected during the fall/winter months of 2007-2008 and 2008-2009, as well as opportunistic observations made by other researchers.

The *Exxon Valdez* Oil Spill Trustee Council (EVOSTC)-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. However, evidence of disease as a significant factor is episodic suggesting a potential for population recovery. In contrast, predation would be continuous, if not increasing, as humpback whale populations in PWS recover. Increased whale predation on herring is consistent with stable isotope analyses indicating PWS whales are primarily piscivores and reports that humpback whale populations in the north Pacific are increasing by 5%–7% per year. In addition, humpback whales exhibit a high degree of fidelity to their foraging grounds. If the number of whales foraging in PWS is increasing, and they preferentially forage on herring, then whales may be removing an increasing biomass from local herring populations. These removals could represent a substantial proportion of the total herring biomass if local whale populations are sufficiently large.

This project continues the work begun under *Significance of Whale Predation on Natural Mortality Rate of Pacific Herring in Prince William Sound* (Restoration project 10080), to determine, if humpback whales could be limiting the recovery of PWS herring and the relevance of whale predation in PWS relative to Sitka Sound and Lynn Canal. Restoration project 100804 identified humpback whales as significant predators on herring in PWS, consuming between 2,639–7,443 tonnes in 2007–2008 representing a predation intensity of 27%-77%. In 2008-2009 whales consumed between 4,388 and 12,989 tonnes and predation intensities ranged between 21% – 63% of the adult biomass present in spring 2008. For comparison the last significant harvest of herring from PWS was 3,904 tonnes in 1998.

Whale attendance patterns were used to estimate whale abundance through mark-recapture analysis. We used the unique marking patterns on whale flukes to identify individual whales. The modeled abundance of 461 (95% C.I. 402,547), is in close agreement with 447 individual whales identified by flukes. Both of these estimates represent the number of whales that were present within the Sound at some point during the study and not necessarily the number of whales occupying PWS at any given time.

The presence of humpback whales within in PWS varies seasonally. Whales are generally associated with large shoals of adult herring. Seasonal trends were monitored using encounter rates (whales seen/nautical miles traveled) during surveys. The typical pattern

of whale movement into the Sound 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 late winter, whale numbers drop off dramatically with the migration to the Hawaiian breeding grounds. In the spring whales return to the Sound to target dense aggregations of 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 did not return to their traditional overwintering grounds in December. 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.

Using encounter rates with (whales seen/NM 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, for recent years, 2012–2015, we detected a 39% decline in the encounter rate within the Sound. This decline may be linked to changes in prey associate with above average water temperature in the Gulf of Alaska or a reduction in herring abundance within the Sound.

Their high energy density, large biomass, and predictable migration patterns in combination with a lack of alternative prey, 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 the Sound are at a higher trophic level than other whales in the Gulf of Alaska. If herring populations decline, we can expect a corresponding decline in the number of whales using the Sound, unless alternative prey such as krill dramatically increases in abundance.

We used biomass data generated by the herring age structured assessment model developed by the Alaska Department of Fish and Game in conjunction with our consumption model to evaluate the impact of humpback whales on the PWS herring population. Whales foraged on herring in large numbers over much of the spring, fall and winter. Our most conservative model, starting with 50 whales, estimated an average of 20% of the pre-spawning adult biomass of herring being consumed over the course of the study. For our high end model, starting with 200 whales, 114% of the pre-spawning adult biomass of herring was consumed. While the high end models overestimates consumption, large influx of whales into the sound would be plausible given the scale of whale movements seen in recent years. Although many factors play into predation intensity (i.e., number of whales, prey availability, attendance patterns) maintaining a high herring biomass provides a buffer to predation.

Humpback whales are a key component of the PWS ecosystem. Their ecological absence from the Gulf of Alaska following intense commercial whaling has ended and populations may now be approaching carrying capacity in the North Pacific. We have demonstrated that herring are an important resource for humpback whales, and that relatively small changes in whale numbers can have a large impact on herring populations when herring abundance is low. If whales skip or delay their southern migration due to nutritional stress, age structured models may not account for increased natural mortality, if there is a dramatic increase in predation during the winter and early spring months after the Guideline Harvest Level is set. Our monitoring efforts have provided information to National Marine Fisheries Service regarding reclassification of humpback whales under the Endangered Species Act, Ecosystems Considerations Chapter for the North Pacific Fishery Management Councils Stock Assessment Reports, Unusual Mortality Events of large whales in the Gulf of Alaska during 2014–2015, and numerous consultations for estimating "takes" under the Marine Mammal Protection Act.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are important predators in marine ecosystems that have the potential to control the productivity of forage populations. The potential is highlighted by the revised status of nine of the 14 worldwide distinct population segments of humpback whales to "not warranted for listing under the Endangered Species Act" in the United States (Department of Commerce 2016). The existence of "recovered" humpback whale populations has motivated growing controversy over their impacts on commercial fisheries. As of 2011, the humpback whale population in the north Pacific was growing at about 5% per year and was estimated to be in excess of 20,000 individuals (Barlow et al. 2011), which prompted concern that whales may be competing for fishery production directly by consuming commercially valuable species or indirectly by consuming prey resources used by harvested species (Gerber et al. 2009, Clapham et al. 2007, Morishita 2006, Pearson et al. 2012). At this time, Gulf Watch Alaska and Glacier Bay National Park have the only funded surveys dedicated to humpback whales in Alaska.

In the Gulf of Alaska this concern is focused on evidence that humpback whales prey on Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus),* juvenile walleye pollock *(Gadus chalcogrammus)* and sand lance *(Ammodytes personatus*) (Witteveen, 2008) in addition to euphausiids. The forage fish species were found to comprise one third of humpback whale diets near Kodiak, 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 (Witteveen et al. 2009). Pacific herring are commercially exploited in Alaskan waters with an ex-vessel value of approximately $20 – $30 million annually for the years 2008–2009 (ADFG 2010), most of which supports the economies of small coastal communities. Many of these harvested herring populations are also preyed upon by humpback whales. Their large size and relatively high metabolic rates in combination with an increase in 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 inter-annual 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, while other populations remain unaffected. 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 (Sigler and Csepp 2007). 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 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 biomass removed in PWS to estimates of herring abundance. To estimate the biomass removed we combined attendance models and observed diets with published data on whale size and metabolic demands. Parameter values for the models were varied in order to provide low and high end estimates that bracketed the range of all potential population estimates.

OBJECTIVES

1. Estimate population of humpback whales through the use of photographic mark-recapture models.
2. Monitor the seasonal trends of humpback whales in Prince William Sound relative to their prey.
3. Estimate inter-annual trends in humpback whale abundance.
4. Determine the diet and dietary shifts of humpback whales.
5. Estimate predation rates on herring by humpback whales.
6. Incorporate mortality rates into herring age structure models.

METHODS

Study Area and Sampling Effort

We monitored humpback whales 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. Depending on weather, surveys were conducted in a clock wise or counter clock wise circuit around PWS. Aerial surveys, other EVOSTC projects, and traditional local knowledge were employed to ensure aggregations of whales in areas that could not directly surveyed, were not being overlooked during boat based surveys.

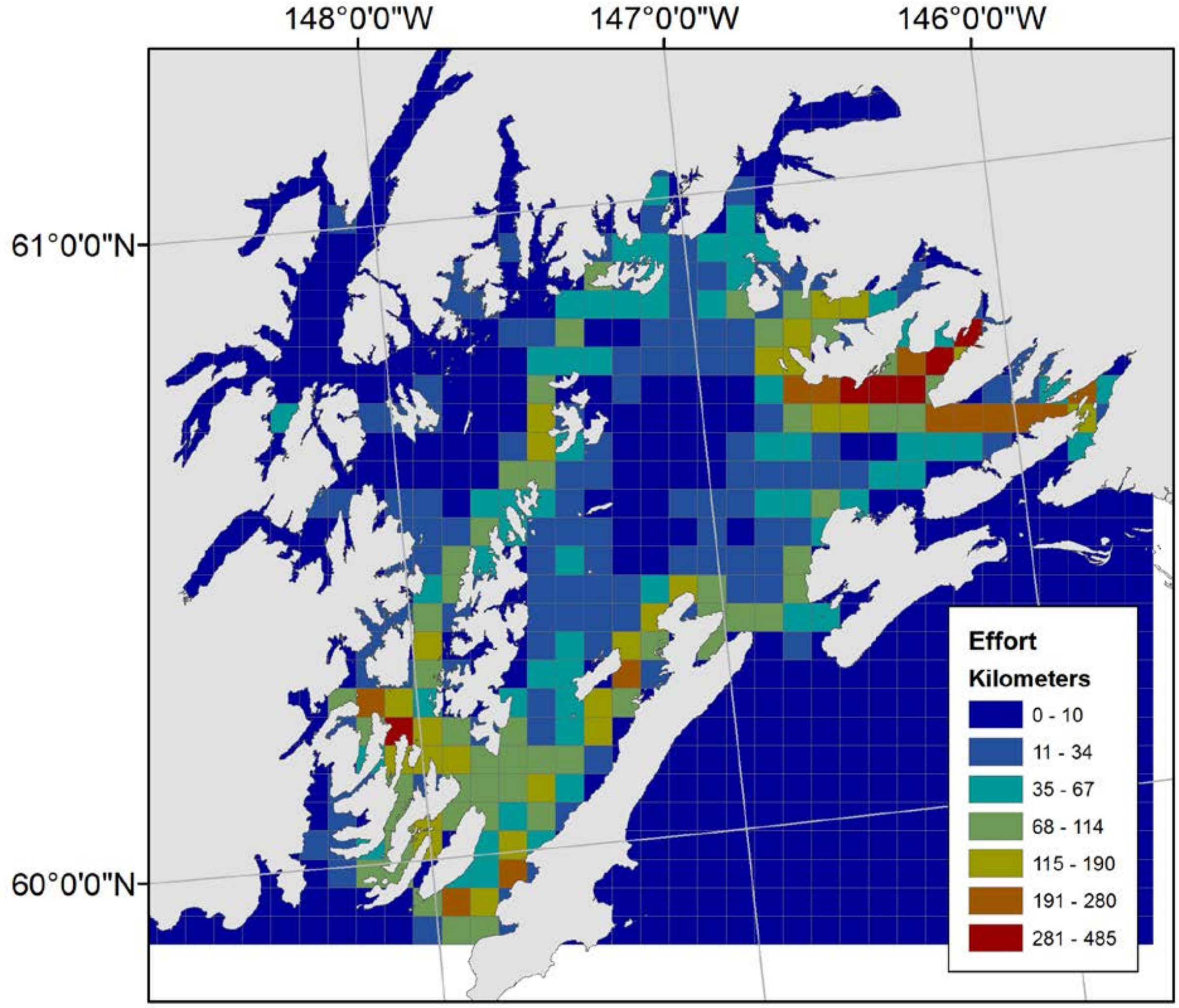

Figure 1. Effort in kilometers surveyed within 5 km grids for humpback whales in Prince William Sound, Alaska for the years 2007–2015.

Estimation of Whale Abundance

To address objective 1, 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). We used these records to develop attendance histories for each whale in each location. Cataloged photographs for PWS include opportunist observations that were not included in other analysis presented here. PWS photographic records for the mark-recapture analysis were collected on 22 boat based surveys (Table 1). Surveys were conducted aboard the 17.7m vessel *M/V Auklet*.

Table 1. A summary of humpback whale survey effort in Prince William Sound, Alaska (including surveys from Restoration Project 100804).

Survey	Season	Distance covered (NM)	Counts of Whales	Whales Photo ID
September-07	Fall	370	15	3
November-07	Winter	193	59	24
January-08	Late winter	359	123	26
September-08	Fall	412	101	44
October-08	Fall	371	58	45
December-08	Winter	287	8	30
January-09	Late winter	313	140	22
March-09	Late winter	381	190	5
October-11	Fall	441	38	33
December-11	Winter	220	3	30
February-12	Late winter	279	29	2
April-12	Spring	259	16	17
September-12	Fall	444	20	38
November-12	Winter	316	107	30
April-13	Spring	507	49	19
September-13	Fall	355	60	41
December-13	Winter	309	98	29
March-14	Spring	435	146	33
July-14	Summer	366	7	9
September-14	Fall	427	80	44
December-14	Winter	209	20	7
April-15	Spring	374	80	19

Photographic Identification

We used Nikon D-300, D-200, and D-70 cameras with 80-200 mm lenses to capture digital images of the ventral side of humpback whale flukes to 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 were also excluded, this is because the capture probability for a calf is complicated by their co-occurrence with their mothers (and is therefore not independent), and the probability of recapture in later years can be difficult as calf flukes tend to change more than adult flukes.

Huggins closed-capture model

In addition to estimating whale abundance by cataloging the number of unique individuals, we also estimated abundance using the Huggins closed-capture model. All modeling was done in program MARK (White and Burnham 1999). Models were structured to consider the population closed during the survey season only. The Huggins style closed-capture model was chosen because it distinguishes between "no sightings" from "no effort" for a given sampling period. This is important because there was not always a consistent number of surveys within a given survey season and it is important that gaps in survey effort are not treated as an absence in humpback whales. Instances where there was no equivalent survey counterpart for a given year were assigned fixed capture probabilities of zero. The Huggins model estimates accounts for whales not seen during surveys, hence it represents an upper limit to the number of whales present.

A suite of competing models of humpback whale abundance were developed for each study area. These included models where capture probabilities covaried with different measures of effort (nautical miles and hours spent on effort), and a model where all capture probabilities were constrained. We evaluated these different models using the Akaike's Information Criterion corrected for small sample sizes (AIC_c) by selecting the model which had the lowest AIC_c value (Burnham and Anderson 2002).

Each year was grouped separately to allow the population to be "open" between survey seasons. This allows for migration and thus poses no requirement for a given level of feeding ground fidelity. In each area, individual capture probabilities were estimated for each survey, and estimates of absolute abundance were derived for each survey year. Misidentification errors were minimized by a relatively small population size. The lower and upper 95% confidence intervals (LCI, UCI) were corrected to consider the number of unique individuals input into the model, *M*. Since *M* can be considered the minimum number of whales, the correction ensures that the LCI no less than this value. This adjustment was made by (Pers. comm. G. White):

$$LCI = \hat{f}_0 / C + M_{t+1} \qquad\qquad UCI = \hat{f}_0 * C + M_{t+1}$$

where $\hat{f}_0$ is the estimated number of animals never seen and C is the correction factor. These are estimated by:

$$\hat{f}_0 = \hat{\bar{N}} - M_{t+1}$$

$$C = \exp\left\{ 1.96 \left[\ln\left(1 + \frac{\operatorname{var}(\hat{\bar{N}})}{\hat{f}_0^{\,2}} \right) \right]^{1/2} \right\}$$

Seasonal Trends in Humpback Whale Abundance

Although mark-recapture models provide an estimate of abundance, they do not describe seasonal trends. Consequently, to address objective 2, we used the average number of unique whales seen each month for establishing seasonal patterns of whale present within PWS. The data used to establish the seasonal attendance patterns included calves and individuals identifiable in poor quality photographs and represent a lower bound to the daily attendance pattern for whales. By identifying individuals, we avoid overestimating whale numbers by double counting. Seasons were delineated by the seasonal behaviors of whales and herring (Table 2). The locations of whales were mapped relative to known concentrations of prey to establish a link between whale movements and their prey. Observations from Restoration Project 100804 were included in this analysis.

Table 2. Seasonal transitions based on whale and herring behavior in Prince William Sound, Alaska.

Season	Period	Days	Characteristics of season
Spring	Mar 15–May 31	78	Returning from breeding grounds, herring spawning.
Summer	Jun 1–Aug 31	92	Numbers drop in PWS as herring disperse.
Fall	Sep 1– - Nov 15	76	Return to PWS with migrating herring.
Winter	Nov16–Dec 31	46	Feed on overwintering herring shoals.
Late Winter	Jan 1–Mar 14	73	Depart for breeding grounds.

Inter-annual Trends in Humpback Whale Abundance

To address objective 3, long term population trends within PWS were evaluated by combining observations from this study and from Restoration Project 100804. Because the mark recapture model may be estimating an area larger than PWS, we used encounter rates with individually identified whales (whales seen/NM traveled) to account for varying effort between years. Linear regression was used to detect inter-annual trends. We used an $\alpha = 0.05$ to determine statistical significance.

Diet and Dietary Shifts of Humpback Whales

To address objective 4, a combination of techniques were 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 echosounder. Prey distinctly visible on 50kHz was presumed to be fish. Prey visible only at 200kHz were presumed to be smaller and categorized as zooplankton. Confirmation and collection of target prey was accomplished using herring jigs, zooplankton tows, cast nets and skim nets (used to clean swimming pools) to collect prey (i.e., fish, scales, or zooplankton) at the surface near feeding whales. Certainty of identification of the target prey was recorded as certain, probable or undetermined. Only cases were the identification was certain or probable were used to identify specific prey.

We identified the trophic level of individual whales and their prey to verify diet using stable isotope analysis. The use of stable isotopes obtained from biopsy tissue samples is a well-established method to obtain diet information from free-ranging whales (e.g., Bowen 1997, Witteveen et al. 2009, Bowen and Iverson 2013). Nitrogen stable isotope ratios (^{14}N /^{15}N; $\delta^{15}N$) increase with increasing trophic level (Vander Zanden and Rasmussen 1999), thereby giving an indication of the trophic level at which individual whales are foraging. In marine coastal environments, carbon stable isotope ratios (^{12}C /^{13}C ; $\delta^{13}C$) are useful for distinguishing between benthic and pelagic bases of the food web; because carbon fixation occurring in benthic organisms results in a greater proportion of the heavy ^{13}C isotope when compared to pelagic carbon fixation (France 1995). In PWS the $\delta^{13}C$ values in consumers are also related to the relative influence of offshore versus coastal feeding (Kline 1999, 2010).

Skin samples for stable isotope analysis were collected from the flank of each whale using a 150 lb crossbow and modified bolt equipped with a stainless steel biopsy dart tip and floatation for retrieval. Photographs were taken at the time of sampling to identify each whale and avoid sample misidentification. All samples were stored on ice after collection until they could be frozen at -20 or -80 °C freezer.

Primary consumers (a composite of multiple individual copepods) were collected to establish a baseline for $\delta^{15}N$ values and to allow for the comparison of trophic level across sites. Copepods *(Calanus* spp.) serve as surrogates for the base of regional food webs and account for regional differences in baseline $\delta^{15}N$ values (Kling et al. 1992, Cabana and Rasmussen 1996, Post 2002, Matthews and Mazumder 2005, Andrews 2010).

Prepared samples were sent to a mass spectrometry facility at University of Georgia for the 2008/09 samples for analysis. FIU prepared the 2014/15 samples for quantification of the ratios of $\delta^{13}C$ and $\delta^{15}N$ for lipid-extracted tissue samples (see Witteveen et al. 2009, 2011, Straley et al. 2018) for details regarding sample preparation and isotope analysis. Lipids consist mostly of carbon and very little nitrogen, therefore variable lipid content in different samples can introduce unwanted variability to $\delta^{13}C$ values which may be interpreted as habitat changes or diet changes. These values were converted to δ notation by comparison against international reference standards.

Stable isotope ratios are presented in δ notation:

$$\delta^{a}X = \frac{R_{sample} - R_{standard}}{R_{standard}} * 1000\ ‰$$

where R is the ratio of the heavy to light isotope (i.e., ^{13}C / ^{12}C). Stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ were analyzed and used to evaluate the relationship between humpback whales and their prey sources and to calculate trophic position similar to the methods of Witteveen et al. (2009).

Trophic levels of individual whales were calculated by taking the difference in δ^{15}N of primary consumers (copepods) from humpback whales and accounting for the trophic enrichment factor determined by Witteveen et al. (2009) using the following equation:

$$Trophic\ Level\ (TL) = 2 + \left(\delta^{15}N_{humpback\ whale} - \delta^{15}N_{copepod}\right)/2.4$$

where 2 is the trophic position of the primary consumer and 2.4 is the average increase in δ^{15}N between trophic levels for marine mammals (Post 2002).

Estimate Predation Rates on Herring by Humpback Whales

The large size of humpback whales prevent direct measurement of ingestion rates, therefore to address objective 5, estimates of annual consumption were derived from seasonal attendance patterns, diet, abundance, and daily consumption rates. Inter-annual variation was accounted for by using different numbers of whales as a starting point for the model based on the number of whales counted during each survey (Table 1). The model was run with 50, 100, and 200 whales. The seasonal trend (Objective 2) was used to vary the proportion of whales within the PWS. 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 (Witteveen et al. 2006, Roman and McCarthy 2010).

$$C = \sum_{t=1}^{5} PnS_tD_tR$$

C = Annual consumption in each year (tonnes of herring).
P = Proportion of whales eating herring.
S_t = Proportion of whales present during each season.
D_t = Number of days in each season.
R = Daily consumption rate.

We used biomass data generated by age structured model to evaluate the impact of humpback whales on the PWS herring population. The results of high-end and low-end models of whale consumption were compared to the estimated adult pre-fishery run biomass for the years 2007, 2008, 2011, 2012, 2013, and 2014 (Pers. comm. S. Moffit).

We estimated the potential biomass removed for each year using six 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 with seasonal estimates of herring abundance yields a measure of the intensity of humpback whale predation.

Incorporate Mortality Rates into Herring Age Structure Models

This objective was not met due to funding limitations. Our intention was for a graduate student to provide abundance estimates and evaluate natural mortality attributed to whales using the PWS herring age structured assessment model. Due to circumstances we couldn't control, these tasks were partially completed but funding lapsed before the analysis was finalized. We sought additional funding though the EVOSTC Cross-Publication Program RFP, but unfortunately the proposal was not funded.

RESULTS

Population Estimates of Humpback Whales

By using the unique markings on the flukes from our surveys and opportunistically collected photographs, we identified 447 individual whales that used the waters of PWS from November of 2006 through April of 2015. Because it is unlikely that we photographed all of the whales in within PWS, this number should be considered a minimum estimate of abundance for the time period.

The estimate of 447 whales derived from photographs of each whale's flukes is in agreement (within the bounds of the confidence intervals) with the results of the Huggins closed-capture model, which accounts for the unseen fraction of the population. The analysis suggested that a model with time variation and heterogeneity would be appropriate. The estimator with this model is called M(th) Chao, which produced an estimate of 461 individuals (95% confidence interval of 402,547). Capture probabilities varied from 0.03 to 0.21. It is important to note that these are estimates of the number whales that have used PWS at some point during the study, but are not resident in the Sound throughout the year.

Estimates of total number of whales (this includes whales that were not photographed) within PWS on each survey ranged from a low of three to a high of 190, with an average of 66 based on counts from our surveys (Fig. 2). Although many factors influence counts of whales (e.g., weather, effort, recounting whales), these values provide a frame of reference for our modeling efforts by estimating the number of whales that were actually within PWS.

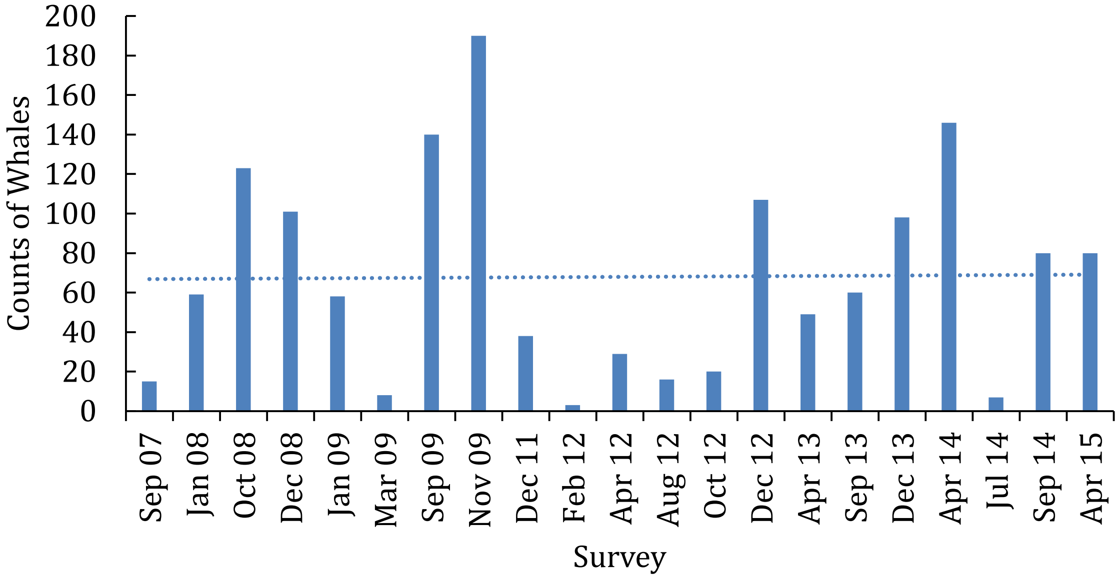

Figure 2. Raw counts of humpback whales in Prince William Sound, Alaska (not corrected for effort). These counts provided an estimate of the whale numbers within the Prince William Sound during each survey. (Aug 12 was an opportunistic survey, distance was not record as a measure of effort).

Seasonal Trends of Humpback Whales in Prince William Sound Relative to Prey

Seasonal trend in whale numbers are influenced by the annual migration to low latitude breeding ground and the movement of herring in PWS. Encounter rates with whales in PWS varied seasonally, peaking in the fall and winter months (Fig. 3). Whale numbers were at their minimum in late January through early March, which coincides with peak numbers of whales in Hawaiian waters.

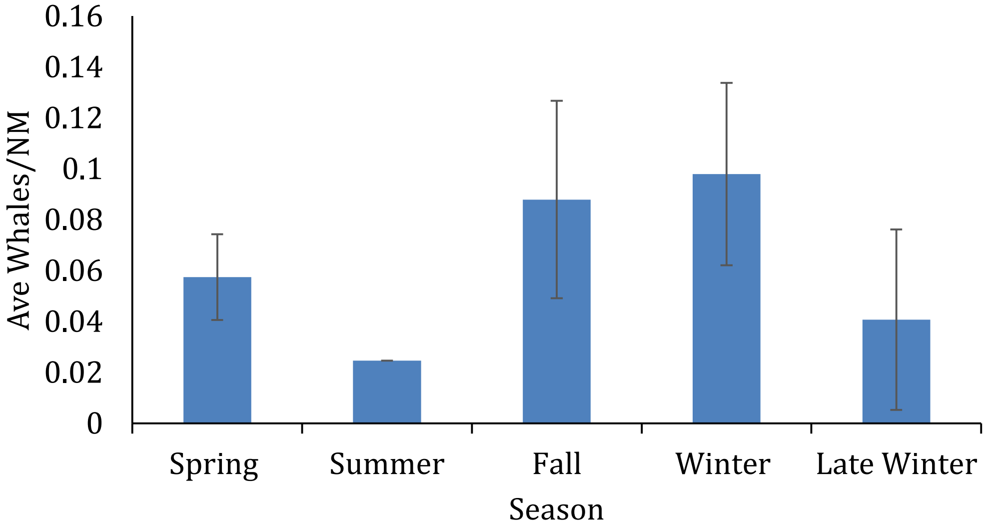

Figure 3. Average seasonal encounter rates (number of whales individually identified/nautical mile surveyed) by season for the years 2007-2015 in Prince William Sound, Alaska (Error bars represent ± 1 SD).

Whales in PWS were generally associated with large shoals of adult herring (Fig. 4). Herring were accompanied by whales as they moved into the Sound during early fall through Montague Strait on their way to overwintering grounds. Whale numbers within the Sound increased during the fall and early winter then drop off dramatically in late winter when they migrate to the Hawaiian breeding grounds. In the spring whales returned to the Sound to feed on spawning herring. After spawning both herring and whales dispersed, resulting in lower whale numbers during the summer months. The distribution of whales within PWS mirror tagged herring movements (Bishop and Eiler 2017)

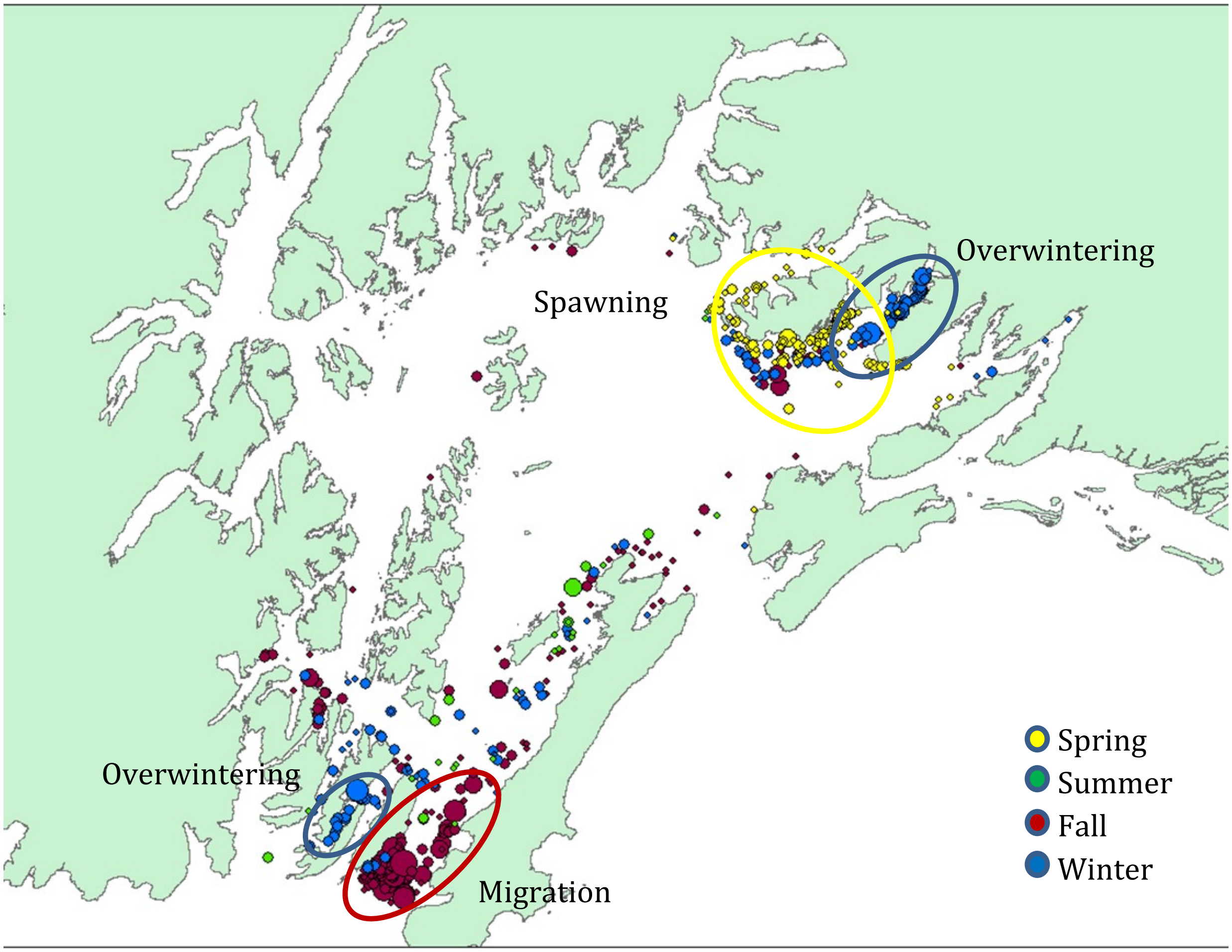

Figure 4. The distribution of humpback whales (solid circles) and important areas for adult herring (open ovals) in Prince William Sound, Alaska (2006–2015).

In December of 2014, whales and herring did not return to the Port Gravina as they had in previous years. Instead, whales were scarce throughout the Sound with the exception of a group of whales feeding on a school of herring was located off the southwest side of Latouche Island. In other years of the study, this area was more typically occupied by whales and herring in the early fall. Deteriorating weather and darkness prevented a complete survey of this area in December 2014. The following spring, April of 2015, large pre-spawning adult herring aggregations were not seen. Herring schools were small, dispersed and mostly found in Port Fidalgo rather than on in the Knowles Head/Hell's Hole area (Figs. 5 and 6). Whale numbers during this survey were lower and less concentrated, as they pursued small fast moving schools. Whales were also found in the Green Island area, an area not typically used during spring of recent years, spawning herring were reported there later in the spring (Pers. comm. M.A. Bishop).

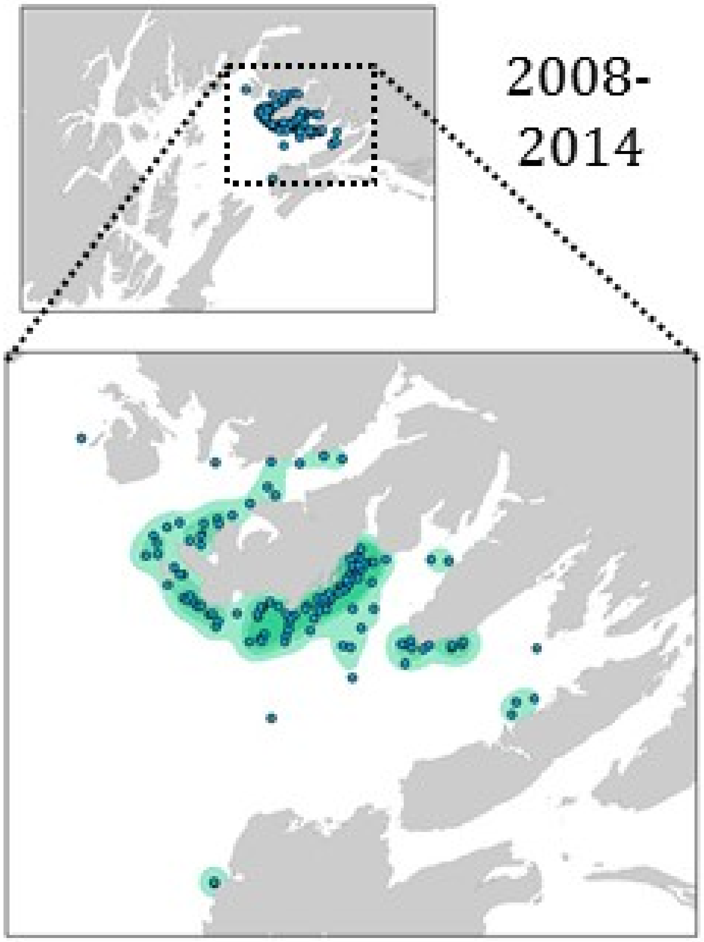

Figure 5. The distribution and density of humpback whales during the herring spawn in Prince William Sound, Alaska for the years 2008–2014 (Surveys in 2009 and 2010 were not funded.).

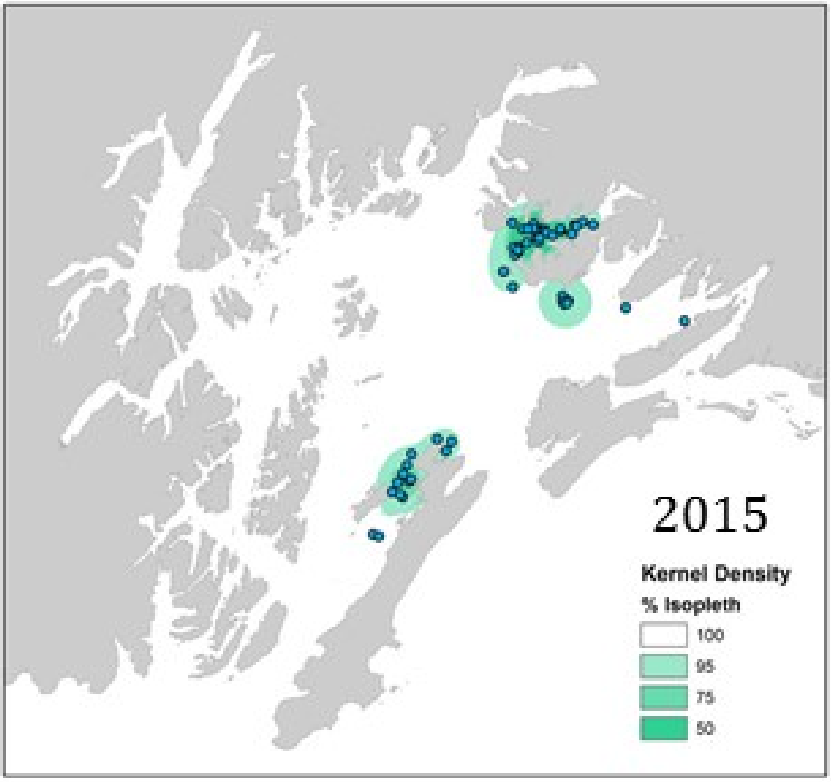

Figure 6. The distribution and density of humpback whales during the herring spawn in Prince William Sound, Alaska for the year 2015.

Inter-annual Trends in Humpback Whale Abundance

We did not detect a significant inter-annual trend in the number of individual whales encountered within PWS from September 2007 through April 2015 (p=0.607; Fig. 7, only one survey was conducted in 2015, during April). However, for recent years, 2012–2015, we observed a 39% decline in the encounter rate (p=0.009; Fig. 8).

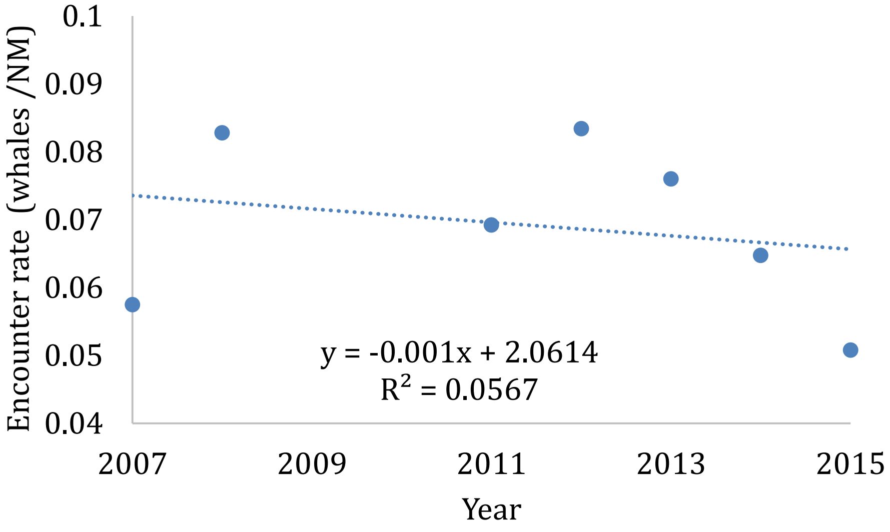

Figure 7. Encounter rates (whales seen/nautical mile surveyed) for the years 2007–2015 Prince William Sound, Alaska (January and early March surveys from 2009 are reported in 2008. These whales are hold overs that have not yet migrated. Surveys in 2009 and 2010 were not conducted.).

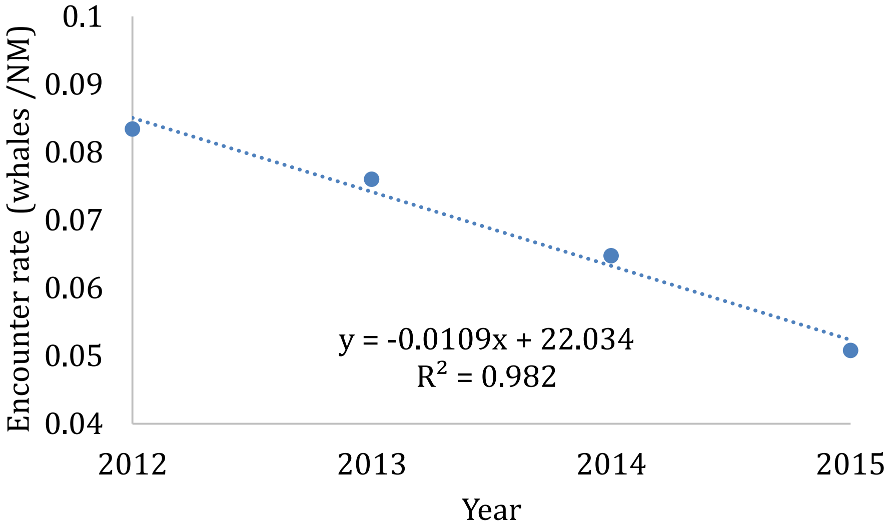

Figure 8. Encounter rates (whales seen/nautical mile surveyed) for the years 2012–2015 in Prince William Sound, Alaska.

Diet and Dietary Shifts of Humpback Whales

Humpback whales in PWS primarily feed on Pacific herring (Table 3). From 1045 observation of foraging whales where prey could be determined, 81.0% were feeding on herring. An additional 11.2% of prey was identified as fish, which may include herring. The proportion of euphausiids varied between years. In 2012 and 2014 the amount of herring observed in the diet was reduced, this was partially the result of abundant age-0 walleye pollock in the Sound (Dorn et al 2015; Arimitsu 2017). The ubiquitous pollock schools, present in these years, made it difficult to determine what species was being targeted by the whales when both herring and pollock were present. Based on observational data, herring were the dominant prey item for humpback whales in all seasons except summer (Table 4).

Table 3. Observed prey from 1045 encounters with foraging humpback whales in Prince William Sound, Alaska from Sept. 2007–April 2015.* Only one survey was conducted in 2015 during April.

	Year							
	2007	2008	2011	2012	2013	2014	2015*	Total
Pacific Herring	77.4%	97.7%	94.4%	56.9%	86.6%	35.1%	70.8%	81.0%
Fish (may include herring)	18.0%	0.2%	2.8%	16.7%	0.0%	45.8%	0.0%	11.2%
Euphausiids	3.8%	1.7%	2.8%	22.2%	11.9%	12.2%	8.3%	5.7%
Zooplankton *(may include euphausiids)*	0.0%	0.4%	0.0%	4.2%	1.5%	3.1%	20.8%	1.4%
Juvenile Coho Salmon	0.8%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.2%
Walleye Pollock	0.0%	0.0%	0.0%	0.0%	0.0%	3.8%	0.0%	0.5%
Number of observations	239	476	36	72	67	131	24	1045

Table 4. Observed prey by season for 1045 humpback whales in Prince William Sound, Alaska from Sept. 2007–April 2015.

	Season				
	Spring	Summer	Fall	Winter	Late Winter
Pacific Herring	81.9%	0.0%	69.8%	83.5%	97.3%
Fish (may include herring)	18.0%	0.0%	19.8%	11.2%	1.8%
Euphausiids	10.6%	100.0%	7.1%	5.0%	0.0%
Zooplankton *(may include euphausiids)*	7.4%	0.0%	1.4%	0.3%	0.9%
Juvenile Coho Salmon	0.0%	0.0%	0.5%	0.3%	0.0%
Walleye Pollock	0.0%	0.0%	1.4%	0.0%	0.0%
Number of observations	94	6	368	358	219

Diets inferred from stable isotope analysis were in agreement with field observations: PWS humpback whales feed at a relatively high trophic level (Fig. 9). Humpback whale isotope values for $\delta^{13}C$ and $\delta^{15}N$ averaged -18.29 ‰ (SE= 0.3) and 14.58 ‰ (SE= 0.15), respectively (Table 5). The forage fish (herring, pollock, and Pacific sand lance) all had similar $\delta^{13}C$ and $\delta^{15}N$ isotope values although herring had highly variable $\delta^{13}C$ values, reflecting seasonal or individual variability in offshore to coastal feeding histories (Kline 2010). Krill had variable isotope values generally lower in $\delta^{15}N$ and $\delta^{13}C$ values than forage fish or humpback whales however some krill and all *Thysanoessa spinifera* were higher in $\delta^{15}N$ values similar to forage fish species (Fig. 9).

PWS mean monthly trophic levels for PWS whales ranged from a low of 3.28 in March 2009 to a high of 5.26 in December 2015 (Fig. 10, Table 6) while the average trophic level for PWS whales was 4.02 (SE=0.08). In 2014 and 2015, the trophic level of humpback whales within PWS was elevated relative to earlier samples.

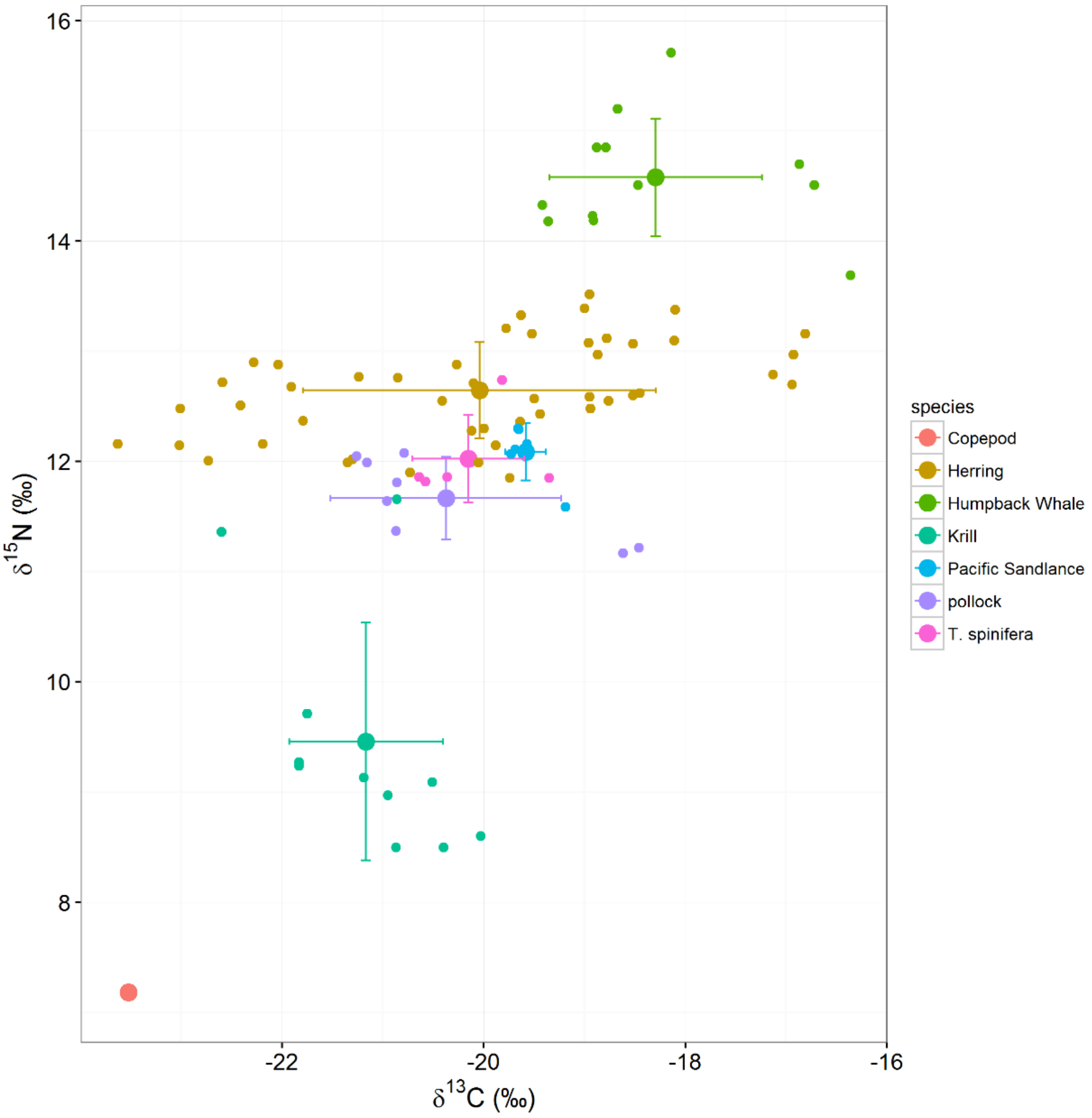

Figure 9. Isotope biplot (δ13C and δ15N) of non-lipid extracted humpback whale skin and whole prey items in Prince William Sound, Alaska, 2014-2015.

Table 5. Mean and 1 SE for δ13C and δ15N values of humpback whales and their prey sources from Prince William Sound, Alaska, 2008-2015. *one sample made up of many individuals

Species	**N**	**Mean δ^{13}C**	**SE δ^{13}C**	**Mean δ^{15}N**	**SE δ^{15}N**
Copepod	1*	-23.52	NA	7.18	NA
Herring	48	-20.04	0.26	12.65	0.06
Humpback Whale	12	-18.29	0.30	14.58	0.15
Krill	12	-21.17	0.23	9.46	0.33
Pacific Sandlance	6	-19.58	0.08	12.09	0.11
Pollock	8	-20.37	0.40	11.67	0.13
Thysanoessa spinifera	5	-20.15	0.25	12.03	0.18

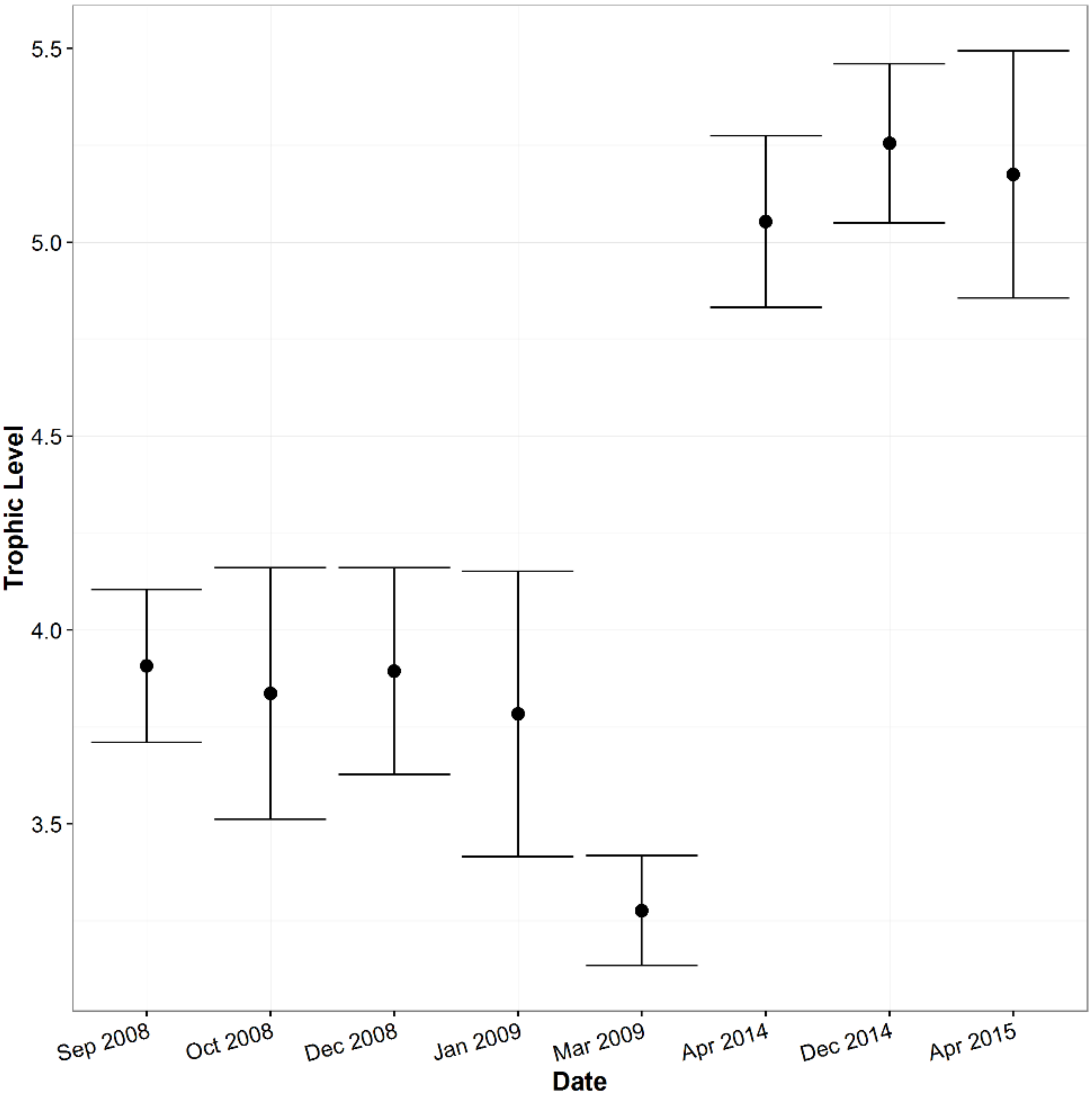

FIGURE 10. Trophic levels reported as monthly means with standard errors (SE) for humpback whales sampled (N=49) in Prince William Sound, 2008 to 2015. Higher trophic levels represent a piscivorous diet, as planktivorous cetaceans have lower trophic levels (2.8 to 3.0; Hoekstra et al. 2002).

Table 6. Mean monthly trophic position and 1SE of humpback whales (N49) in Prince William Sound, Alaska, 2008-2015.

Year	N	Month	Mean Trophic level	SE Trophic level
2008	9	Sep	3.91	0.07
2008	11	Oct	3.84	0.10
2008	11	Dec	3.89	0.08
2009	9	Jan	3.78	0.12
2009	2	Mar	3.28	0.10
2014	3	Apr	5.05	0.13
2014	2	Dec	5.26	0.15
2015	2	Apr	5.18	0.23

Fall adult herring are the most energy dense prey available to humpback whales in PWS (Fig. 11), their abundance, schooling behavior, and predictability (during spawning, migration and overwintering) are other characteristics that increase their status as the preferred prey. As adult herring numbers drop during summer months, other prey such as krill and age-0 herring become more important (Table 4).

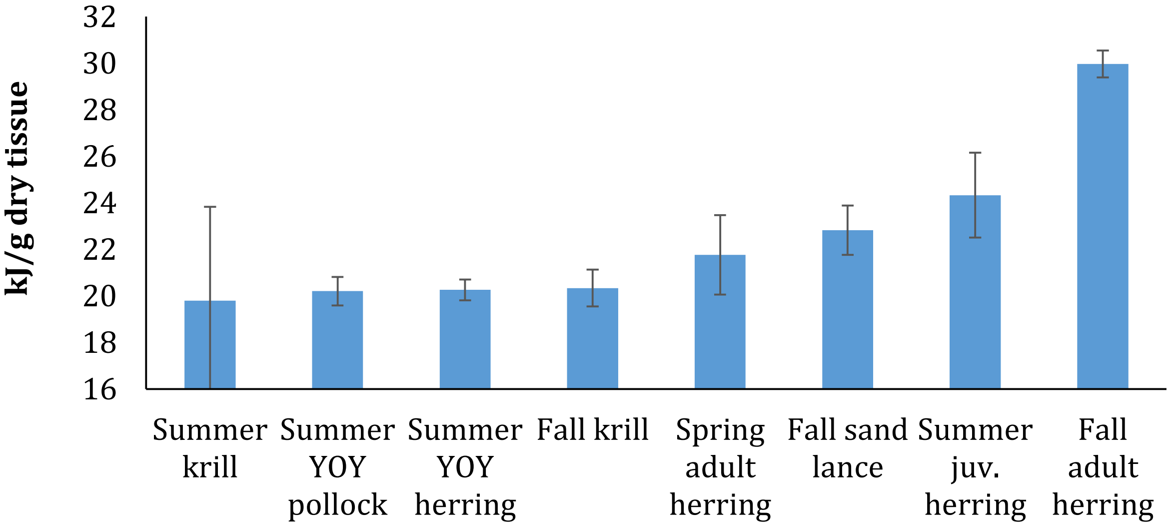

Figure 11. Average energy density (kJ/g of dry mass) of humpback whale prey in Prince William Sound, Alaska (error bars represent ±1SE).

Predation Rates on Herring by Humpback Whales

Over the course of this study whales fed primarily on herring in PWS (Table 3). This translates into average of 2,695 (SD= 876) to 4,454 (SD = 500) tonnes of herring /year if we assume a starting point of 50 whales (Fig. 12). When 200 whales are used as a starting point, they have the potential of consuming an average of 10,779 (SD. = 3504) to 17,817(SD = 2001) tonnes of herring /year, essentially all of the adult herring in PWS (Fig. 12).

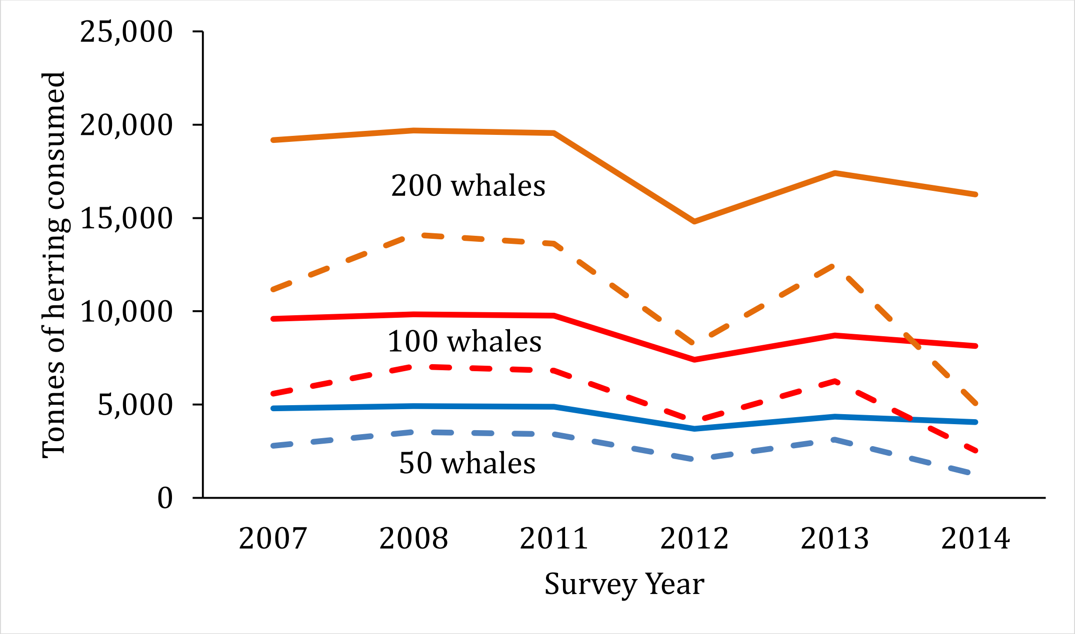

Figure 12. Modeled consumption of herring in Prince William Sound, Alaska based on the observed diet composition for 50 (blue), 100 (red), and 200 (green) whales. Low estimates (dashed lines) exclude other fish and use Witteveen's consumption value of 338 kg/whale/day (Witteveen et al. 2006). High estimates (solid lines) treat other fish as herring and use Roman's daily consumption value of 471kg/whale/day (Roman and McCarthy 2010).

Although many factors play into predation intensity (e.g., number of whales, diet, and attendance patterns) maintaining a high herring biomass provides a buffer to whale predation when predation intensity is variable. Whales foraged on herring in large numbers over much of the spring, fall and winter in PWS. Our most conservative model, starting with 50 whales, estimated an average of 20% of the pre-spawning adult biomass of herring in PWS being consumed by whales over the course of the study. For our high end model, starting with 200 whales, 114% of the pre-spawning adult biomass of herring was consumed (Table 7). For comparison, the last significant harvest of herring from PWS was 3,904 tonnes in 1998 approximately 20% of the spawning biomass (ADFG 2010). While the high end models overestimates of consumption, a large influx of whales into PWS is plausible given scale of whale movements seen in recent years.

Table 7. Modeled percent of pre-spawning adult herring biomass (from age structured model) removed by in Prince William Sound, Alaska based on the observed diet composition for a peak number of 50, 100, and 200 whales. Low estimates exclude other fish and use Witteveen's consumption value of 338 kg/whale/day (Witteveen et al. 2006). High estimates treat other fish as herring and use Roman's daily consumption value of 471kg/whale/day (Roman and McCarthy 2010).

Biomass Year	Biomass (mt)	50 low	50 high	100 low	100 high	200 low	200 high
2007	8,293	33.7%	35.0%	40.8%	70.1%	81.6%	140.1%
2008	13,688	25.7%	27.9%	40.0%	55.9%	80.0%	111.7%
2011	19,237	17.7%	28.8%	40.2%	57.6%	80.3%	115.2%
2012	16,964	12.1%	27.7%	30.8%	55.4%	61.6%	110.9%
2013	13,350	23.4%	21.4%	30.8%	42.9%	61.6%	85.8%
2014	20,295	17.7%	28.8%	40.2%	57.6%	80.3%	115.2%

DISCUSSION

Population estimates of humpback whales

The population of humpback whales in PWS has increased dramatically since the 1980s (Teerlink et al. 2015). This trend paralleled the population growth observed across the North Pacific (Calambokidis et al. 2008). 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 (Fig. 13);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, whales rely on blubber reserves accumulated on the feeding grounds. 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 other leave and return later in the season. This pattern accounts for the year-round presence of humpbacks in Alaska's waters.

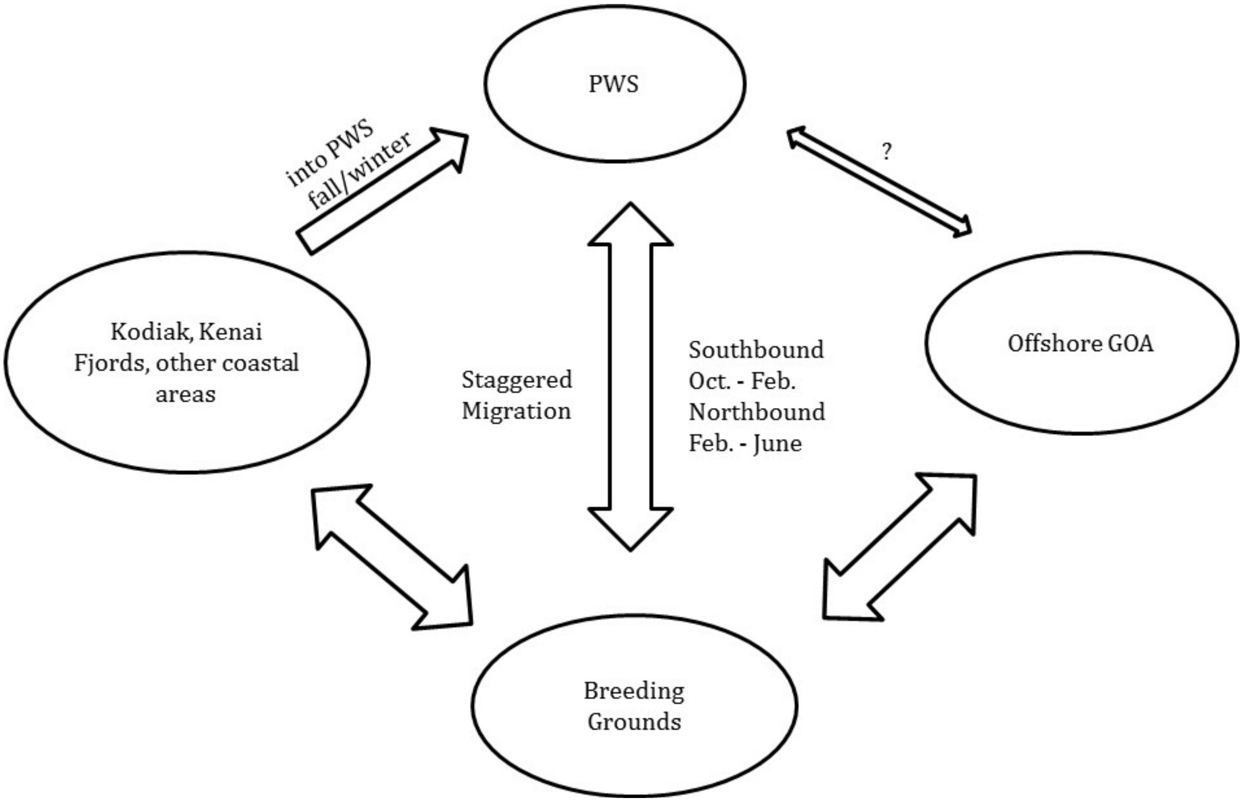

Figure 13. A conceptual model of the factors influencing the number of whales present in Prince William Sound, Alaska. Maybe a short explanation of what the ? means – factors that we still don't understand that influence movement between offshore GOA and PWS? Thanks.

The distribution and abundance of prey influences where humpbacks will be found on the feeding grounds. Mitochondrial DNA suggests that there are separate feeding aggregations across the Gulf of Alaska (i.e., whales in southeastern Alaska are generally not the same individuals that forage in PWS; Baker et al. 2013). Thus, movement in and out of the PWS, with some exceptions, is limited to whales that reside in the northern Gulf of Alaska. Although we have little data on prey resource outside of the Sound, euphausiids production in the Gulf of Alaska, eulachon runs on the Copper River, and herring are probably influencing PWS whale numbers.

Seasonal Trends

The seasonal trends for the majority of humpback whales in PWS are influenced by the movements of adult herring into and around the Sound. (i.e., spawning, migration into the sound, and over-wintering). At these times herring form large shoals that are predictable in time and space providing a high energy resource for whales just prior to the southern migration and as they return from to the Gulf of Alaska after two to four months of fasting (Darling and McSweeney 1985). Throughout this study, groups of whales were associated with large shoals of adult herring.

The timing of whale movements into and within PWS mirrors the herring life cycle. Whale numbers increase in the spring as they return from the breeding grounds to feed on spawning herring. As the herring disperse following spawning, whale numbers within the Sound drop. In the fall, herring aggregate near Montague Entrance and are accompanied by an increasing number of whales. The whales follow the herring into the over-wintering bays, such as Port Gravina, and remain there until they leave for the breeding grounds in late winter. Whales were seen feeding on other prey types including krill and juvenile herring, however, it is unlikely these prey types are driving the movements of the majority of whales in PWS. One prey type we did not evaluate was juvenile salmon. Our surveys did not overlap with the outmigration of salmon from PWS. Anecdotal reports of whales feeding near hatchery release sites suggest that juvenile salmon may be important prey for whales when herring and krill are scarce.

We considered other factors that may affect the number of humpback whales in PWS such as predation, competition and anthropogenic effects (Fig. 14). Killer whales are the only potential predator on humpback whales in PWS. Although we have seen aggressive interactions between humpback and killer whales it is unlikely that predation risk is great enough to influence humpback numbers within the Sound. There is potential for competition between whales, other marine mammals, marine birds and fish for forage fish and krill. We were not able to evaluate the impacts of interspecific competition on whale numbers; this is an area of concern that warrants further investigation.

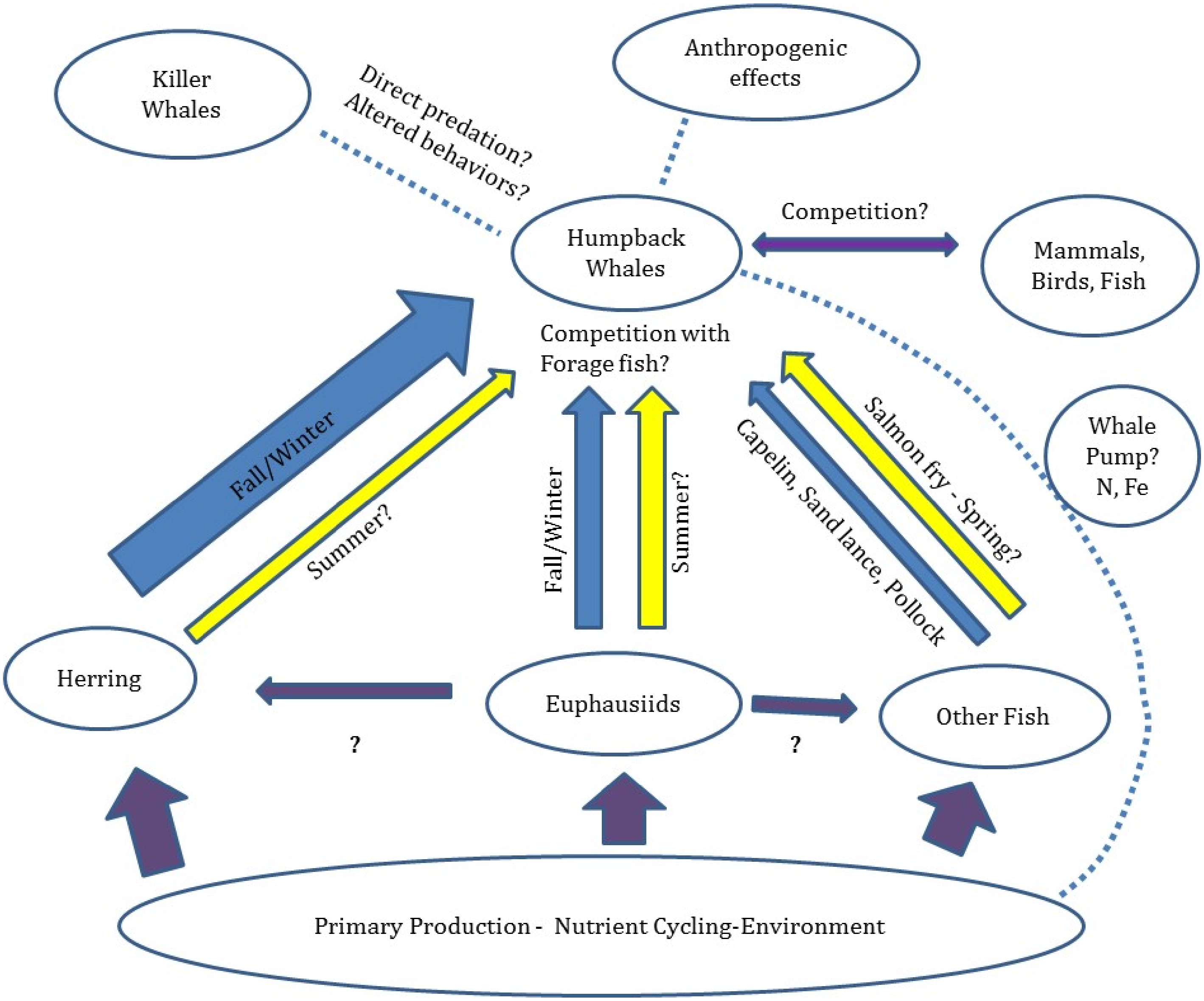

Figure 14. A conceptual model of top-down and bottom-up factors that affect humpback whale numbers in Prince William Sound, Alaska.

Inter-annual Trends

Given the seasonal variation in humpback whale number within PWS, identifying inter-annual trends abundance presents a challenge. Because our surveys were limited to the waters with PWS we are unable to account for whales outside of the Sound. Weather conditions also play into assessing inter-annual trends. By examining encounter rates, we standardized for varying effort between years and eliminate the possibility of counting the same animal more than once. Although the inter-annual trend from 2007-2015 was not statistically significant, the last four year of this series represented a 39% decline in encounter rates. These later years correspond to anomalous oceanographic events in the

North Pacific (“The Blob”, El Niño) and poor primary production (Zador and Yasumiishi 2016, Di Lorenzo 2016).We surmise that this climatic forcing event influenced changes in prey and may account for the decline in encounter rates in recent years. Large shoals of herring have consistently overwintered in Port Gravina since at least 2008, when we began been monitoring humpback whale predation on herring. Avian and mammalian predators feed heavily upon these shoals during the fall and winter months when little alternative prey is available. During our December 2014 survey, we did not locate any large schools of overwintering herring and the number of herring predators was greatly reduced. The 2015 spawning event also proved to be unusual, we did not locate large shoals herring typical of the area in spring, whales were present, but targeting small, fast moving herring schools. Continued monitoring is needed to determine if this trend is the result of a decline in the herring biomass within PWS, a response to warmer water or a combination of the two.

Diet and Dietary Shifts of Humpback Whales

Their high energy density, large biomass and predictable migration patterns make adult herring the most important forage species for humpback whales in PWS. We consistently observed humpbacks feeding on adult herring during the spring, fall and winter months. 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.

Higher trophic levels are indicative of a more piscivorous (e.g., foraging exclusively on herring) diet; as planktivorous (e.g., foraging exclusively on krill) cetaceans have lower trophic levels (TL 2.8 to 3.0, Hoekstra et al. 2002). These data confirmed the visual prey observations of a fish (herring) diet for the whales feeding in PWS. Whales biopsied in April 2014, December 2015, and April 2015 were found at trophic levels higher than expected although analysis of herring and krill isotope data suggests that this could be caused by the presence of carnivorous krill feeding on copepods and extending the food chain length in coastal waters of Prince William Sound compared to more oceanic waters to the west (Arimitsu 2016). The increase in whale trophic level occurred during an unusual mortality event for large whale in the Gulf of Alaska. Trophic level data should be interpreted with caution as trophic level increases can be attributed to starvation in animals (Gannes et al. 1997). Therefore, further investigation and collaboration is needed to explain the increase in whale trophic level.

A lack of alternative prey, such as krill, may have driven PWS individuals into becoming herring specialists relative to their counterparts in southeastern Alaska and the Bering Sea, where krill are the dominant prey. However, from 2012-2014 we did see an increase in the number of whales of feeding on krill, suggesting an increase in the krill biomass during these years. Corresponding to the increase in krill, was an increase in age-0 pollock during 2012 and 2014. Pollock were so abundant and widely distributed during these years that it was difficult to determine what the whales were feeding on. Generally during the two big pollock years there were always herring present when whales were feeding, but in many cases pollock were also present, we couldn’t say with certainty what species were being targeted. We did encounter large schools of age-0 pollock with no whales associated with them, suggesting that herring were the primary target. We made several observations of whales feeding on krill with schools of adult herring nearby, implying that krill may be important prey to PWS whales when available. When selecting prey, whales are making a tradeoff between energy content, abundance, and the cost of locating and capturing prey (Fig. 15). For humpbacks, which feed on many individuals at once, school density as well as the energetic value of the prey become important considerations in prey selection.

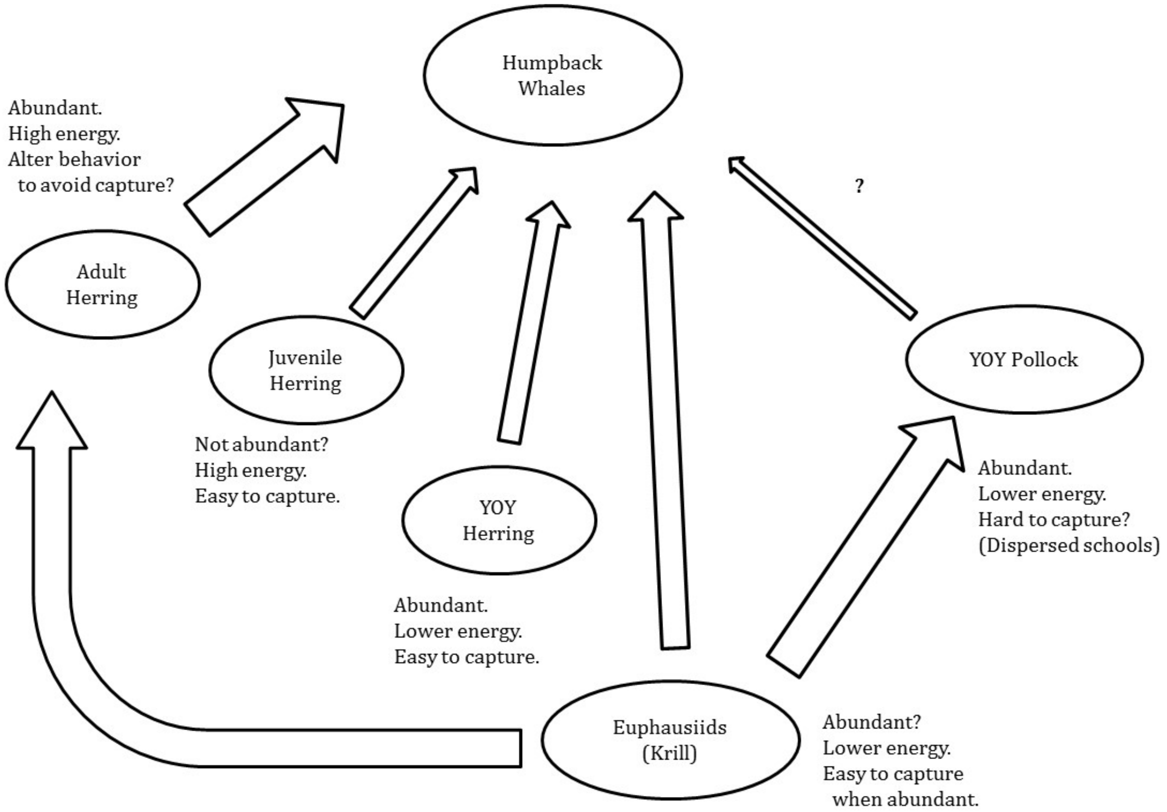

Figure 15. A conceptual model of the factors influencing humpback whales prey selection in Prince William Sound, Alaska.

Predation Rates on Herring by Humpback Whales

The estimated biomass of herring removed by humpback whales was strongly influenced by the number whales within PWS. The challenge is determining a starting point, the number of whales present, for the model. Our population estimate from the mark-recapture model and unique IDs are over estimates of the number of whales with the boundaries of PWS. They represent the number of whales that make use of the Sound (i.e., the whales in the spring may not be the same whales seen in the fall). The number of unique whales seen on each survey underestimates the number of whales present; because we know that we did not photograph every whale. Using the number of whales seen on each survey provides a better reference point for starting the model, although there are still biases (whales not seen or whales counted more than once) between three and 190 whales were counted, knowing the seasonal trends, we selected 50, 100, and 200 whales as reasonable starting points for the model.

Identifying prey posed less of a challenge. Herring schools generally present a distinct signal on echosounders, they are easily captured using nets and jigs, and their scales are often found near foraging whales. Stable isotope analysis supports a diet high in fish for PWS humpbacks. In 2012 and 2014 age-0 pollock were so abundant that they we couldn't be certain which species was being targeted. Based on their higher energy density and denser schooling behavior, it is likely that herring were preferred over pollock as prey. For those years, including fish with herring is probably a reasonable assumption.

At the current biomass, the PWS herring population is vulnerable to whale predation. Even at our lowest estimate, 12% of the pre-spawning adult biomass is being consumed. A major concern is the sensitivity of the consumption model to whale numbers: movements of 50 to 100 whales into or out of a feeding area are common and appear to be occurring more frequently during the recent warm water events in the Gulf of Alaska. The number of whales used in our consumption model represent high and low estimates for whales in PWS, however shifts in whale distribution can be sudden. For example, in 2015 approximately 50 humpbacks moved into Kachemak Bay and were apparently feeding on juvenile herring (Pers. comm. K. Holderied). In southeastern Alaska, 150 -200 whales were missing from Seymour Canal during the fall and winter of 2016 (Pers. comm. L. Barr, S. Carey, and D. Rogers). Seymour Canal has consistently been an important late season (September through January) feeding area (Straley 1990), and the fall of 2016 was the first time since the 1970s that no whales were seen. During winter of 2016-2017 an additional 50-70 whales may have overwintered in Sitka Sound feeding on herring. Given the scale of these whale movements, and the low biomass of PWS herring, there is the potential for dramatic and rapid fluctuation in herring mortality due to predation.

Several aspects of humpback whale and herring biology further exacerbate the potential for whale predation on herring. For example, the schooling behavior of herring makes them attractive prey to humpbacks even at low population levels. Humpback whales are generalists, capable of feeding at many trophic levels if needed. However, there are individuals that specialize in certain prey types, including herring. With energy stores that exceed other predators and alternative prey, whales can maintain predation pressure for a long period of time even when herring abundance is low.

CONCLUSIONS

Humpback whales are a key component of the PWS ecosystem. Their ecological absence from the Gulf of Alaska following intense commercial whaling has ended and populations may now be approaching carrying capacity in the North Pacific. The recovery of this population coincided with major perturbations in PWS:1964 earthquake, 1976/1977 regime shift, introduction of hatcheries, *Exxon Valdez* oil spill, collapse of the herring fisheries, and increased abundance of pollock. These massive changes in their environment appeared to have little impact on the population growth of humpback whales. However, recent events may be a cause for concern. We have demonstrated that herring are an important resource for PWS humpback, and that relatively small changes in whale numbers can have a big impact on herring populations when herring abundance is low. Warm water in the Gulf of Alaska from 2014 -2016 put additional stress on the Gulf of Alaska ecosystem. During our December 2014 survey we did not locate any large schools of overwintering herring and the number of herring predators was greatly reduced. The 2015 spawning event also proved to be unusual, we did not locate large shoals herring typical of the area in spring, whales were present, but targeting small, fast moving herring schools. Anecdotal reports suggest a similar situation during the 2016 spawn. These observations may have been a precursor to an Unusual Mortality Event being declared by NMFS for fin and humpback whales in the Gulf of Alaska. Surveys in southeastern Alaska during August of 2016 found reduced calf production and "skinny whales", suggesting bottom up pressures on humpback populations.

Following over 40 years of population growth, it appears that humpback whales may now be experiencing the effects of bottom-up forcing. This will increases pressure on struggling herring stocks if whales skip or delay their migration. The current herring age structure assessment models may not account increased natural mortality, after the Guideline Harvest Level is set, if there is a dramatic increase in predation during the winter and early spring months due to an influx of whales.

ACKNOWLEDGEMENTS

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The Wildlife Society, Juneau, AK. April 5-7 2011: Moran John R., Janice M. Straley, Ron A. Heintz, Kevin M. Boswell, and Johanna J. Vollenweider. *Commensalism during the Alaskan winter: humpback whales deliver deepwater prey to air breathing predators.*

Hollings Scholar program summer 2011: Elizabeth Parker, Bonita Nelson (Mentor), Dr. Ron Heintz & John Moran (Co-Principal Investigators). *Seasonal and Annual Variation in Energy Density of a North Pacific Euphausiid (Thysanoessa raschii).*

Top-down control of herring workshop, Juneau AK. Sept. 19, 2011. John R. Moran, Janice M. Straley, Stanley D. Rice, Ron Heintz, Terrence J. Quinn II, and Suzanne F. Teerlink. *Late-season abundance and seasonal trends of humpback whales on three important wintering grounds for Pacific herring in the Gulf of Alaska.*

NOAA's Juneau Marine Naturalist Symposium, Juneau, AK. May 9-10, 2011: Moran, John R., Janice M. Straley, Ron A. Heintz, Kevin M. Boswell, and Johanna J. Vollenweider. *Commensal Feeding with Humpback whales.*

Endangered Species Day, Juneau, AK. May 20, 2011: Moran, John R., Janice M. Straley, Ron A. Heintz, Kevin M. Boswell, and Johanna J. Vollenweider. *Commensalism during the Alaskan winter: humpback whales deliver deepwater prey to air breathing predators (general public version).*

Advisory Panel to the Western Pacific Fishery Management Council, Honolulu, HI. 25 June, 2012. *Invited speaker.*

154th meeting of the Western Pacific Fishery Management Council, Honolulu, HI. June 25-28, 2012. *Invited speaker.*

Fishers Forum Honolulu, HI. June 27, 2012: Managing for Recovery of the North Pacific Humpback Whales. *Invited speaker.*

19th Biennial Conference on the Biology of Marine Mammals Tampa, FL. 27 November – 2 December 2011: Moran, John R; Straley, Janice M; Rice, Stanley D; Heintz, Ron A; Quinn II, Terrance J; Teerlink, Suzanne F. *Late-season abundance and seasonal trends of humpback whales on three important wintering grounds for Pacific herring in the Gulf of Alaska.*

19th Biennial Conference on the Biology of Marine Mammals Tampa, FL. 27 November – 2 December 2011: Straley, Jan; Moran, John; Vollenweider, Johanna; Boswell, Kevin; Heintz, Ron; McLaughlin, Kate and Andy; Rice, Stanley. *A comparison of the diet, habitat use and impact of humpback whale predation upon three overwintering herring populations in the Gulf of Alaska.*

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(Megaptera novaeangliae) predation on Pacific herring (Clupea pallasii) populations in the Gulf of Alaska.

Alaska Marine Science Symposium Anchorage, AK, Jan 2012: John R Moran, Stanley D Rice, Janice M Straley, Kevin M Boswell, and Ron A Heintz. *Significance of Whale Predation on Natural Mortality Rate of Pacific Herring.*

Alaska Marine Science Symposium Anchorage, AK, Jan 2012: Kevin M. Boswell, Johanna J. Vollenweider, John M. Moran, Ron A. Heintz, Jason K. Blackburn, and David J. Csepp. *Humpback Whale Foraging Structures Winter Schooling Behavior of Pacific Herring and Facilitates Commensal Predation by Multiple Predators***.**

Guest lecturer - University of Eastern Finland Nov. 2014. John Moran. *Living in a Humpback Whale World*.

Invited speaker - Wildlife photo-ID workshop, Joensuu, Finland Nov. 2014. John Moran. *Challenges of Photo ID during the Alaskan Winter.*

Alaska Marine Science Symposium Anchorage, AK. Jan 2015: John R. Moran, Janice M. Straley and Mayumi L. Arimitsu. *Humpback whales as indicators of herring movements in Prince William Sound.*

Juneau Marine Naturalist Symposium, Juneau, AK. May 2015: John Moran*. Seabirds as indicators of humpback whale prey.*

National Stranding Meeting April 2016: Kate Savage, Bree Witteveen, John Moran, Stephen Raverty, Kathy Burek Huntington, Deborah Fauquier, Kate Wynn, Fran VanDolah, Paul Cottrell, Mandy Migura, Aleria Jensen. *2015 Gulf of Alaska Large Whale Unusual Mortality Event.*

Society for Marine Mammals Biennial Conference San Francisco, CA. December 2015: Kelly Cates Shannon Atkinson, John Moran, Adam Pack, and Jan Straley. *Do testosterone levels of humpback whales suggest breeding activity in summer feeding grounds?*

Alaska Marine Science Symposium Anchorage, AK. Jan 2016: Mandy Lindeberg, Mayumi Arimitsu, Mary Anne Bishop, Dan Cushing, Rob Kaler, Kathy Kuletz, Craig Matkin, John Moran, John Piatt, and Jan Straley. *Response of Top Predators and Prey to Changes in the Marine Environment: Gulf Watch Alaska's Pelagic Monitoring Program.*

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Alaska Marine Science Symposium Anchorage, AK. Jan 2016: Kevin Boswell, Mark Barton, Alexandra Brownstein, Jan Straley, and John Moran**.** *Stable Isotope Analysis* *of Humpback Whales (Megaptera novaeangliae) to Confirm Diet during Winter Foraging.*

Alaska Marine Science Symposium Anchorage, AK. Jan 2016: John Moran and Jan Straley. *Missing Herring: Water Temperature, Relocation or Dinner?*

Alaska Marine Science Symposium Anchorage, AK. Jan 2016: Jan Straley and John Moran Bird Killers of Prince William Sound: A Foraging Strategy Used by Humpback Whales to Detect Schooling Fish.

GoA 2015 Anomalies Workshop Anchorage, AK. January 2016: John Moran*. Fish Anomalies in the Gulf of Alaska, 2014 & 2015 Highlights.*

Invited Speaker. Maui Whale Tales Kapalua, Hawaii February 2016: John Moran. *Hawaii's Humpbacks: What are they doing in Alaska?*

UAS Guest lecturer February 2016: John Moran. Impacts of a recovering humpback whale population.

Alaska Marine Science Symposium Anchorage, AK. Jan 2017: John R. Moran, Matthe.B. O'Dell, Danielle M. S. Dickson, Janice M. Straley and Mayumi L. Arimitsu. *Seasonal distribution of Dall's porpoise in Prince William Sound, Alaska.*

PICES - Drivers of Dynamics of Small Pelagic Fish Resources, Victoria BC March 2017: John Moran, Kevin Boswell and Janice Straley. *Humpback whales ruin a perfectly good overwintering strategy for Pacific herring in Alaska.*

Other Outreach

PWSSC Community Lecture Series, Field Notes radio program, Gulf Watch Alaska Virtual Field Trip, Gulf Watch Project brochure, KCAW Public Radio Interview, NOAA Video -The Science Behind: Whale Recovery in Alaska. 2013.

Personal Communications

Lou Barr - *F/V Gavia* Juneau, AK.

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Shawn Carey – NMFS/AKRO Juneau, AK

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Steve Moffitt – ADFG Cordova, AK.

Dennis Rogers – *M/V Northern Song* Petersburg, AK.

Gary White - Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO.

Online Resources

EVOSTC Long-Term Monitoring Program –
http://www.evostc.state.ak.us/index.cfm?FA=projects.gulfwatch

Gulf Watch Alaska – http://www.gulfwatchalaska.org/

Gulf of Alaska Data Portal – http://portal.aoos.org/gulf-of-alaska.php

Humpback Whales of Southeastern Alaska - http://www.alaskahumpbacks.org/index.html

Appendix 1

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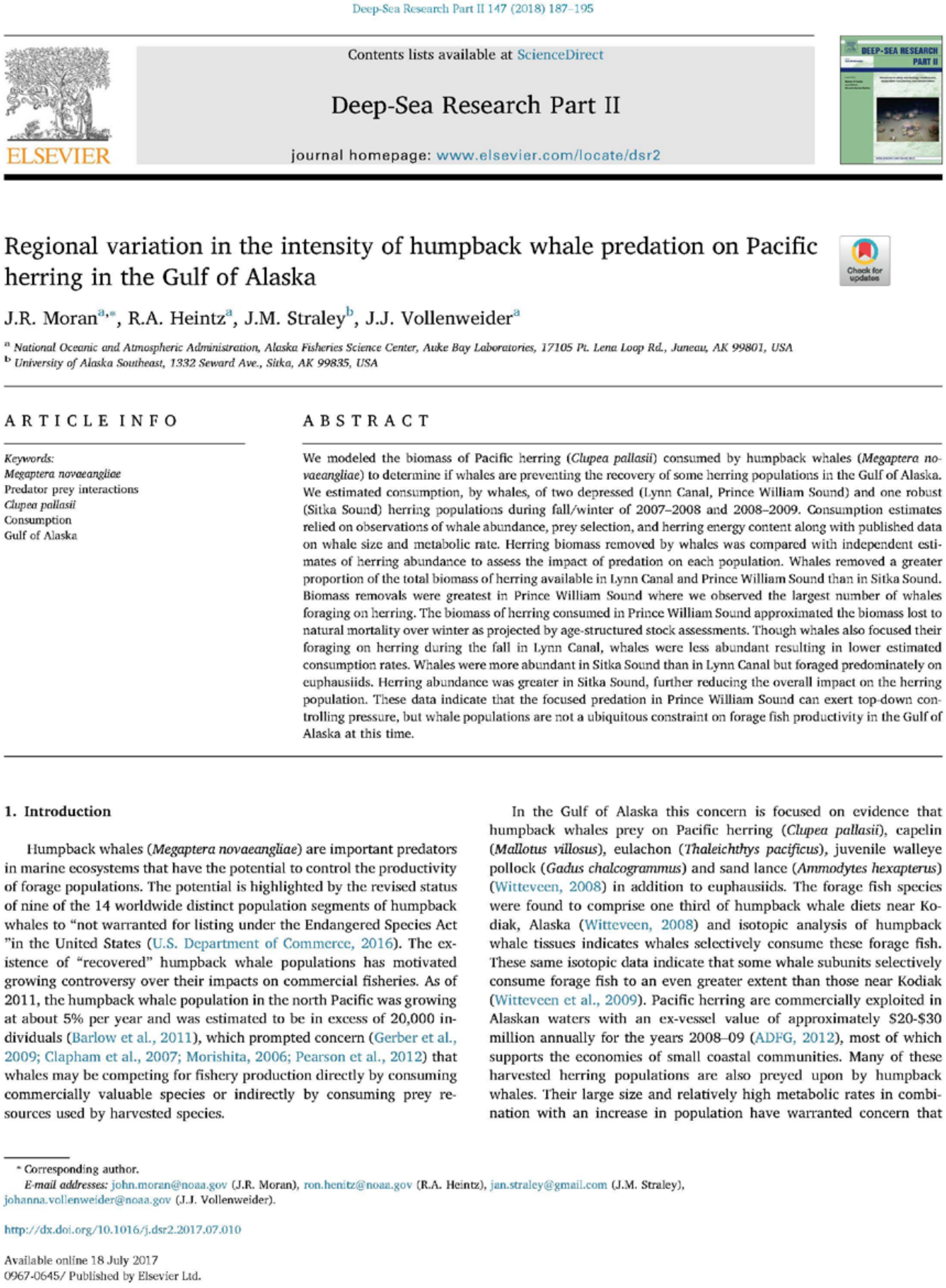

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Regional variation in the intensity of humpback whale predation on Pacific herring in the Gulf of Alaska

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ABSTRACT

We modeled the biomass of Pacific herring (*Clupea pallasii*) consumed by humpback whales (*Megaptera novaeangliae*) to determine if whales are preventing the recovery of some herring populations in the Gulf of Alaska. We estimated consumption, by whales, of two depressed (Lynn Canal, Prince William Sound) and one robust (Sitka Sound) herring populations during fall/winter of 2007–2008 and 2008–2009. Consumption estimates relied on observations of whale abundance, prey selection, and herring energy content along with published data on whale size and metabolic rate. Herring biomass removed by whales was compared with independent estimates of herring abundance to assess the impact of predation on each population. Whales removed a greater proportion of the total biomass of herring available in Lynn Canal and Prince William Sound than in Sitka Sound. Biomass removals were greatest in Prince William Sound where we observed the largest number of whales foraging on herring. The biomass of herring consumed in Prince William Sound approximated the biomass lost to natural mortality over winter as projected by age-structured stock assessments. Though whales also focused their foraging on herring during the fall in Lynn Canal, whales were less abundant resulting in lower estimated consumption rates. Whales were more abundant in Sitka Sound than in Lynn Canal but foraged predominately on euphausiids. Herring abundance was greater in Sitka Sound, further reducing the overall impact on the herring population. These data indicate that the focused predation in Prince William Sound can exert top-down controlling pressure, but whale populations are not a ubiquitous constraint on forage fish productivity in the Gulf of Alaska at this time.

1. Introduction

Humpback whales (*Megaptera novaeangliae*) are important predators in marine ecosystems that have the potential to control the productivity of forage populations. The potential is highlighted by the revised status of nine of the 14 worldwide distinct population segments of humpback whales to “not warranted for listing under the Endangered Species Act ”in the United States (U.S. Department of Commerce, 2016). The existence of “recovered” humpback whale populations has motivated growing controversy over their impacts on commercial fisheries. As of 2011, the humpback whale population in the north Pacific was growing at about 5% per year and was estimated to be in excess of 20,000 individuals (Barlow et al., 2011), which prompted concern (Gerber et al., 2009; Clapham et al., 2007; Morishita, 2006; Pearson et al., 2012) that whales may be competing for fishery production directly by consuming commercially valuable species or indirectly by consuming prey resources used by harvested species.

In the Gulf of Alaska this concern is focused on evidence that humpback whales prey on Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), juvenile walleye pollock (*Gadus chalcogrammus*) and sand lance (*Ammodytes hexapterus*) (Witteveen, 2008) in addition to euphausiids. The forage fish species were found to comprise one third of humpback whale diets near Kodiak, 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 (Witteveen et al., 2009). Pacific herring are commercially exploited in Alaskan waters with an ex-vessel value of approximately $20-$30 million annually for the years 2008–09 (ADFG, 2012), most of which supports the economies of small coastal communities. Many of these harvested herring populations are also preyed upon by humpback whales. Their large size and relatively high metabolic rates in combination with an increase in population have warranted concern that

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humpback whales could be removing 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 inter-annual 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 populations, while other populations remain unaffected. 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 (Sigler and Csepp, 2007). Humpback whales have been observed foraging on large, dense, overwintering shoals of herring in southeastern Alaska and Prince William Sounds (Boswell et al., 2016; Straley et al., in this issue).

The objective of this report is to examine the extent to which humpback whale predation impacts Pacific herring populations in the Gulf of Alaska during the fall and winter months. The study focuses on three Pacific herring populations; Lynn Canal and Prince William Sound, which are depressed and have been closed to commercial fishing since 1982 and 1993, respectively (Thynes et al., 2016; Sheridan et al., 2014), and Sitka Sound which appears healthy with current harvest levels are near historic highs (Thynes et al., 2016). By comparing the impact of humpback whale predation on these populations it is possible to examine the feasibility of the hypothesis that humpback whales are inhibiting the recovery of herring in Lynn Canal and Prince William Sound. Specifically, we compared the proportion of herring consumed by humpback whales in each location calculated as consumption rates of humpback whales relative to estimates of herring biomass derived from stock assessments. Consumption rates of humpback whales are modeled by combining observations of 1) whale abundance, 2) prey selection, 3) prey energy content, 4) whale size, and 5) whale metabolic rates at each location. These estimates of consumption are related to assessments of the herring stock biomass in each location to determine the relative intensity of whale predation on these populations.

2. Methods

We estimated the proportion of Pacific herring biomass consumed by humpback whales from Lynn Canal, Prince William Sound, and Sitka Sound (Fig. 1) for the winters of 2007–2008 and 2008–2009. The study period spanned September 15 to March 15, the time frame in which we observed herring begin to aggregate and form overwintering shoals, hereafter referred to as "winter". We estimated the biomass removed for each location and winter using two contrasting modeling scenarios to provide a range of uncertainty. The large size of humpback whales prevents direct measurement of ingestion rates; therefore, estimates of consumption were derived from the allometry between whale size and metabolic requirements. The model scenarios represent different estimators of humpback metabolic rates and consequently a range of high and low consumption requirements. Dividing the resulting consumption ranges by estimates of total herring population biomass yields a measure of the intensity of humpback whale predation on the herring populations in each location. Details of the model components and associated parameters are described below.

2.1. Biomass removal model

The biomass removal model relies on both published data and data collected in the field, including estimates of whale metabolic rates, whale sizes, diet composition, and energy content of herring. The model is given in Eq. (1).

$$C = \sum_{t=1}^{182} \frac{p_t \sum_{i=1}^{100} K\left(\frac{n_t}{100} w_i\right)^{\beta}}{ED_t} \tag{1}$$

In Eq. (1) C is the total biomass removed by whales over the of the 182 days of the "winter" study period; p_t is the proportion of the whales known to be eating herring on the tth day of the study period, n_t is the number of whales foraging on the tth day, w_i is the mass of a whale in the ith size class, k and β are allometric parameters describing the metabolic rate of whales in the ith size class and ED_t is the energy density of herring on the tth day of study period. Different modeling scenarios to define the range of biomass removals relied on different combinations of n_t, K and β. Multiple combinations of these parameters resulted in multiple values of C, which represents the consumption scenario of a single winter in a specific location. Each scenario was simulated 50 times and a set of simulations is referred to as an experiment. The locations studied include Lynn Canal, Sitka Sound and Prince William Sound (Fig. 1). The two winters were 2007–2008 and 2008–2009. Details of parameters used in the biomass removal model and how they are used to estimate predation intensity are described below.

2.2. Whale abundance

Whale abundance (n_t) was calculated using the number of unique individuals present in a given area on each day of the study and scaled upward based on mark-recapture abundance estimates. Observations of individual whales and mark-recapture estimates of whale abundance are given in Straley et al. (in this issue). Briefly, monthly surveys were conducted in each location for two field seasons. For each winter there is a mark-recapture estimate of the total number of whales present throughout the winter and five to six observations of the number of unique whales present on specific days. From the latter values, models were developed to describe the daily abundance of whales at each location by piecewise regression. Linear models relating the number of unique whales to the number of days that had elapsed from the start of the survey period were fit between visual observations. The daily abundance of whales in Prince William Sound was not estimated for the winter of 2007–2008 because only three surveys were conducted over a limited spatial area (Straley et al., in this issue). Instead, the daily abundance observed in 2008–2009 was scaled to the 2007–2008 mark recapture estimate. The observed daily abundance ($n_{t\ observed}$) was scaled using the mark recapture estimates ($\hat{n}_{aw}$) for a given area (a) and winter (w) using the following equation:

$$\sum n_t = \sum \alpha n_{t\ observed} \tag{2}$$

where α is a coefficient that minimizes

$$\hat{n}_{aw} - Maximum\,(n_t) \tag{3}$$

Summing the daily abundance estimates over a survey period indexes the relative foraging effort, which is termed "whale days".

2.3. Prey selection

Estimates of the proportion of whales feeding on herring relied on direct observations of prey being consumed, remains after feeding, and acoustic mapping of the prey fields using a 50/200 kHz frequency echosounder. Samples were collected to verify species identities whenever possible. The proportion of groups foraging on herring on a given day of the study was modeled from the visual observations. The study period was divided into six 30-day periods beginning on 15 September. The proportion of groups foraging on herring observed during each period was used to estimate p_t for each day within a period. Values of p_t for each period and location (Table 1) were derived from observations combined from both winters in each location (Straley et al., in this issue) and were estimated as the proportion of whales

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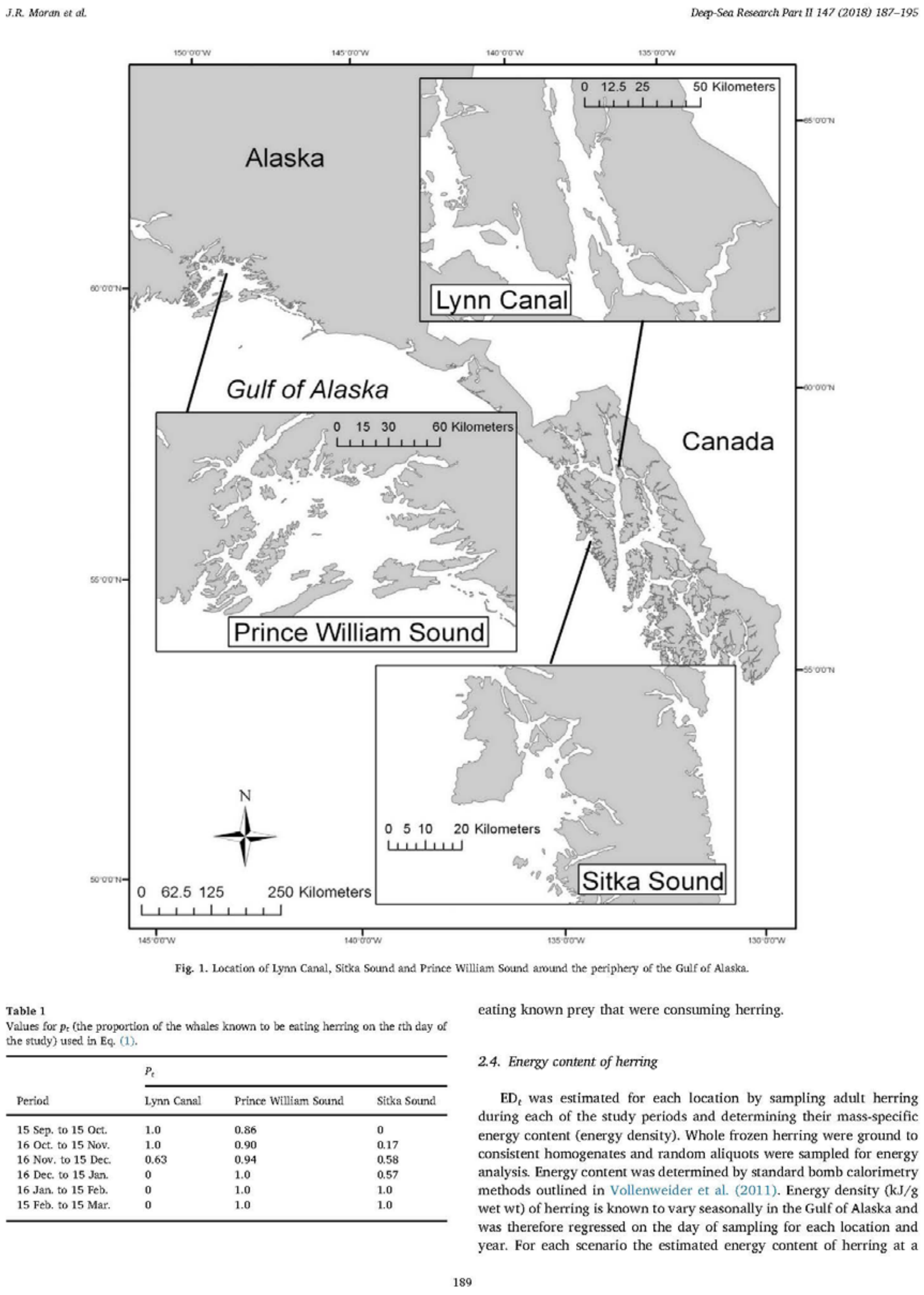

Fig. 1. Location of Lynn Canal, Sitka Sound and Prince William Sound around the periphery of the Gulf of Alaska.

Table 1
Values for p_t (the proportion of the whales known to be eating herring on the tth day of the study) used in Eq. (1).

	P_t		
Period	Lynn Canal	Prince William Sound	Sitka Sound
15 Sep. to 15 Oct.	1.0	0.86	0
16 Oct. to 15 Nov.	1.0	0.90	0.17
16 Nov. to 15 Dec.	0.63	0.94	0.58
16 Dec. to 15 Jan.	0	1.0	0.57
16 Jan. to 15 Feb.	0	1.0	1.0
15 Feb. to 15 Mar.	0	1.0	1.0

eating known prey that were consuming herring.

2.4. *Energy content of herring*

ED_t was estimated for each location by sampling adult herring during each of the study periods and determining their mass-specific energy content (energy density). Whole frozen herring were ground to consistent homogenates and random aliquots were sampled for energy analysis. Energy content was determined by standard bomb calorimetry methods outlined in Vollenweider et al. (2011). Energy density (kJ/g wet wt) of herring is known to vary seasonally in the Gulf of Alaska and was therefore regressed on the day of sampling for each location and year. For each scenario the estimated energy content of herring at a

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given location was randomly selected from the 95% confidence interval for the tth day.

2.5. Whale weight

As current sizes of humpback whales are not available, a simulation was initiated by converting a set of randomly selected humpback whale lengths to mass. A set of 100 lengths were randomly selected from a normal distribution with mean = 12.30 m and s.d. = 1.34. This distribution corresponds to the length distribution for humpback whales harvested along the coast of British Columbia (Nichol and Heise, 1992). Each length in the distribution (L_i) was converted to mass using the relationship

$$w_i = \frac{0.0158 L_i^{2.95}}{100} \qquad (4)$$

where w_i is the mass is in kg and L_i in m (Lockyer, 1976). The same size distribution was used throughout a simulation.

2.6. Whale metabolic rate

Many models of whale consumption in the primary literature were found to derive from 18 independent sources (Appendix A). Nine of those models described allometric relationships between the size of marine mammals and their metabolic rates, six models related size to ingestion rate and three models related size to heat loss and ventilation rate. Included in the metabolic rate allometries were six models based on the Kleiber curve. The remaining three metabolic rate allometries were derived from doubly labeled water – isotope ratio (DW-IR) methods. DW-IR studies are considered the most accurate methods for estimating field metabolic rates (Sparling et al., 2008). To compare the estimated metabolic rates from the various models, we used the reported or observed values of K and β in a simulation of the modeling scenario estimating consumption (Eq. (1)) using n_t for Prince William Sound in 2008–2009.

2.7. Herring biomass estimates and predation intensity

Predation intensity was calculated by dividing the estimate of herring consumption by estimates of herring spawning stock biomass. The Alaska Department of Fish and Game estimates spawning stock biomass of herring for Sitka Sound and Prince William Sound using age-structured models as part of their annual stock assessments. These estimates derive from annual surveys conducted on the spawning grounds each spring and index the biomass of herring available for consumption after spawning. Predation intensity in Prince William Sound and Sitka Sound on a given survey is calculated using the herring biomass from the previous spring as estimated in the stock assessments. There is no age-structured model for Lynn Canal, so predation intensity is based on monthly acoustic surveys conducted in conjunction with the whale abundance surveys (Boswell et al., 2016). Daily consumption was summed over a given month and divided by the acoustically determined estimate of herring biomass to estimate predation intensity.

3. Results

3.1. Whale abundance

Humpback whales were generally most abundant in all locations in the first half of each year's survey from September through December. Timing of peak abundance depended on both year and location. In Sitka Sound the peak abundance of whales was observed in November during the first survey (2007–2008) and in October during the second survey (2008–2009) (Fig. 2). Peak abundance in Lynn Canal tended to be earlier, occurring in September in the first survey and October during the second survey. In Prince William Sound whales remained at high abundance throughout the fall of the second survey and only began declining after December (Fig. 2). While the daily abundance for first survey in Prince William Sound was not estimated, the largest number of whales was observed in December.

There was much more foraging effort exerted by humpback whales in Prince William Sound than the other areas as a result of their prolonged period of peak abundance there. The total number of humpback whales present in Prince William Sound over the 182 survey days in (2008–2009) was more than threefold that of Sitka (18,719 vs. 5114 whale days) and more than ninefold that of Lynn Canal (2019 whale days) (Table 2).

3.2. Prey selection

Humpback whale prey choice depended on the season and location sampled. In Lynn Canal and Prince William Sound whales foraged almost entirely on herring in the first months of the survey. While few whales were observed foraging on herring after December in Lynn Canal, whales in Prince William Sound continued to focus on herring throughout the entire survey period. In contrast, humpback whales in Sitka focused on euphausiids early in the winter and switched to herring later (Straley et al., in this issue).

3.3. Energy content of herring

Herring energy content tended to be highest when whales were most abundant. In fall the peak energy levels were near 10 kJ per g (wet weight) when averaged across the locations and years (Fig. 3). In Lynn Canal and Prince William Sound herring were available throughout the survey (Fig. 3) and their energy declined as time progressed. In contrast, herring were not available to sample in Sitka Sound until later in the survey. However, the absence of herring early in the survey had little effect on their energy content later as indicated by comparisons of herring from Lynn Canal and Sitka Sound (Fig. 3). For example, Sitka Sound herring averaged 7.6 kJ/g in January 2009 compared with 7.3 kJ/g for Lynn Canal herring in early February.

3.4. Whale metabolic rates and consumption

Comparison of humpback whale consumption using the 18 published metabolic rate models produced estimates of consumption ranging between 1500 and 16,000 t of herring. The highest consumption estimates were derived from allometries involving DW-IR studies, while Kleiber's model based on basal metabolic rate approximated the lowest estimates. We excluded the highest value derived from an ingestion rate allometry which was developed for all vertebrates. Similarly, we excluded some of the lowest values which assumed basal metabolic rates and do not account for foraging activity.

From the range of available metabolic rate models, we selected two different allometric models to estimate the daily energy needs of foraging humpback whales that encompassed the range of published estimates of whale metabolic rates (Appendix A). The first model, herein referred to as the low-end model (Perez and McAlister, 1993), is based on Kleiber's (1961) observation that the allometric scalar in the relationship between mass and basal metabolic rate is near the ¾ power. This relationship holds over several orders of magnitude and offers the promise of extrapolating the metabolic rate for species for which it cannot be measured directly. The second model, herein referred to as the high-end model (Acquarone et al., 2006), extrapolates data from doubly labeled water experiments involving otariids and odobenids weighing up to 1300 kg to estimate field metabolic rates of humpback whales.

Metabolic rate under the low-end model predicts average daily metabolic cost. It estimates metabolic demand from mass using values of 209 and 0.75 for K and β, respectively. The value for K has been adjusted upwards from Kleiber's basal metabolic rate model to reflect

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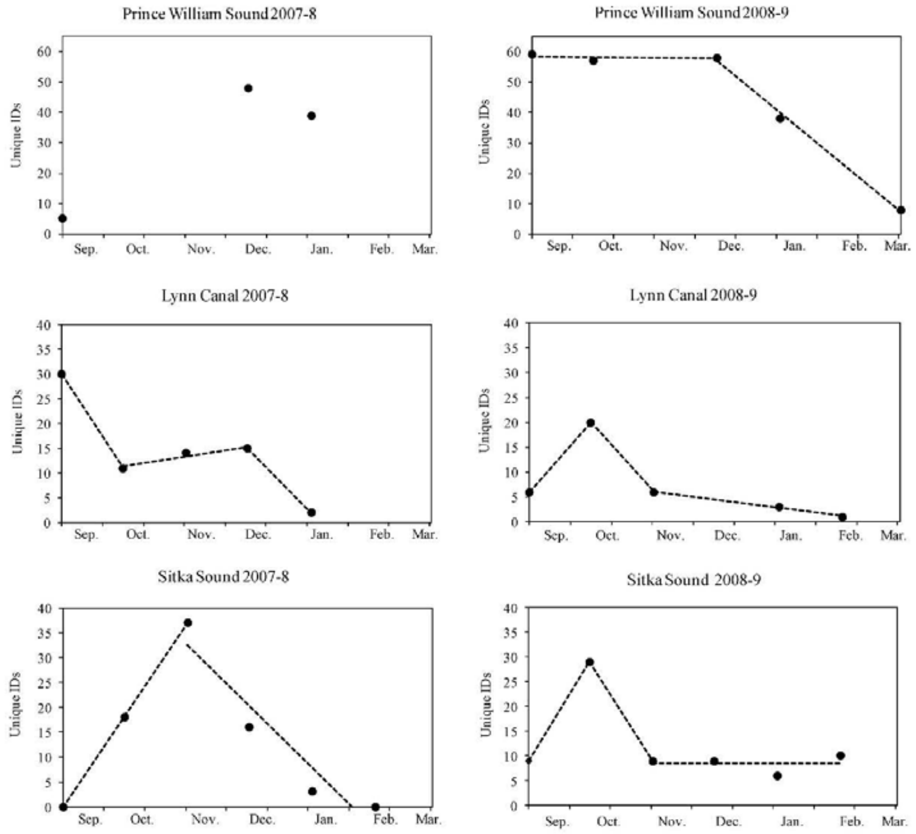

Fig. 2. Daily abundances of humpback whales in Lynn Canal, Sitka Sound and Prince William Sound. The daily abundance for Prince William Sound in 2007–2008 was not estimated because only three surveys were conducted over a limited spatial area. The study period spanned between September 15 (day 1) and March 15 (day 182).

Table 2
Range of estimated herring biomass removed from Lynn Canal (LC), Sitka Sound (SS), and Prince William Sound (PWS) under the Perez and McAlister (low-end) and Acquarone (high-end) models. The biomass of herring consumed is the median value from 50 simulations. Predation intensity is estimated as the median biomass consumed divided by the total herring biomass observed in the spring previous to the modeled survey period.

Location	Survey period	Whale days	Herring consumed (t)	Total herring biomass (t)	Predation intensity
LC	07–08	2940	732–1987	1461	50–136%
	08–09	2019	501–1335	499	100–267%
SS	07–08	7190	1018–2776	101,209[b]	1–3%
	08–09	5114	813–2168	108,192[b]	1–2%
PWS	07–08	8915	2639–7443	9650[a]	27–77%
	08–09	18,719	4388–12,989	20,737[a]	21–63%

[a] Steve Moffitt, personal communication, Alaska Department of Fish and Game.
[b] Sherri Dressel, personal communication, Alaska Department of Fish and Game.

the additional cost of activity. The adjustment is based on observations of respiration in captive gray whales (Wahrenbrock et al., 1974). These estimates underestimate demand during winter foraging periods, because humpback whales must secure sufficient energy reserves during to fuel a fast that lasts at least two months (Gabrielle et al., 1996; Mate et al., 1998). During this period humpback whales migrate to their calving grounds, mate and return to the foraging grounds. Some of the returning females will be accompanied by suckling calves. Thus additional costs not predicted by the low-end model include late-term gestation and lactation.

The high-end model estimates the field metabolic rate from mass using values of 1.1 and 0.83 for K and β, respectively (Acquarone et al., 2006). Field metabolic rates for otariids and odobenids may be more consistent with balaenopterids because otariids and odobenids also fast for periods during the year. Field metabolic rates measured with doubly labeled water include routine metabolic rates as well as costs associated with foraging, digestion and growth. In addition, many of the observations in the high-end model included lactating females. For each simulation, estimates of metabolic demand based on the high-end model were randomly selected from the 95% prediction interval. Neither the low-end nor the high-end models explicitly estimate costs associated with gestation or lactation. In addition, both models assume 100% of ingested prey is digested.

3.5. *Predation intensity*

In Lynn Canal most of the whale foraging effort on herring was focused on the beginning of the survey period when whales were abundant and herring were relatively scarce. Overall, humpback whales consumed between 732 and 1987 t of herring in 2007–2008 and 501–1335 t in 2008–2009 (Table 2). In November 2007 whales

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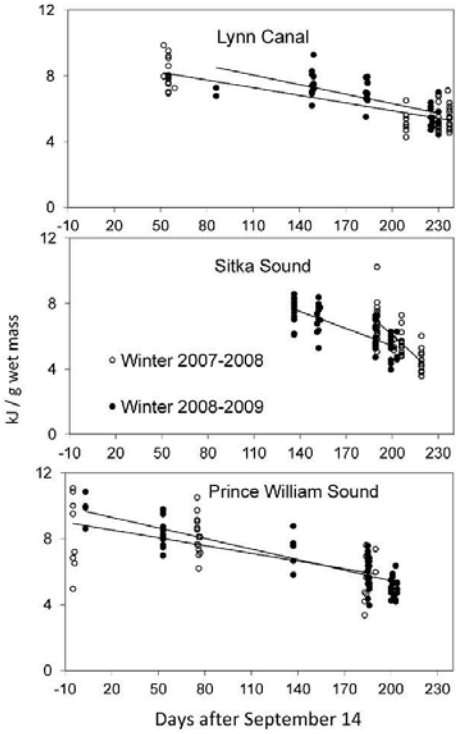

Fig. 3. Energy loss in herring from Lynn Canal, Sitka Sound and Prince William Sound during the winters of 2007–2008 and 2008-009. Elapsed days is the same scale as in Fig. 2.

Table 3
Estimated monthly herring biomass removed from Lynn Canal in 2007 under the Perez and McAlister (1993) (low-end) and Acquarone et al. (2006) (high-end) models. The biomass of herring consumed is the median value from 50 simulations. Predation intensity is the predicted biomass of herring removed in a given month divided by the estimated biomass of herring present at that time as determined by acoustic surveys.

Month	Herring consumed (t)	Total herring biomass (t)	Predation intensity
November	202–542	9043	2.2–6%
December	89–240	41,334	< 1%

consumed approximately one-third of the total biomass consumed over the study period. Comparing whale consumption with the herring biomass present in November yielded estimates of predation intensity ranging between 2.2% and 6.0% (Table 3). In December, the mass of herring consumed declined as whales departed, but herring biomass increased substantially. Thus, predation intensity dropped to less than 1% regardless of the modeling scenario. After December no whales were observed consuming herring.

In Sitka Sound humpback whales were abundant in fall but their foraging effort focused on euphausiids. Consequently, predation intensity on herring was very low. In absolute terms whales only slightly more tonnage of herring in Sitka than in Lynn Canal (Table 2) even though whales were more abundant in Sitka Sound. In Sitka Sound humpback whales consumed 1018–2776 and 813–2168 t in 2007–2008 and 2008–2009, respectively (Table 2). This represented less than 3% of the total biomass of herring available. The biomass consumed was far less than the biomass removed in the Sitka Sound sac roe harvest: 14,616 and 15,012 t in 2007 and 2008, respectively (ADFG, 2012)

Whales foraged in large numbers over much of the winter in Prince William Sound, resulting in significant predation intensity (Table 2). In absolute terms, whales consumed between 2639 and 7443 t in 2007–2008 representing a predation intensity of 27–77%. In, 2008–2009 whales consumed between 4388 and 12,989 t and predation intensities ranged between 21% and 63% of the total biomass present in spring 2008. For comparison the last harvest of herring from Prince William Sound was 3904 t in 1998 (ADFG, 2010).

4. Discussion

Increased predation intensity by humpback whales in Lynn Canal and Prince William Sound relative to Sitka Sound is consistent with the hypothesis that humpback whales are a limiting factor in the recovery of herring in Alaska when populations are depressed. In Sitka Sound, where the herring population is commercially fished, humpback whales consume less than 3% of the spawning stock biomass. In contrast, whales in Prince William Sound consumed 21–77% of the spawning stock biomass. In Lynn Canal, predation intensities in November 2007 ranged between 2 and 6% when the seasonal herring biomass was increasing (as herring moved into the area) and local whale abundance was declining. Presumably predation intensity was higher in September and October when herring abundance was lower (Sigler and Csepp, 2007) and whale abundance higher.

It is important to recognize that predation intensities reported are reflective of only half the year. This work was conducted during the fall and winter months and humpback whales also feed on herring during the spring and summer. Therefore predation estimates presented here are conservative and the impact of whale predation could be significantly greater. Another point of uncertainty in our estimates relates to juvenile herring. As in any stock assessment, estimates of spawning stock biomass in each location does not account for juveniles and only indexes a portion of the total number of herring present. Total biomass of herring is larger than the spawning stock values used here to estimate predation intensity, which would have the effect of causing our estimates of predation intensity to be overestimates. On the other hand, juvenile herring are preyed upon by whales, but it is not certain to what extent whales forage on them.

It is important to note that whales are not suspected of causing population declines in Lynn Canal or Prince William Sound. The herring population in Lynn Canal was closed to fishing in 1981. The cause for its failure is unknown, but habitat loss and overfishing have been identified as important factors (Carls et al., 2008). In Prince William Sound the herring population crashed following an epizootic involving viral hemorrhagic septicemia virus (Carls and Rice, 2007). Rather, results from our study indicate that humpback whales exert top-down control in populations that are in a depressed abundance already, regardless of the reason they are depressed.

4.1. *Identification of the most appropriate consumption estimate*

The true whale consumption rate of herring is likely closer to the low-end estimate than the high-end estimate. This is because recent observations (Leaper and Lavigne, 2007; Boyd, 2002) indicate that field metabolic rates for whales should be near the basal rates predicted by Kleiber's model (Kleiber, 1961). The reasons given for the convergence of field and predicted basal metabolic rates derive from the reduced cost of locomotion in large whales (Boyd, 2002), metabolic depression associated with periods of fasting (Leaper and Lavigne, 2007) and the observation that heat loss rates in whales are lower than basal metabolic rates (Folkow and Blix, 1992).

These arguments for reduced metabolic rates in whales contrast sharply with predictions of field metabolic rates generated from doubly labeled water studies. Sparling et al. (2008) indicated that carefully

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conducted doubly labeled water studies can accurately predict field metabolic rates in pinnipeds. While the high-end model relies on doubly labeled water studies conducted specifically on marine mammals, it does not include observations published in contemporary or more recent publications. Re-examination of the data reported by Acquarone et al. (2006), Boyd (2002) and Nagy et al. (1999) indicates the allometric slope should be 0.79, not 0.82 as reported (Appendix A). Consequently, doubly labeled water studies produce and an allometric relation that differs from the Kleiber model by a factor of 6.5 (Appendix A). The low-end model we employed differs from Kleiber's model by a factor of 2.24. The latter estimate is more in line with the conclusions drawn by Boyd (2002), Folkow and Blix (1992), and Leaper and Lavigne (2007).

One explanation for the higher values predicted by doubly labeled water studies is that the low-end model does not account for the metabolic cost of lactation. Some of the studies referenced by Acquarone et al. (2006), Boyd (2002) and Nagy et al. (1999) involved lactating pinnipeds. However most of these were otariids and lactation in humpback whales is more analogous with the intensive lactation of phocids (Oftedal, 1997). Humpback whales have been estimated to output 2000 MJ/d as milk during mid-lactation (Oftedal, 1997). For a 30 t female, this is about 200 MJ more than her average daily metabolic cost as predicted by the low-end model. Thus for lactating females, average daily metabolic demand is higher than Kleiber's model by a factor of approximately 4.5, still less than the value predicted by the high-end model. Costs associated with gestation are somewhat lower than those of lactation (Lockyer, 2007). If they are assumed to equal lactation then gestating and lactating females would have metabolic demands roughly twice that predicted by the low-end model. If all females in the population were either gestating or lactating then metabolic demands would be approximately 50% greater than those calculated under the model. Thus accounting for lactation and gestation conservatively results in predicted consumption rates that are about 3.3 times the consumption estimated under the Kleiber model, which is about half the estimate of the high-end model and about 1.4 times the estimate of our low-end model.

4.2. *Impacts of whale predation on Lynn Canal herring*

Dramatic seasonal changes in the abundance of herring in Lynn Canal obscure the impact of whales on this population. Monthly acoustic surveys conducted during the winter of 2007–2008 (Straley et al., in this issue) revealed a pattern consistent with that of Sigler and Csepp (2007), which indicates a biomass of herring in midwinter (December to February) that swamps the local spawning stock biomass. It is unclear if the large winter shoal represents a mixture of discrete spawning stocks or the local Lynn Canal spawning stock is a component of a much larger population. If the Lynn Canal spawning stock is a discrete population, then whales have a large impact. Most of the whale foraging occurred early in our sampling period when a relatively small biomass of herring would be present. For example, between 2001 and 2004 Sigler and Csepp (2007) found that the biomass of herring present in October ranged between 700 and 1200 t, approximately equal to the estimated spawning stock biomass (Carls et al., 2008). If the herring present in October represented the local spawning population, then humpback whales are consuming somewhere near 16–29% of the spawning stock in a single month. Alternatively, if these fish represented a small fraction of a much larger spawning stock, then predation intensity would be much lower. For example, the biomass removed in 2007–2008 (732–1987 t) represents $< 1\%$ of the peak herring biomass (91,000 t) observed in February (Straley et al., in this issue).

Early in the survey period humpback whales were the dominant predators of herring in Lynn Canal. Between 2001 and 2004 the greatest number of Steller sea lions (*Eumetopias jubatus*) never exceeded 800 animals (Womble and Sigler, 2006) and they were most abundant between October and February. Based on average size of sea lions, the sea lion biomass likely never exceeded 800 t. Whales were abundant between September and December and their maximum biomass was twice that of Steller sea lions in 2007 and 50% more in 2008. Though herring are a conspicuous prey item of sea lions, consumption of herring by sea lions is likely a quarter to a half that of whales. Ectothermic predators have even less effect on herring. Walleye pollock, the most abundant piscivorous predator, had biomass estimates of less than 637 t between 2001 and 2004 (Sigler and Csepp, 2007). The proportion of herring in pollock diet is relatively low (Yang and Nelson, 2000; Urban, 2012) and therefore not likely to contribute significantly to herring mortality relative to that imposed by whales.

4.3. *Impacts of humpback whale predation on Prince William Sound herring*

Estimates of predation intensity in Prince William Sound provide the best evidence for humpback whales limiting the recovery of a depressed herring population. Whales removed a biomass approximating the State of Alaska's Guideline Harvest Level for herring in Prince William Sound, which ranges from zero to 20% of the spawning biomass when spawning biomass exceeds 22,000 t (State of Alaska, 1998). This level of fishing mortality is considered sustainable and occurs in addition to natural mortality. Between 2001 and 2006 natural mortality over winter accounted for the loss of 1800 to 5500 t of adult herring (Marty et al., 2010). The biomass consumed by humpback whales over the winters of 2007–2008 and 2008–2009 falls within this range, suggesting that humpback whales account for the majority of the winter mortality of adult herring in Prince William Sound. While the hypothesis that humpback whale predation is a factor limiting the recovery of herring is feasible based on the estimates provided herein it is much less certain whether whale consumption adds significantly to current levels of mortality and if herring mortality is currently unsustainable.

4.4. *Impacts of whale predation on Sitka Sound herring*

The consumption of Sitka Sound herring by humpback whales is underestimated here. Whale predation on herring in Sitka Sound was not significant until late in the survey, when herring began staging prior to spawning. It is not known where the herring were located in fall to early winter or if whales were foraging on them before they arrived in Sitka Sound. The number of unique whales increased slightly in February 2009 when herring arrived in Sitka Sound, presenting the possibility that some individuals were traveling with the herring. Consequently, some level of predation occurred outside our study area. Nevertheless, predation intensity would have to increase tenfold to equal that of the other locations.

4.5. *Conclusion*

By remaining in Alaskan waters during the fall and winter months, humpback whales can exploit large shoals of lipid-rich herring. Late season predation had varying effects on the different herring stocks examined in this study. The shoaling behavior of overwintering and pre-spawning herring in predictable locations increases their vulnerability to humpback whale predation. When these shoals are large relative to the number of whales, then impacts to the local herring stock is minimal. However, when herring abundance is low, their tendency to aggregate continues to make an attractive target for foraging whales. Predation effects on herring can be minimized if the shoaling behavior is delayed until humpback whales begin their winter migration to calving grounds. Thus, the late arrival of herring in Sitka Sound coupled with their large biomass led to a minimal effect of whale predation. This contrasts with Prince William Sound, where there was a significant spatial and temporal match between whales and a depressed herring population. This temporal and spatial match between whales and herring resulted in whales removing a significant proportion of the spawning stock biomass. Therefore, the interplay between herring

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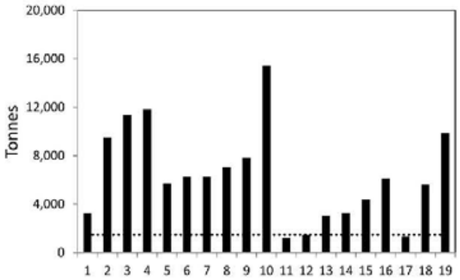

Fig. A1. Estimated total consumption for a single simulation of the winter of 2008–2009 in Prince William Sound using values of K and β found in different reports. The horizontal line depicts the estimate produced by Klieber's (1961) relation for basal metabolic rate. Models are classified as being derived from doubly labeled water isotope ratio studies (DW-IR), ingestion rate allometries (Ingestion), metabolic rate allometries (Kleiber) or alternative approaches (Other). Published models are found in: 1. Nagy et al. (1999) (all mammals), 2. Current pinniped FMRs with walrus, 3. Nagy et al. (1999) (mammalian carnivores), 4. Acquarone et al. (2006), 5. Trites et al. (1997), 6. Armstrong and Siegfried (1991), 7. Sigurjónsson and Víkingsson (1997), 8. Innes et al. (1987), 9. Reilly et al. (2004), 10. Nagy (2001), 11. Boyd (2002). 12. Kleiber (1961), 13. Laidre et al. (2007), 14. Lockyer (1981), 15. Perez and McAlister (1993), 16. Sigurjónsson and Víkingsson (1997), 17. Folkow and Blix (1992), 18. Blix and Folkow (1995), 19. Armstrong and Siegfried (1991).

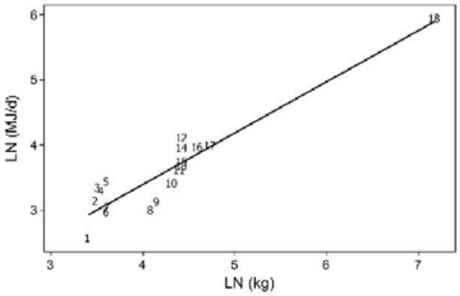

Fig. A2. Comparison (natural log- natural log) of body weights (kg) and current published metabolic (MJ/d0 rates of foraging pinnipeds and walrus based on DW-IR studies. Symbol numbers : 1. Trillmich and Kooyman (2001), 2. Costa and Gentry (1986), 2. Costa et al. (2000), 3. Costa et al. (1989a), 4. Costa et al. (1985), 5. Arnould and Boyd (1996), 6. Costa et al. (1985), 7. Sparling et al. (2008), 8. Costa and Gales (2003), 9. Costa and Gales (2003), 10. Costa et al. (1991), 11. Costa et al. (1989b) Abstract, 12. Costa et al. (1989a), 13. Costa et al. (1985), 14. Costa et al. (1985), 15. Reilly and Fedak (1991), 16. Costa and Gales (2000), 17. Reilly et al. (1996), 18. Acquarone et al. (2006).

shoaling behavior, stock size and whale attendance patterns dictate the extent to which whales can be expected to directly impact Alaska's herring fisheries. We suggest that managers use caution when setting quotas for herring and consider the effects of a recovering whale population on depressed or declining stocks.

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Appendix A

Rationale for selecting allometric models

The models used for our analysis were selected after a review of published allometries. We identified 10 different models describing the allometric relationship between the size of marine mammals and metabolic rate, six models relating size to ingestion rate and three other models relating size to heat loss and ventilation rate (Fig. A1). Included in the metabolic rate allometries were six models based on the Kleiber curve, which includes the Perez model. The remaining four metabolic rate allometries were derived from doubly labeled water-isotope ratio (DW-IR) methods, which included the high-end model. Also included were Nagy et al. (1999) values for all mammals and mammalian carnivores, which were derived in his review. Some authors employed multiple techniques, including Sigurjónsson and Víkingsson (1997) and Armstrong and Siegfried (1991). Our review also indicated that the high-end model did not include all of the contemporary and more recent DW-IR studies of pinnipeds, so we created a model

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based on the existing DW-IR studies of foraging pinnipeds including Acquarone's walrus observations. The allometric model is shown below in Fig. A2 and referred to as "current pinniped FMRs" in Fig. A1.

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Appendix 1

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Appendix 2

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Seasonal presence and potential influence of humpback whales on wintering Pacific herring populations in the Gulf of Alaska

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ABSTRACT

This study addressed the lack of recovery of Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska, in relation to humpback whale (*Megaptera novaeangliae*) predation. As humpback whales rebound from commercial whaling, their ability to influence their prey through top-down forcing increases. We compared the potential influence of foraging humpback whales on three herring populations in the coastal Gulf of Alaska: Prince William Sound, Lynn Canal, and Sitka Sound (133–147°W; 57–61°N) from 2007 to 2009. Information on whale distribution, abundance, diet and the availability of herring as potential prey were used to correlate populations of overwintering herring and humpback whales. In Prince William Sound, the presence of whales coincided with the peak of herring abundance, allowing whales to maximize the consumption of overwintering herring prior to their southern migration. In Lynn Canal and Sitka Sound peak attendance of whales occurred earlier, in the fall, before the herring had completely moved into the areas, hence, there was less opportunity for predation to influence herring populations. North Pacific humpback whales in the Gulf of Alaska may be experiencing nutritional stress from reaching or exceeding carrying capacity, or oceanic conditions may have changed sufficiently to alter the prey base. Intraspecific competition for food may make it harder for humpback whales to meet their annual energetic needs. To meet their energetic demands whales may need to lengthen their time feeding in the northern latitudes or by skipping the annual migration altogether. If humpback whales extended their time feeding in Alaskan waters during the winter months, the result would likely be an increase in herring predation.

1. Introduction

The number of North Pacific humpback whales (*Megaptera novaeangliae*) has increased in the past four decades to over 21,800 whales in 2006 (Barlow et al., 2011) with an annual population growth rate of 4–7% (Calambokidis et al., 2008). Most humpback whales within the Alaskan population are seasonal migrants, moving from high latitude feeding areas to low latitudes for breeding. While on the feeding areas, humpbacks form discrete maternally-directed and genetically-distinct feeding aggregations (Baker et al., 1985, 1986). This means that calves will return as juveniles and adults to the same feeding area where their mothers introduced them. In the Gulf of Alaska (GOA), two feeding aggregations of humpback whales have been documented: Southeast Alaska/Northern British Columbia (in this paper shortened to Southeast Alaska) and the Northern GOA.

The prey base for humpback whales in the North Pacific is diverse, ranging from large zooplankton to schooling fish and varies by location, season and possibly individual preference (Witteveen et al., 2011). Well-documented North Pacific humpback whale prey include: Pacific herring (Boswell et al., 2016; Krieger and Wing, 1986), multiple species of krill *Thysanoessa* spp., *Euphausia pacifica* (Burrows et al., 2016; Krieger and Wing, 1986; Nemoto, 1957; Szabo, 2015), juvenile salmon *Oncorhynchus* spp. (Chenoweth et al., 2017), capelin *Mallotus villosus*, Pacific sandlance *Ammodytes hexapterus*, juvenile walleye pollock *Theragra chalcogramma*, (Krieger and Wing, 1986; Witteveen et al., 2008; Rice et al., 2011), eulachon *Thaleichthys pacificus*, Pacific sandfish *Trichodon trichodon*, surf smelt *Hypomesus pretious* (Witteveen et al., 2008) and myctophids *Stenobrachius leucopsarus* (Neilson et al., 2015).

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Appendix 2

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While the increase in humpback whale numbers in the North Pacific is a success story (Barlow et al., 2011), it may be having an effect on its prey populations. Furthermore, as humpback whales continue to recover globally, perhaps to above pre-whaling levels (Ivashchenko et al., 2016), their ecological impact increases (Baker and Clapham, 2004; Ripple et al., 2014). The ability for these large predators to influence their prey through top-down forcing (Baum and Worm, 2009; Bowen, 1997) might become a significant concern for management agencies, especially considering commercial fisheries interests target the same species. In the GOA, some Pacific herring stocks have remained depressed long after commercial fishing stopped (Rice et al., 2011). The hypothesis that predation by humpbacks might be impeding a rebound of herring makes sense for areas where humpback whale populations have significantly rebounded. Thus, linkages between humpback whales and fisheries in the GOA have frequently focused on direct competition for herring (Boswell et al., 2016; Heintz et al., 2010; Liddle, 2015; Teerlink, 2011).

The general behavior of herring is to gather in fall, after the water column becomes mixed and then overwinter deep in the bays and channels often near their spawning areas (Brown et al., 2002; Boswell et al., 2016; Hay, 1985). The maturing adults gradually enter bays and deep channels, forming 1arge, deep aggregations that remain as loosely aggregated schools for several weeks to months before spawning (Barnhart, 1988). Consequently, herring become vulnerable to whale predation when both overlap temporally and spatially. In Alaskan waters, the overlap begins during the fall, when herring begin to move to deeper water for the purposes of winter foraging. Some humpbacks follow the herring and others begin their migration to the southern breeding areas. By winter, all herring have moved into deeper water for overwintering (Boswell et al., 2016; Sigler and Csepp, 2007; Sigler et al., 2017) and a few whales may continue to forage. In early spring, herring become active, moving to shallower depths, in preparation for spawning, and whales begin returning from breeding areas.

In our study, three areas (Fig. 1) have in common humpback whales that forage upon shoals of Pacific herring during the fall and winter, however, the extent of prior knowledge about whales and herring in the fall and winter varied across each area. In Prince William Sound (PWS), within the northern GOA, there was little information available on the overlap of humpback whales and herring during the fall and winter (Day and Prichard, 2004; Hall, 1979). Interviews with fishermen and others with local knowledge documented herring presence in fall and winter (Brown et al., 2002). During 1994–1996, herring surveys reported humpback whales and herring were together during the fall and winter (from Matkin and Hobbs as reported in Okey and Pauly, 1999). However, the number of whales, geographic distribution, and seasonal trends were unknown in PWS, which provided impetus for this present study.

The relationships between humpback whales and herring were better understood in Southeast Alaska, where humpbacks were observed foraging on densely-aggregated herring during several winters (Straley et al., 1994). In Sitka Sound (SS), year-round studies on humpback whales to assess the relationship between humpbacks and potential prey (herein for our purposes "prey") have been conducted since the early 1980s (Liddle, 2015; Straley, 1990; Straley et al., 1994). Those studies documented the number of humpbacks foraging on both herring and euphausiids (termed krill for this study) during the fall and winter (Straley, 1990; Straley et al., 1994), but the proportion of herring and krill in the diet remained unknown. In Lynn Canal (LC), humpback presence has been documented year-round from shore-based observations (T. Quinn, University of Alaska Fairbanks, unpublished data), but the numbers of whales using this entire area during the fall and winter, and the target prey were unknown.

In this paper, we report on humpback whales in the three areas: PWS, LC, and SS. Specifically, we identified and counted humpback whales in each area during the fall and winter, observed and characterized their feeding behavior, and applied isotopic analyses to corroborate diet (Witteveen et al., 2009). We documented temporal and spatial patterns of humpback whales and herring to assess how the predator-prey relationship varied demographically.

2. Materials and methods

2.1. *Study areas*

Located along the perimeter of the GOA, Prince William Sound, Lynn Cana, and Sitka Sound are distinct geographically (Fig. 1) and oceanographically. PWS, the most northern study site (60.5°N 147.0°W), has relatively protected waters characterized by a complex coastline of glacial fjords and islands, with an area of approximately 4500 km^2. The other study areas are located in Southeast Alaska, which is a mosaic of islands adjacent to the mainland of Canada, deeply incised with glacial fjords, many passageways, and bays. SS is situated mid-way along the outer coast of Baranof Island (57.0°N 135.5°W), encompassing approximately 450 km^2 and is directly exposed to the elements of the GOA. LC (58.4°N 134.8°W), is a long north-south oriented deep trench located to the north and east of SS in the inside waters of Southeast Alaska. The LC study area encompasses approximately 500 km^2 and includes the waters of southern LC and the adjacent waters of northern Stephens Passage.

Adult herring typically congregate near the spawning grounds several weeks to months before spawning (Barnhart, 1988; Boswell et al., 2016; Sigler and Csepp, 2007). Spawning occurs in SS in mid-March to early April (Thynes et al., 2016), in LC in April (Thynes et al., 2016) and PWS in late March to May (Norcross et al., 2001).

In our study areas, herring populations are now and historically have been managed as an important target of commercial fishing (Carlson, 1980). Sizes of each herring population were available from the spring spawning biomass estimates conducted by the state of Alaska (Gordon et al., 2009) and winter biomass estimates from independent researchers (Boswell et al., 2016). For example, in 2009, in PWS, herring spring spawning biomass was estimated at 19,500 t (Steve Moffit, Alaska Department of Fish and Game, pers. comm.). The two study areas in Southeast Alaska, SS and LC, had spawning biomass estimates of 68,511 and 453 t, respectively (Gordon et al., 2009). However, in LC in February 2009 the overwintering herring biomass estimate was 32,295 (± 3020 SE) tonnes (Boswell et al., 2016), a substantial increase from the spawning biomass, indicating this area supported many spawning aggregations of herring that dispersed prior to spawning in LC. In SS, the overwintering biomass in February 2009 was estimated to be 82,970 (± 12,960 SE) tonnes (Rice et al., 2007). Only SS has sustained a herring fishery in recent years, including the years of our study. Prince William Sound and LC had not recovered from low biomass levels (Rice et al., 2007) and did not meet minimum biomass levels to sustain a commercial fishery.

2.2. *Whale survey effort*

In PWS, eight surveys were conducted aboard the 18-m vessel M/V *Auklet*, starting and ending in Cordova, circumnavigating PWS for a total survey distance total of 4587 km (Table 1a). Each survey lasted five to six days covering roughly the same route with at least two trained observers aboard. One observer, at a minimum, was present in the wheelhouse along with skipper looking for signs of whale activity during all daylight hours. Total distance traveled each day was recorded on a handheld Garmin72 GPS and tallied for the entire survey. In Sitka Sound and LC, 46 and 25 surveys, respectively, were conducted during day trips from small boats (< 10 m) with two observers aboard. A GPS recorded the track line for a total survey distance of 2282 km for LC and 1110 km for SS. When daylight and weather conditions limited surveys, effort was focused on areas with higher concentrations of whales (Table 1b and c). Although as effort increases, the number of whales identified reaches an asymptote (the actual number of whales in

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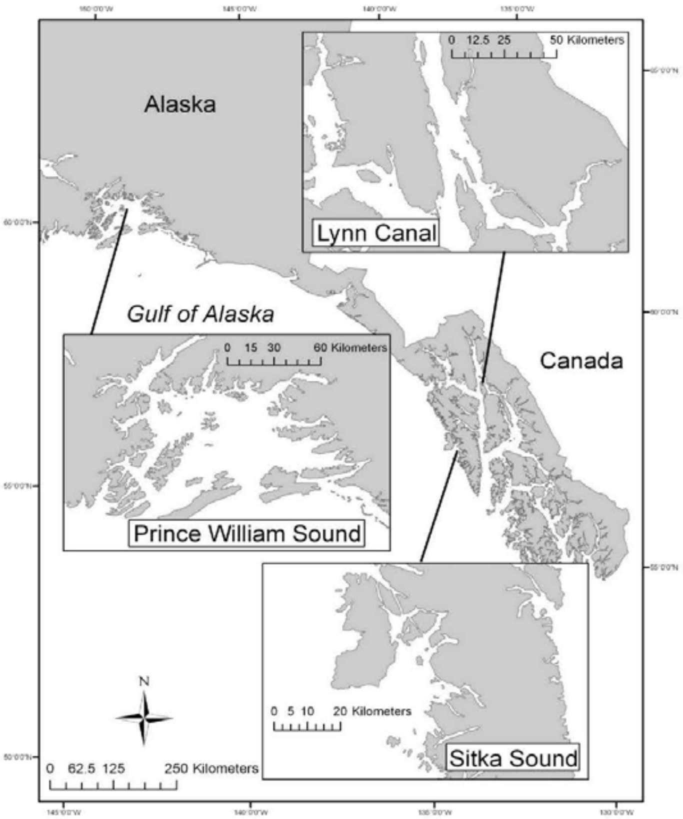

Fig. 1. Locations of the Prince William Sound, Lynn Canal, and Sitka Sound study areas.

the area), we were unable to parameterize the nonlinear relationship between counts and effort, and thus results are presented without standardization for effort.

2.3. *Monthly whale observations across the fall and winter seasons*

Data were tabulated monthly. Each year the first month started 15 September–14 October and the last month was 15 February–14 March. Not all study areas had monthly surveys each year, resulting in 8, 10 and 11 months of data tabulated for PWS, LC, and SS, respectively (Table 1a–c).

2.4. *Groups of whales, behavior determination and age class*

Whales were considered part of a group if they dove and surfaced in synchrony for four or more surfacing's and were in close association, usually within a body length of each other. Whales were considered as a single whale if not in close association with one or more whales. Sometimes numerous whales (from ten to 50) would feed in one area giving the appearance of a group of whales feeding and in association with one another. While these whales may join other whales and dive in synchrony briefly for one or two dive cycles, the associations are very fluid, implying no consistency to the association with another whale. These whales were recorded as single whales.

The behavior of each group was recorded. Whale behaviors were recorded as: 1) feeding: defined as diving and surfacing repeatedly in the same area with prey visible on the echosounder or seen within the water; 2) sleeping: defined as resting or motionless at or just below the surface; 3) traveling: defined as directed swimming in one direction or 4) milling: defined as moving in an unspecified direction, sometimes with an erratic path of travel or circling, giving the appearance searching. Also recorded, if possible, were whale age classes (calf, adult, or juvenile). An adult is a whale over five years old, a calf is a whale less than a year old in close association with the presumed mother, and a juvenile is a whale whose birth year is known and age is 1–5 years old (Clapham, 2009).

2.5. *Photo-identification of individual whales*

If daylight and sea conditions allowed, whales were approached for photographing the ventral surface of their flukes for individual identification based on distinctive color patterns (after Katona et al., 1979). We used Nikon D-300, D-200, and D-70 cameras equipped with 80–200 mm zoom or 300 mm fixed lenses to capture digital images of the flukes and other body features and marks. Photo-IDs were cataloged and entered into a relational database that allowed us to make monthly and yearly tallies for comparisons across both years of the study.

2.6. *Overwintering whales*

Humpbacks can achieve their southerly migration from Alaska to Hawaii in as little as 36 days (Gabriele et al., 1996). However, B. Mate (unpublished data, Oregon State University, Newport, OR) recorded a 30-day transit from Hawaii to mid British Columbia, Canada from

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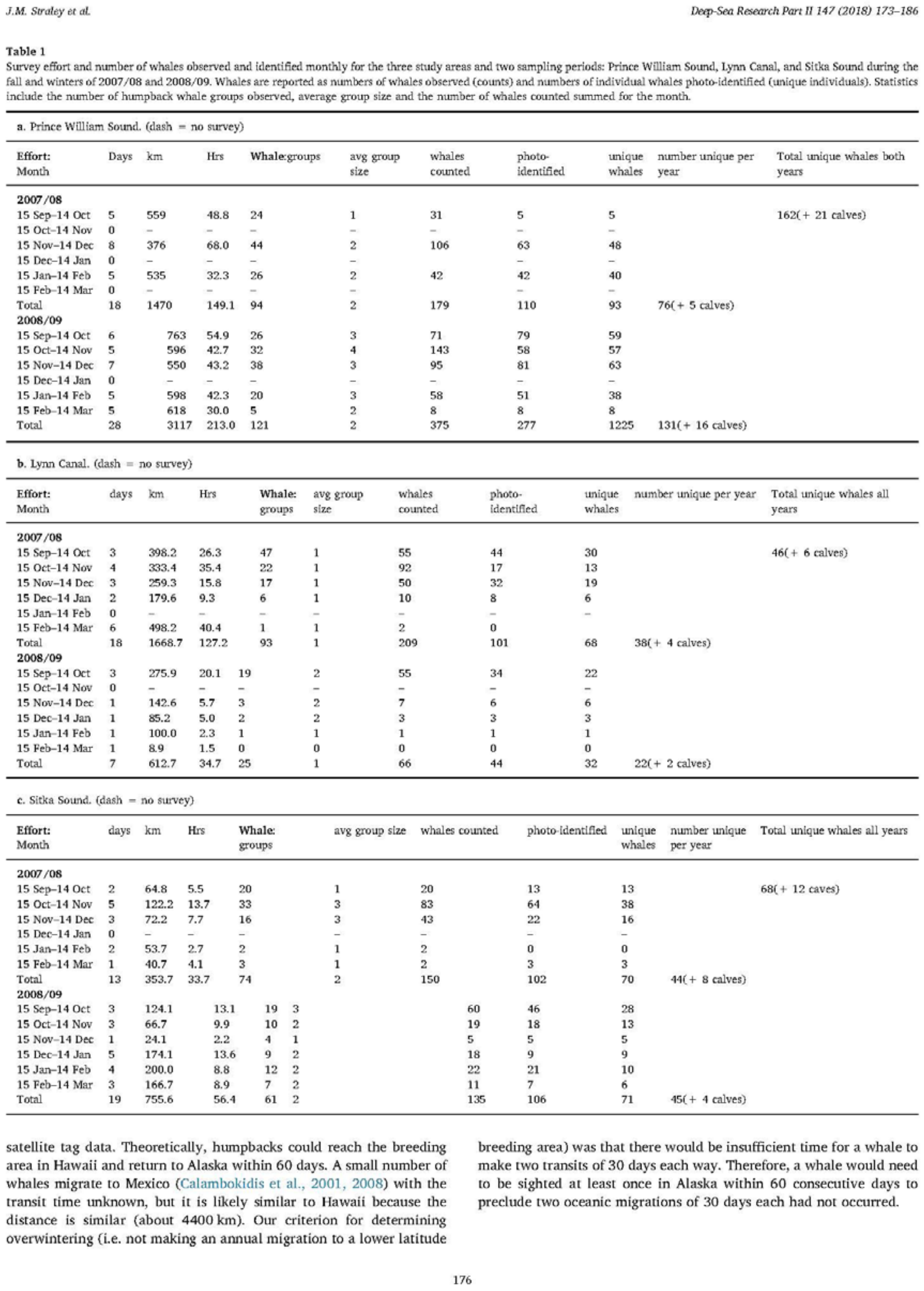

Table 1
Survey effort and number of whales observed and identified monthly for the three study areas and two sampling periods: Prince William Sound, Lynn Canal, and Sitka Sound during the fall and winters of 2007/08 and 2008/09. Whales are reported as numbers of whales observed (counts) and numbers of individual whales photo-identified (unique individuals). Statistics include the number of humpback whale groups observed, average group size and the number of whales counted summed for the month.

a. Prince William Sound. (dash = no survey)

Effort: Month	Days	km	Hrs	**Whale**:groups	avg group size	whales counted	photo-identified	unique whales	number unique per year	Total unique whales both years
2007/08										
15 Sep–14 Oct	5	559	48.8	24	1	31	5	5		162(+ 21 calves)
15 Oct–14 Nov	0	–	–	–	–	–	–	–		
15 Nov–14 Dec	8	376	68.0	44	2	106	63	48		
15 Dec–14 Jan	0	–	–	–	–		–	–		
15 Jan–14 Feb	5	535	32.3	26	2	42	42	40		
15 Feb–14 Mar	0	–	–	–	–		–	–		
Total	18	1470	149.1	94	2	179	110	93	76(+ 5 calves)	
2008/09										
15 Sep–14 Oct	6	763	54.9	26	3	71	79	59		
15 Oct–14 Nov	5	596	42.7	32	4	143	58	57		
15 Nov–14 Dec	7	550	43.2	38	3	95	81	63		
15 Dec–14 Jan	0	–	–	–	–	–	–	–		
15 Jan–14 Feb	5	598	42.3	20	3	58	51	38		
15 Feb–14 Mar	5	618	30.0	5	2	8	8	8		
Total	28	3117	213.0	121	2	375	277	1225	131(+ 16 calves)	

b. Lynn Canal. (dash = no survey)

Effort: Month	days	km	Hrs	**Whale:** groups	avg group size	whales counted	photo-identified	unique whales	number unique per year	Total unique whales all years
2007/08										
15 Sep–14 Oct	3	398.2	26.3	47	1	55	44	30		46(+ 6 calves)
15 Oct–14 Nov	4	333.4	35.4	22	1	92	17	13		
15 Nov–14 Dec	3	259.3	15.8	17	1	50	32	19		
15 Dec–14 Jan	2	179.6	9.3	6	1	10	8	6		
15 Jan–14 Feb	0	–	–	–	–	–	–	–		
15 Feb–14 Mar	6	498.2	40.4	1	1	2	0			
Total	18	1668.7	127.2	93	1	209	101	68	38(+ 4 calves)	
2008/09										
15 Sep–14 Oct	3	275.9	20.1	19	2	55	34	22		
15 Oct–14 Nov	0	–	–	–	–	–	–	–		
15 Nov–14 Dec	1	142.6	5.7	3	2	7	6	6		
15 Dec–14 Jan	1	85.2	5.0	2	2	3	3	3		
15 Jan–14 Feb	1	100.0	2.3	1	1	1	1	1		
15 Feb–14 Mar	1	8.9	1.5	0	0	0	0	0		
Total	7	612.7	34.7	25	1	66	44	32	22(+ 2 calves)	

c. Sitka Sound. (dash = no survey)

Effort: Month	days	km	Hrs	**Whale:** groups	avg group size	whales counted	photo-identified	unique whales	number unique per year	Total unique whales all years
2007/08										
15 Sep–14 Oct	2	64.8	5.5	20	1	20	13	13		68(+ 12 caves)
15 Oct–14 Nov	5	122.2	13.7	33	3	83	64	38		
15 Nov–14 Dec	3	72.2	7.7	16	3	43	22	16		
15 Dec–14 Jan	0	–	–	–	–	–	–	–		
15 Jan–14 Feb	2	53.7	2.7	2	1	2	0	0		
15 Feb–14 Mar	1	40.7	4.1	3	1	2	3	3		
Total	13	353.7	33.7	74	2	150	102	70	44(+ 8 calves)	
2008/09										
15 Sep–14 Oct	3	124.1	13.1	19	3	60	46	28		
15 Oct–14 Nov	3	66.7	9.9	10	2	19	18	13		
15 Nov–14 Dec	1	24.1	2.2	4	1	5	5	5		
15 Dec–14 Jan	5	174.1	13.6	9	2	18	9	9		
15 Jan–14 Feb	4	200.0	8.8	12	2	22	21	10		
15 Feb–14 Mar	3	166.7	8.9	7	2	11	7	6		
Total	19	755.6	56.4	61	2	135	106	71	45(+ 4 calves)	

satellite tag data. Theoretically, humpbacks could reach the breeding area in Hawaii and return to Alaska within 60 days. A small number of whales migrate to Mexico (Calambokidis et al., 2001, 2008) with the transit time unknown, but it is likely similar to Hawaii because the distance is similar (about 4400 km). Our criterion for determining overwintering (i.e. not making an annual migration to a lower latitude breeding area) was that there would be insufficient time for a whale to make two transits of 30 days each way. Therefore, a whale would need to be sighted at least once in Alaska within 60 consecutive days to preclude two oceanic migrations of 30 days each had not occurred.

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2.7. Whale abundance estimation using the Huggins closed-capture model

Abundance of humpbacks was estimated based on numbers of individually photo-ID'd whales as described above. The first photo-ID of each whale was the 'mark' and a "recapture" of the whale was a photograph taken on a subsequent day. This formed the basis of the mark-recapture abundance calculation methodology (Hammond, 1986; Stevick et al., 2001). Bias resulting from matching errors of images of insufficient quality could influence the estimate of abundance using mark-recapture models. To help minimize this error, all images were quality coded using angle of the flukes relative to the camera (with the ventral surface of the flukes being perpendicular to the camera being the highest quality), sharpness of the image, and percent of the flukes visible (i.e. not under water or out of frame) as criteria. Images were ranked as good, fair, poor, or of insufficient quality (Straley et al., 2009). Photographs deemed poor or of insufficient quality were excluded from the mark-recapture analysis. Photographs of the flukes of humpback calves were also excluded, because the initial photo-ID capture probability and therefore, the recapture probability for calves, is complicated by their co-occurrence with their mothers and is therefore not independent (Teerlink, 2011). The probability of recapture in later years can be difficult because pigmentation patterns of calf flukes tend to change more than those of adult flukes, thus leading to overall abundance errors (Hammond, 1986). Appendices A–C provide the photo-ID "capture" history data for individuals for the three study areas, including the number of images (filtered for quality) used in the analysis.

Whale abundances were estimated using the Huggins closed-capture model (Huggins, 1989). All modeling was done in program MARK (White and Burnham, 1999). The closed-capture modeling setting was used to estimate abundance in each area with populations assumed to be closed during the survey season only (i.e. no new recruitment or emigration) (Seber, 1982). The Huggins closed-capture model was chosen because it distinguishes between "no sightings" from "no effort" for a given sampling period. This is important because there was not always a consistent number of surveys within a given survey season for a particular area, and it is important that gaps in survey effort are not treated as an absence of humpback whales. Instances where there was no equivalent survey at that time of year for a given year were assigned capture probabilities of zero. A suite of models for comparing humpback whale abundance was developed for each study area. These included models where capture probabilities co-varied with different measurements of effort (kilometers traveled vs. hours spent), and a null model where all capture probabilities were constrained (one estimate for the entire study, Table 2). We had no additional information to correct effort. We independently evaluated each model using the Akaike's Information Criterion corrected for small sample sizes (AIC_c) where competing models are ranked by goodness of fit and model complexity. By selecting the model that had the lowest AICc value we avoid over parameterization (Burnham and Anderson, 2002).

For all survey areas, each year was grouped separately to allow the population to be "open" between surveys. This allows for migration and thus poses no requirement for a given level of foraging ground fidelity. In each area, individual capture probabilities were estimated for each survey (available in appendices), and estimates of absolute abundance were derived for each survey year. Identification errors were minimized given the relatively small population size, and quality-coded images.

The lower and upper 95% confidence intervals (LCI, UCI) of the abundance estimate were based on the number of unique individuals seen, M_{t+1}, which ensures that the LCI was no less than this value. This adjustment (Gary C. White, Colorado State University, pers. comm.) is

$$LCI = \hat{f}_0 / C + M_{t+1} \tag{1}$$

$$UCI = \hat{f}_0 {}^{*} C + M_{t+1}, \tag{2}$$

for which $\hat{f}_0$ is the estimated number of animals never seen and C is a correction factor.

These parameters were estimated by:

$$\hat{f}_0 = \hat{N} - M_{t+1}$$

$$C = \exp\left\{1.96\left[\ln\left(1 + \frac{\mathrm{var}(\hat{N})}{\hat{f}_0^2}\right)\right]^{1/2}\right\} \tag{3}$$

Table 2

Huggins closed-capture modeling results for Prince William Sound (PWS), Southern Lynn Canal (LC), and Sitka Sound (SS). Standard errors of the abundance estimates are in parenthesis. Models are ranked best to worst for each region. The most parsimonious model estimate's lower and upper lower bounds of the 95% confidence interval are given in brackets.

	Model	AICc	ΔAICc	Parameters	2007/08 Estimate	2008/09 Estimate
PWS	Effort (time)	598.43	–	3	64 (30.7) [55–77]	135 (11.9) [129–142]
	Effort (distance)	599.67	1.24	3	65 (31.0)	135 (11.9)
	Null	601.54	3.11	2	67 (32.1)	135 (12.0)
LC	Effort (time)	411.70	–	4	52 (6.4) [47–58]	35 (8.7) [31–43]
	Effort (distance)	431.66	19.96	4	53 (6.8)	36 (8.8)
	Null	445.50	33.80	3	54 (7.3)	36 (8.9)
SS	Effort (time)	491.75	–	4	95 (24.2) [87–106]	68 (11.9) [62–75]
	Effort (distance)	495.75	4.00	4	96 (24.6)	68 (11.9)
	Null	496.29	4.54	3	97 (24.6)	68 (12.1)

2.8. Numbers of whales and seasonal distribution

During fall and winter inclement weather conditions and limited daylight often made imaging whales difficult, hence the images of individual whales represented only a partial count of the whales' present. Therefore, we estimated the numbers and identified the distribution of all whales, regardless if imaged or not, across a season in each location. We wanted to avoid double counting whales and only counted the number of unique whales seen each day. The daily surveys in LC and SS provided counts of the number of whales seen each day. There was little chance of double counting individuals because whales were typically concentrated in one area and effort consisted of short daylight hours providing a narrow observation window.

In PWS, obtaining a tally of the whales observed each day was more challenging because the multi-day survey transected the sound and whales could travel from area to area. We estimated the distance over time using the whale maximum swimming speed of 8kts/hour, and excluded whales that, based on the distance and time, could have traveled to the next area. By totaling the number whales observed each month, we calculated the minimum number of whales present in study area.

Although mark-recapture models provide an estimate of abundance, they do not describe seasonal trends. Consequently, we used the number of unique whales seen each month for establishing seasonal patterns, then adjusted the pattern to account for the estimated number of whales present. The data used to describe the seasonal attendance pattern, included calves because by fall calves have become intermittently independent and become more independent with age (Straley, unpublished data). By fall calves were feeding on the same prey as other whales. We also included individuals identifiable in poor quality images. This number represents a lower bound to the daily attendance

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pattern for whales in each location. Daily attendance was estimated by fitting linear models to the observed numbers. Inflection points for linear models were determined visually. Whale attendance patterns in PWS were not estimated for the winter of 2007/08 because only three surveys were conducted over a limited spatial area, consequently we relied on the attendance pattern observed in 2008/09.

We used the attendance patterns to establish a lower bound (as described above) and the Huggins estimate of abundance to establish the upper bound to the whale attendance pattern. The number of whales present on the t^{th} day (N_t) based on the observed attendance pattern is referred to as $N_{t\ low}$. The number of whales present as predicted by the upper bound is referred to as $N_{t\ high}$.

The Huggins estimate for a given area (a) and winter (w) ($\hat{N}_{aw}$) was used to adjust the observed attendance patterns to reflect the best estimate of the number of whales present on any given day ($N_{t\ high}$). These latter estimates were calculated using:

$$\sum N_{t\ high} = \sum \alpha N_{t\ low} \tag{4}$$

where α is a coefficient that minimizes

$$\hat{N}_{aw} - Maximum\,(N_{t\ high}) \tag{5}$$

2.9. Foraging observations and identification of diet

2.9.1. Whale foraging behavior

Groups of whales were analyzed for foraging behavior and diet. The average group size for each area, for both years, was the same. For PWS and SS, whales were recorded as singles or in groups of 2–4 with the average group size consisting of two whales (Table 1a and c). In LC, some whales were seen in pairs but most were recorded as alone and not part of a group (Table 1b). While other whales were counted, we only determined the diet of the groups (or single whales in LC) because these whales were more closely observed specifically to see what they were eating. Humpbacks within groups were assumed to be foraging if prey consumption was directly observed in surface events (e.g. lunges, bubble nets etc.; Jurasz and Jurasz, 1979). Foraging was inferred if whales were documented repeatedly diving in the same location or along a trajectory or path such as along a shoreline or other barrier (ocean bottom) and if prey were observed on the echosounder tracing (Fig. 2a and b). Often other herring predators (sea lions and birds) were present, as well. All whales in a group were presumed to be foraging on the same prey. Other behaviors observed were resting, traveling, and milling, but only foraging behavior was analyzed for the purposes of this paper.

2.9.2. Prey type identification from direct observations

When groups of whales were located and believed to be feeding, we attempted to identify prey. Direct observations of prey being consumed, remains of prey seen in the water and/or floating at the surface after a presumed foraging event, and sonar mapping of the potential prey fields observed on a shipboard (Lowrance) dual-frequency (50/200 kHz) echosounder were used to identify prey likely targeted by humpbacks. Whales were sometimes observed diving through the layer of prey on the sounder tracing (Fig. 2a and b). The dual-frequency sounder provides a tool for eliminating or confirming prey based on target strength and transducer frequency. Prey distinctly visible on the sounder tracing using the 50-kHz frequency was presumed to be fish (Fig. 2a; De Robertis et al., 2010). Prey visible only using the 200-kHz frequency was presumed to be zooplankton (Fig. 2b, Ressler et al., 2012). Confirmation of target prey was accomplished using herring jigs, zooplankton tows (333 µm-mesh), cast nets and skim nets (used to clean swimming pools) to collect fish or scales near foraging whales at the surface. Confidence in the identification of the target prey was recorded as "certain" (prey were captured), "probable" (presumed from the echo sounder trace), or "undetermined."

2.9.3. Proportion of prey type in the groups of whale diet

The proportions of each prey type in the diet of groups of whales observed foraging were summed by group totals across months from mid-September to mid-February each year. All whales in a group were presumed to feed on the same prey, hence the group totals were used for identifying the proportion of prey in the diet. Therefore, each month, the number of groups of whales feeding on herring, krill, both or undetermined was calculated as a percentage of the total prey observed for all groups each month.

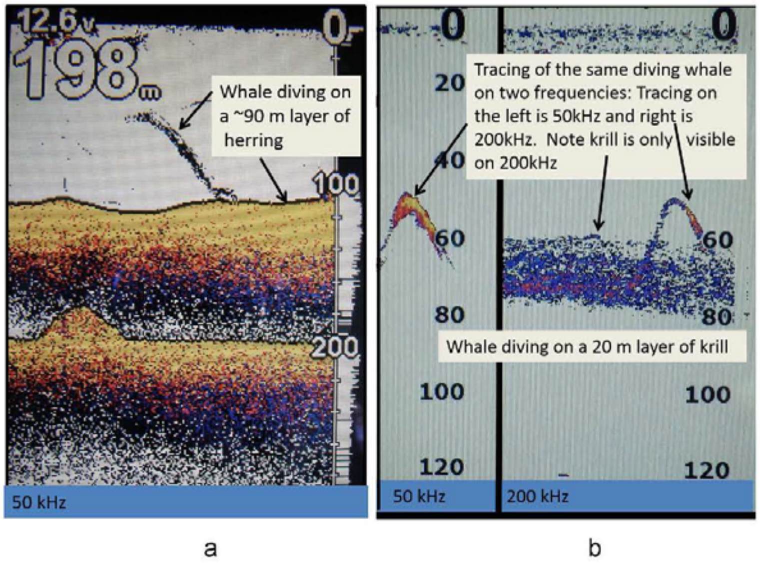

Fig. 2. a. This image is of a Lowrance echo sounder equipped with a 50 kHz transducer used to help identify prey. The tracing shows a 90 m layer of herring almost to the ocean bottom (198 m) with a whale diving into top of the herring. **b.** The two images show the dual frequency Lowrance echosounder with both frequencies visible. The far right image is a whale diving into a 20 m layer of krill visible on the 200 kHz frequency tracing. The image adjoining (directly left of the 200 kHz image) is the 50 kHz tracing with only the whale visible. Krill are too small to be visible at 50 kHz.

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2.10. Identification of the diet of feeding humpback whales using stable isotopes

Use of stable isotopes obtained from biopsy tissue samples is a well-established method for obtaining diet information from free-ranging whales (e.g. Bowen and Iverson, 2013; Witteveen et al., 2009). Nitrogen stable isotopes ($^{15}N/^{14}N$; $\delta^{15}N$) are fractionated as they move through the food web becoming more enriched in the heavy isotope, ^{15}N, and therefore less negative, with each trophic level (Vander Zanden and Rasmussen, 1999), thereby giving an indication of the trophic level at which individual whales are foraging. The ratios of nitrogen stable isotope (^{15}N /^{14}N) provides a measure of trophic level with the ratios becoming less negative or more enriched with increasing trophic position. This enrichment occurs because of the preferential excretion of ^{14}N in metabolic processes (Minagawa and Wada, 1984) resulting in a higher $\delta^{15}N$ value. Typically, humpback whales that feed in the same geographical area, and are genetically distinct, belong to the same feeding aggregation, feed at similar trophic levels, and share isotopic signatures (Witteveen et al., 2009, 2011).

Biopsies from the side or flank of the whale were collected in PWS during 2008/09 and in Southeast Alaska during 2008/09 and the fall of 2009 using a 150-lb. crossbow, and modified bolt, equipped with a stainless-steel biopsy dart with flotation for retrieval. Skin samples were separated from any blubber collected within the dart. Images were taken of each whale at time of biopsy sampling to avoid a sample incorrectly identified as to which whale was sampled. Samples were stored on ice after collection until transferred to a − 20 to − 80 °C freezer.

Primary consumers (copepods) were collected to establish a baseline for nitrogen stable isotope ratios and to allow the comparison of trophic levels represented in prey samples taken across feeding aggregations. Copepods serve as a surrogate for characterizing secondary producers for regional food webs and accounts for regional differences in baseline $\delta^{15}N$ values (Andrews, 2010; Cabana and Rasmussen, 1996; Kling et al., 1992; Matthews and Mazumder, 2005; Post, 2002).

Skin samples and copepods were sent to a mass spectrometry facility (University of Georgia) for quantification of the ratios of $\delta^{13}C$ and $\delta^{15}N$ in lipid-extracted tissue samples. These values were converted to δ notation by comparison against international reference standards.

A comparison to the $\delta^{15}N$ of primary consumers (copepods) allowed us to estimate the trophic position of individual whales (Witteveen et al., 2009, 2011) using the following equation:

$$\text{Trophic Level (TL)} = 2 + (\delta^{15}\text{ N humpback whale} - \delta^{15}\text{N primary consumer})/2.4 \qquad (6)$$

where 2 is the trophic position of a primary consumer and 2.4 is the average increase in ^{15}N between trophic levels for marine mammals (Hobson et al., 1994; Post, 2002). Higher trophic levels of 3.5–4.0 are indicative of a more piscivorous diet (i.e. foraging exclusively on herring – Witteveen et al., 2011) as planktivorous cetaceans (i.e. foraging exclusively on krill) cetaceans have lower trophic levels (TL 2.8–3.0; Hoekstra et al., 2002).

2.11. Statistical analysis

To determine if diet changed across months, prey identification data were pooled by years (by month and location) for groups of humpback whales. Only data where prey was identified were used in the analysis. A logistic regression (Program R v.3.4.0 software) was used to test the probability of herring as the primary prey across months changed for humpback whales in each study area. Month was an ordinal variable, with the first month starting in mid-September/mid-October and ending in mid-February/mid-March of the following year.

3. Results

3.1. Whale observations

During the fall and winters of 2007/08 and 2008/09, Prince William Sound (PWS) had higher numbers of whales observed (554) and more individuals photo-identified (162 + 21 calves) than in Lynn Canal (LC) (275 whales observed, 42 + 6 calves photo-identified) or Sitka Sound (SS) (285 whales observed, 68 + 12 calves photo-identified) (Table 1a–c). In PWS the number of individuals observed each month in the fall of 2008 was consistent 57–63) before declining in the winter of 2009 to 38 in February, with only 8 individuals observed in March 2009 (Table 1a). Insufficient surveys in 2007/08 in PWS did not provide enough data to determine the peaks and declines in abundance. In LC, twice as many individuals were identified during the first season than during the second season when effort was reduced (Table 1b). In SS where effort also varied across years, nearly the same number of individuals was identified across years (Table 1c).

Across both years, a smaller geographic area was surveyed in LC and SS compared to PWS (Fig. 1). However, SS and LC encompassed 100% of the whale presence seasonally, in part because there were not areas missed where whales were present and not surveyed. In PWS, whales were scattered throughout the sound, but with large concentrations of whales found in a few key areas. A small number of whales were missed because the entire sound was not surveyed due to weather or time limitations.

3.2. Whales forgoing annual migration, and overwintering in Alaska

During this study, we confirmed that four whales in PWS and two whales in SS did not make the winter migration to lower latitudes. These whales represent less than 2% of the number of individuals identified during this study. Two of the PWS whales that overwintered were a mother and her last year's calf (now a yearling). The two whales that overwintered in SS were adults of unknown sex. We did not confirm any whales overwintering in LC.

3.3. Whale abundance estimated using the Huggins closed-capture model

The estimates of abundance best fit the effort (time) model for all areas (Table 2). In PWS, the effort (distance) model was not significantly worse than the effort (time) model. However, the difference in the estimated number of whales changed by one whale, hence the effort (time) model was selected because the difference was minimal. The number of individuals used in the mark recapture analysis (Appendices A–C) was smaller than the overall counts reported in Table 1 because the data used in the model were filtered for quality and calves were excluded. The estimates were higher than the numbers of individuals used in the analysis (photo-identified and filtered for quality, with calves excluded) in 2007/08 and 2008/09 (Table 2). In PWS, the estimated 2007/08 abundance was 64 individuals, or 55–77 whales within the 95% confidence limits. During 2008/09, the estimate was 135 whales, with 129–142 within the 95% confidence limits (Table 2). In LC, during 2007/08 the estimate of abundance was 52 whales, with a 95% confidence interval of 47–58 whales, and during 2008/09 the abundance estimate was 35 whales, with a 95% confidence interval of 31–43 whales (Table 2). In SS, the 2007/08 estimate was 95, with a 95% confidence interval of 87–106 whales, and during 2008/09, the abundance was estimated at 68 whales, with a 95% confidence interval of 62–75 whales (Table 2). All the models described similar magnitude and error (Table 2).

3.4. Seasonal trends in peak whale attendance patterns

Generally, for all areas, whale numbers were highest during the fall and declined during winter. However, the seasonal trends for the timing

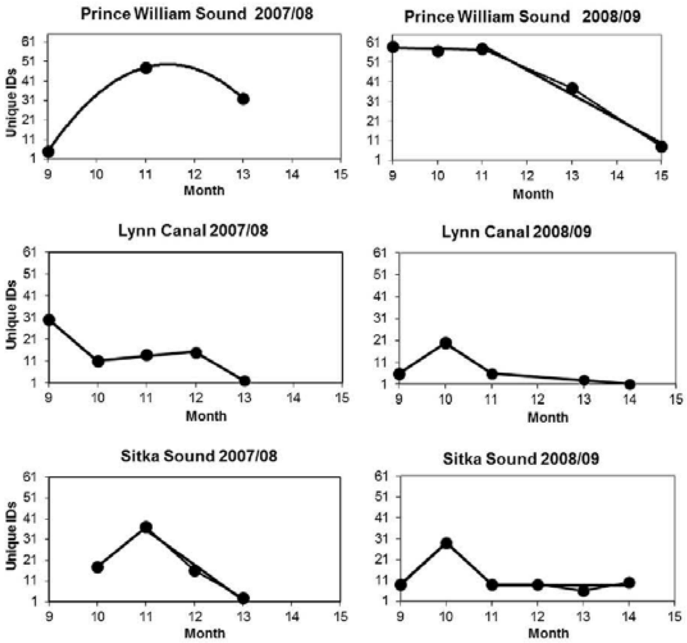

Fig. 3. Late season attendance patterns of humpback whales in Prince William Sound, Lynn Canal and Sitka Sound. Points show the number of unique whales identified in each location during each month from September (month 9) to March (month 15). The attendance pattern for Prince William Sound in 2007/08 was not modeled because only three surveys were conducted over a limited spatial area.

of peak attendance depended on year and location. In PWS, attendance was high throughout the fall, declining in late December-early January (Fig. 3). While the attendance pattern for the first year (2007/08) in PWS was not estimated (due to a reduced survey design), the largest number of individuals was observed in December 2007, and the next year, 2008/09, peak attendance occurred in December. Peak attendance in LC was earlier, occurring during September within the first survey period of the study (2007/08) and October during the second survey period (2008/09), prior to the arrival of deep dense aggregations of herring. In SS, the peak attendance of whales was observed in November during the first survey period (2007/08) and during October within the second survey period (2008/09).

3.5. Foraging behavior observations

In PWS, the majority of the groups (163 of 215 total groups) of whales we encountered were foraging (76% of all observations; Table 3a). Most of the foraging groups were feeding upon herring with minimal foraging on krill observed (Table 4a, Fig. 4a). The proportion of herring as prey type did not change significantly across months ($p = 0.36$).

In LC, fewer total groups (118) were documented feeding than in PWS (163) but a higher proportion (86%) of the groups were observed foraging (Table 3b). Herring were identified as prey in 100% of the foraging groups in seven of the 10 months surveyed across the two study years. Krill, mixed or unknown prey type were identified as prey in the three other months. The probability of herring as prey type did not vary significantly across months for groups where prey were identified ($p = 0.07$) (Table 4b, Fig. 4b).

In SS, 135 groups of whales were encountered with 94% observed foraging (Table 3c). In contrast to PWS and LC, krill was the dominant prey type in both years until later in the season when whale abundance had declined and herring was the only prey type identified (Table 4c, Fig. 4c). In SS, there was a significant increase in herring as prey type across the seasons ($p < 0.001$). During the fall, most groups of whales were observed to prey upon krill, while during the winter, the majority of groups preyed upon herring. The same groups of whales found feeding on krill in the fall were observed feeding on herring in winter.

3.6. Identification of the diet of feeding humpback whales using stable isotopes

During the fall and winter of 2008/09 in PWS, 42 biopsy tissue (skin and blubber) samples were collected from feeding humpback whales. Only nine Southeast Alaska samples were collected during the fall and winter of 2008/09; hence, the sample size was supplemented with 38 samples collected during the fall of 2009.

Prince William Sound mean monthly trophic levels ranged from a low of 3.4 in March to a high of 4.0 in September and December; the overall mean trophic level was 3.8 (± 0.12 SE) (Table 5). Southeast Alaska mean monthly trophic levels ranged from 3.0 to 3.5 with an overall mean trophic level of 3.4 (± 0.10 SE). These data were consistent with visual prey observations of a fish (herring) diet for the whales feeding in PWS and a diet of krill and herring for whales feeding in Southeast Alaska during the fall and winter (Fig. 5).

4. Discussion

The presence of humpback whales on high latitude foraging areas in winter is not a new finding. In Norway, Ingebritsen (1929) reported the capture of pregnant female humpbacks in early winter. Berzin and Rovnin (1966) reported humpback whales in the eastern Aleutian Islands in December. In Southeast Alaska, Straley (1990) first documented humpback whales in the fall and winter in the late 1970s. Conducting winter fieldwork in the Gulf of Alaska (GOA) is logistically challenging, it is an essential period that should be considered when evaluating the impact of humpback whales on overwintering herring populations.

Whale populations in the North Pacific have increased steadily for the last several decades (Calambokidis et al., 2001, 2008); hence, the

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Table 3
Numbers of groups of whales observed foraging or involved in other behaviors each month, 2007/08 and 2008/09, in Prince William Sound, Lynn Canal, and Sitka Sound.

a. Prince William Sound. (dash = no survey)

Group behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	19	–	30	–	22	–	71
	2008/09	23	23	30	–	13	3	92
	Totals	42	23	60	–	35	3	163
Other	2007/08	5	–	14	–	4	–	23
	2008/09	3	9	8	–	7	2	29
	Totals	8	9	22	–	11	2	52

b. Lynn Canal. (dash = no survey)

Group behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	46	18	9	5	–	0	78
	2008/09	18	–	2	2	1	0	23
	Totals	64	18	11	7	1	0	101
Other	2007/08	1	4	8	1	–	1	15
	2008/09	1	–	1	0	0	0	2
	Totals	2	4	9	1	0	1	17

c. Sitka Sound. (dash = no survey)

Group behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	20	31	16	–	2	3	72
	2008/09	15	10	4	7	12	7	55
	Totals	35	41	20	7	14	10	127
Other	2007/08	0	2	0	–	0	0	2
	2008/09	4	0	0	2	0	0	6
	Totals	4	2	0	2	0	0	8

impact of predation on herring or other forage species may be increasing as humpback populations recover. In this study, we compared the potential foraging pressure exerted by humpback whales by identifying and estimating the number of whales present in three areas in the GOA where herring overwinter. Estimates of the number of whales in each study area were derived from mark-recapture models. Although we attempted to meet the assumptions of the mark-recapture models, our analysis of humpback abundance is subject to some bias (White and Burnham, 1999). Weather, heterogeneity in whale behavior (some whales were easier to 'capture' with a good photograph than others), capture probabilities, migration (some whales leave earlier and some later for the breeding areas, hence not all individuals were equally available for 'capture'), and local knowledge of whale distribution all influence mark-recapture estimates (Hammond, 1986; Stevick et al., 2001).

Despite the potential for bias in the mark-recapture estimates, we believe our abundance estimates are robust for Lynn Canal (LC) and Sitka Sound (SS) for both years, and Prince William Sound (PWS) during 2008/09, given the agreement between estimated population abundance and the number of individuals identified in each study area (Tables 1a–c and 2). Although the abundance estimate for PWS during 2007/08 (64 whales) was higher than the number of individuals photo-identified (filtered for quality) and used as input data in the model, we believe the data collected during 2007/08 were problematic. The problems arise from the counts of observed non-calf whales (76 whales), which was three times higher than the 22 whales (filtered data) used in the model. In addition, the 76-whale count was higher than the abundance estimate of 64 whales. It is likely this discrepancy is due to the survey methodology. In LC and SS, the decision to conduct a survey was selected on a day-to-day basis allowing for better choice of conditions for surveying. Surveys in PWS were conducted from a chartered vessel on dates selected in advance. Consequently, some surveys were conducted in marginal weather and sea-state conditions. In PWS, this resulted in fewer photographs that passed quality codes for the mark recapture model, leading to an underestimate of abundance. During 2008/09, two more surveys were conducted than for 2007/08, considerably improving the quality and amount of data collected.

Identification of target prey can be difficult. An advantage of sampling in the fall and winter months is that the number of prey taxa vs. those available in summer is lower. The two primary prey groups accessible for humpbacks in our study areas in fall and winter are herring and krill (Astthorsson, 1990). Identifying trophic levels through stable isotope analysis supported our observations that herring were the primary prey in the fall and winter in PWS. However, the lower trophic level for the two whales sampled in March could be reflective of whales just returning from the breeding areas where some minimal feeding by humpbacks is believed to occur (e.g. off Hawaii, Baird et al., 2000; off Mexico, Gendron and Urban, 1993; Goodyear, 1993).

The seasonal attendance pattern of humpbacks is equally important as the overall numbers of individual whales. Knowing how whales were distributed in relation to the herring distribution is essential for understanding the potential magnitude of predation. In PWS, the attendance patterns of whales were synchronized with the formation of shoals of overwintering herring observed in the late fall and early winter. Thus, it appears that the presence of whales in PWS coincided with the peak of herring abundance, allowing whales to maximize the consumption of overwintering herring prior to their southern migration. The overlap of whale presence and the peak of herring did not happen in LC and SS because whale numbers in Southeast Alaska declined, as herring were still moving into LC and SS. More individuals were identified in PWS and the target prey identified as primarily herring during 2008/09 suggested whales could pose a threat to herring recovery within PWS.

In Alaska, there are whales that are present in every month of the year, giving the appearance of year-round attendance of individual humpback whales, however, most humpback whales migrate annually

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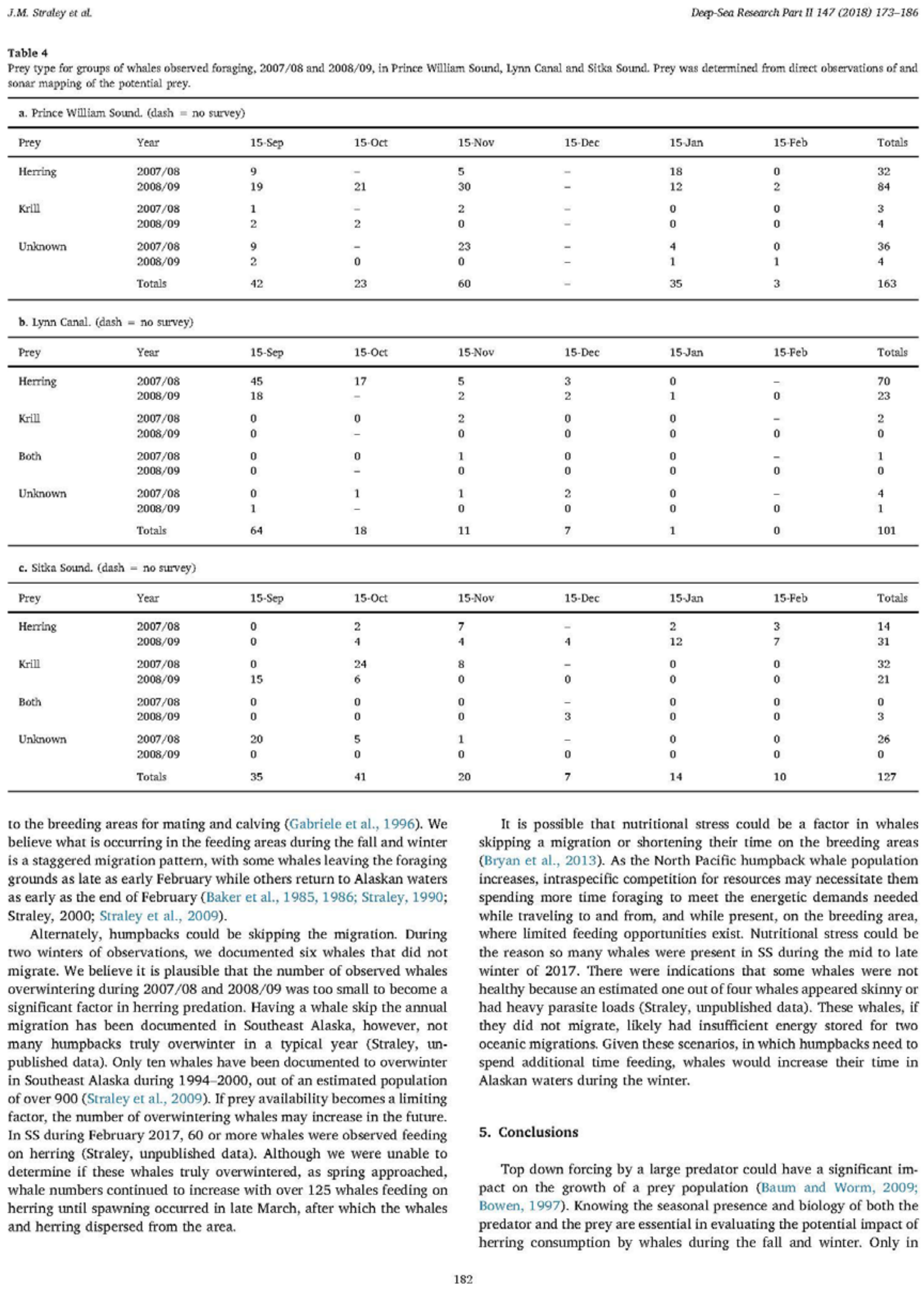

Table 4
Prey type for groups of whales observed foraging, 2007/08 and 2008/09, in Prince William Sound, Lynn Canal and Sitka Sound. Prey was determined from direct observations of and sonar mapping of the potential prey.

a. Prince William Sound. (dash = no survey)

Prey	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Herring	2007/08	9	–	5	–	18	0	32
	2008/09	19	21	30	–	12	2	84
Krill	2007/08	1	–	2	–	0	0	3
	2008/09	2	2	0	–	0	0	4
Unknown	2007/08	9	–	23	–	4	0	36
	2008/09	2	0	0	–	1	1	4
	Totals	42	23	60	–	35	3	163

b. Lynn Canal. (dash = no survey)

Prey	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Herring	2007/08	45	17	5	3	0	–	70
	2008/09	18	–	2	2	1	0	23
Krill	2007/08	0	0	2	0	0	–	2
	2008/09	0	–	0	0	0	0	0
Both	2007/08	0	0	1	0	0	–	1
	2008/09	0	–	0	0	0	0	0
Unknown	2007/08	0	1	1	2	0	–	4
	2008/09	1	–	0	0	0	0	1
	Totals	64	18	11	7	1	0	101

c. Sitka Sound. (dash = no survey)

Prey	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Herring	2007/08	0	2	7	–	2	3	14
	2008/09	0	4	4	4	12	7	31
Krill	2007/08	0	24	8	–	0	0	32
	2008/09	15	6	0	0	0	0	21
Both	2007/08	0	0	0	–	0	0	0
	2008/09	0	0	0	3	0	0	3
Unknown	2007/08	20	5	1	–	0	0	26
	2008/09	0	0	0	0	0	0	0
	Totals	35	41	20	7	14	10	127

to the breeding areas for mating and calving (Gabriele et al., 1996). We believe what is occurring in the feeding areas during the fall and winter is a staggered migration pattern, with some whales leaving the foraging grounds as late as early February while others return to Alaskan waters as early as the end of February (Baker et al., 1985, 1986; Straley, 1990; Straley, 2000; Straley et al., 2009).

Alternately, humpbacks could be skipping the migration. During two winters of observations, we documented six whales that did not migrate. We believe it is plausible that the number of observed whales overwintering during 2007/08 and 2008/09 was too small to become a significant factor in herring predation. Having a whale skip the annual migration has been documented in Southeast Alaska, however, not many humpbacks truly overwinter in a typical year (Straley, unpublished data). Only ten whales have been documented to overwinter in Southeast Alaska during 1994–2000, out of an estimated population of over 900 (Straley et al., 2009). If prey availability becomes a limiting factor, the number of overwintering whales may increase in the future. In SS during February 2017, 60 or more whales were observed feeding on herring (Straley, unpublished data). Although we were unable to determine if these whales truly overwintered, as spring approached, whale numbers continued to increase with over 125 whales feeding on herring until spawning occurred in late March, after which the whales and herring dispersed from the area.

It is possible that nutritional stress could be a factor in whales skipping a migration or shortening their time on the breeding areas (Bryan et al., 2013). As the North Pacific humpback whale population increases, intraspecific competition for resources may necessitate them spending more time foraging to meet the energetic demands needed while traveling to and from, and while present, on the breeding area, where limited feeding opportunities exist. Nutritional stress could be the reason so many whales were present in SS during the mid to late winter of 2017. There were indications that some whales were not healthy because an estimated one out of four whales appeared skinny or had heavy parasite loads (Straley, unpublished data). These whales, if they did not migrate, likely had insufficient energy stored for two oceanic migrations. Given these scenarios, in which humpbacks need to spend additional time feeding, whales would increase their time in Alaskan waters during the winter.

5. Conclusions

Top down forcing by a large predator could have a significant impact on the growth of a prey population (Baum and Worm, 2009; Bowen, 1997). Knowing the seasonal presence and biology of both the predator and the prey are essential in evaluating the potential impact of herring consumption by whales during the fall and winter. Only in

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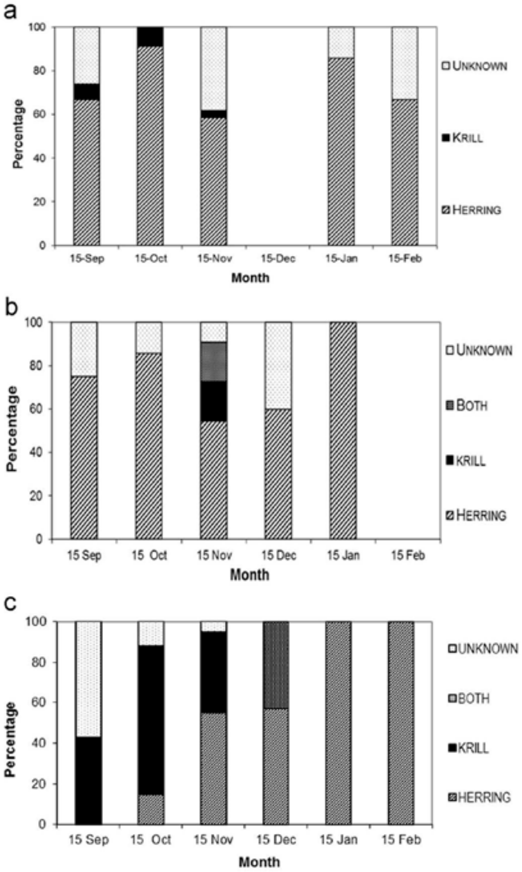

Fig. 4. a. Proportion of prey type observed by groups (N = 163) of foraging humpback whales in Prince William Sound each month during the combined fall and winters, 2007/08 and 2008/09. b. Proportion of prey type observed by groups (N = 101) of foraging humpback whales in Lynn Canal each month during the combined fall and winters, 2007/08 and 2008/09. c. Proportion of prey type observed by groups (N = 127) of foraging humpback whales in Sitka Sound each month during the combined fall and winters, 2007/08 and 2008/09.

Table 5
Trophic levels (TL) reported as monthly means with standard errors (SE) for humpback whales sampled in Prince William Sound (PWS) and Southeast Alaska, 2008–2009.

		PWS			SEAK		
Year	Month	TL	SE	n	TL	SE	n
2008	Sep	4.0	0.06	9			
	Oct	3.9	0.09	11	3.4	0.19	5
	Dec	4.0	0.08	11			
2009	Jan	3.9	0.13	9			
	Feb				3.5		1
	Mar	3.4	0.10	2	3.5	0.19	3
	Sep				3.0	0.07	15
	Nov				3.1	0.07	23
Overall		3.8	0.12	42	3.3	0.10	47

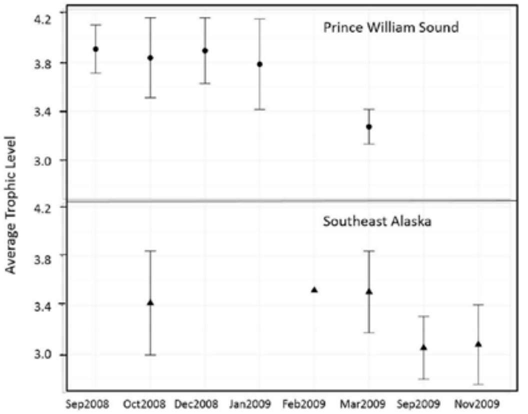

Fig. 5. Trophic level values with standard errors for humpback whales foraging in Prince William Sound (PWS) (n = 42) from the fall and winter 2008/09 and in southeastern Alaska (SEAK) (n = 47) from fall and winter 2008/09 and fall 2009.

Prince William Sound did it appear that whales might have had an impact on overwintering herring populations aggregated into deep layers. That is, peak whale attendance occurred when herring were available as prey. In Lynn Canal and Sitka Sound peak attendance of whales occurred earlier in the fall before the herring had completely moved into each area, hence, there was less potential for predation to have influenced herring populations. North Pacific humpback whales in the Gulf of Alaska may be experiencing nutritional stress from reaching or exceeding carrying capacity. Humpbacks might need to spend more time feeding in the northern latitudes by spending less time on the breeding areas or skipping the annual migration altogether. This would lead to more humpback whales present on the feeding areas during the winter months and increase predation pressure on herring populations.

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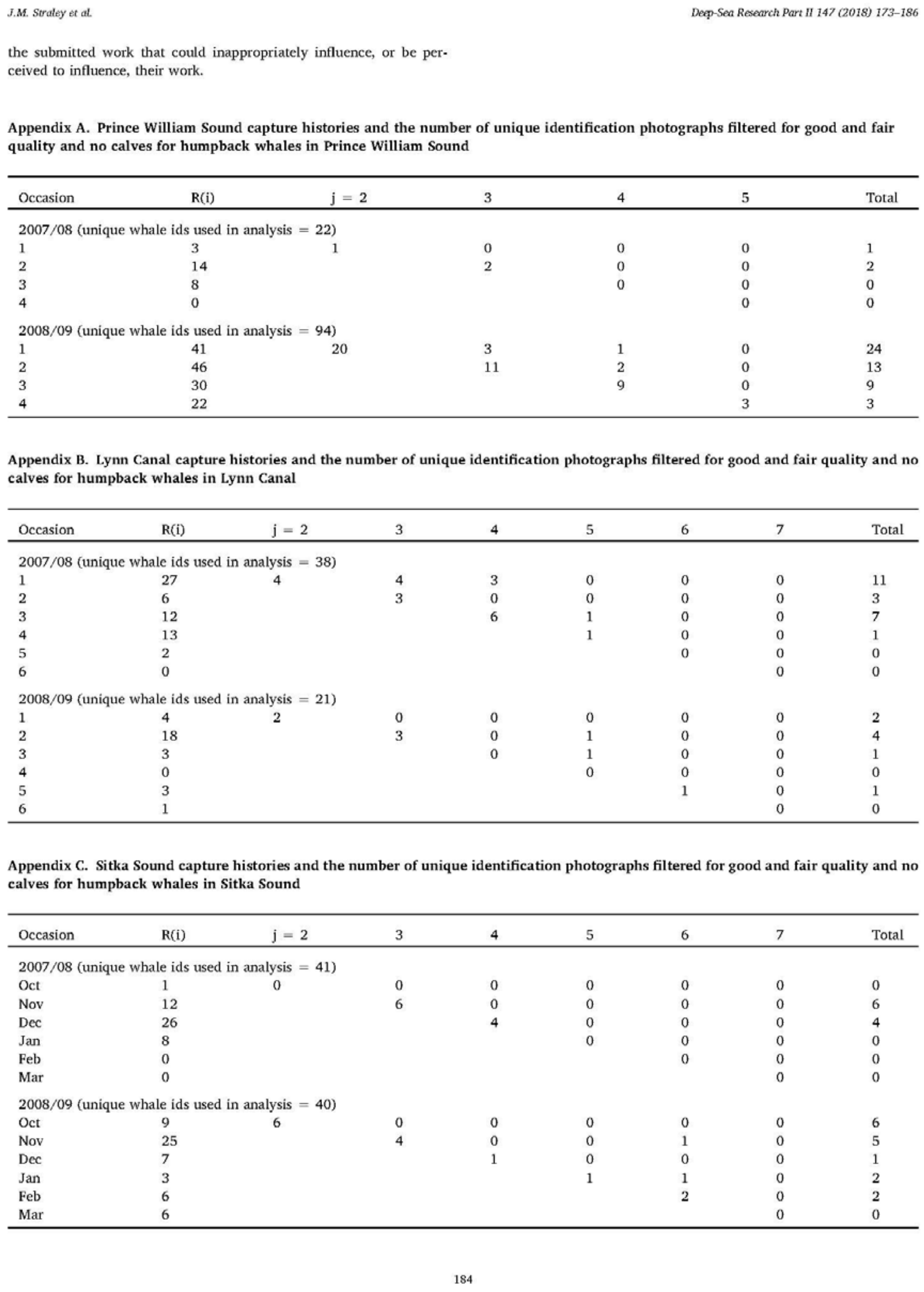

the submitted work that could inappropriately influence, or be perceived to influence, their work.

Appendix A. Prince William Sound capture histories and the number of unique identification photographs filtered for good and fair quality and no calves for humpback whales in Prince William Sound

Occasion	R(i)	j = 2	3	4	5	Total
2007/08 (unique whale ids used in analysis = 22)						
1	3	1	0	0	0	1
2	14		2	0	0	2
3	8			0	0	0
4	0				0	0
2008/09 (unique whale ids used in analysis = 94)						
1	41	20	3	1	0	24
2	46		11	2	0	13
3	30			9	0	9
4	22				3	3

Appendix B. Lynn Canal capture histories and the number of unique identification photographs filtered for good and fair quality and no calves for humpback whales in Lynn Canal

Occasion	R(i)	j = 2	3	4	5	6	7	Total
2007/08 (unique whale ids used in analysis = 38)								
1	27	4	4	3	0	0	0	11
2	6		3	0	0	0	0	3
3	12			6	1	0	0	7
4	13				1	0	0	1
5	2					0	0	0
6	0						0	0
2008/09 (unique whale ids used in analysis = 21)								
1	4	2	0	0	0	0	0	2
2	18		3	0	1	0	0	4
3	3			0	1	0	0	1
4	0				0	0	0	0
5	3					1	0	1
6	1						0	0

Appendix C. Sitka Sound capture histories and the number of unique identification photographs filtered for good and fair quality and no calves for humpback whales in Sitka Sound

Occasion	R(i)	j = 2	3	4	5	6	7	Total
2007/08 (unique whale ids used in analysis = 41)								
Oct	1	0	0	0	0	0	0	0
Nov	12		6	0	0	0	0	6
Dec	26			4	0	0	0	4
Jan	8				0	0	0	0
Feb	0					0	0	0
Mar	0						0	0
2008/09 (unique whale ids used in analysis = 40)								
Oct	9	6	0	0	0	0	0	6
Nov	25		4	0	0	1	0	5
Dec	7			1	0	0	0	1
Jan	3				1	1	0	2
Feb	6					2	0	2
Mar	6						0	0

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Appendix 2

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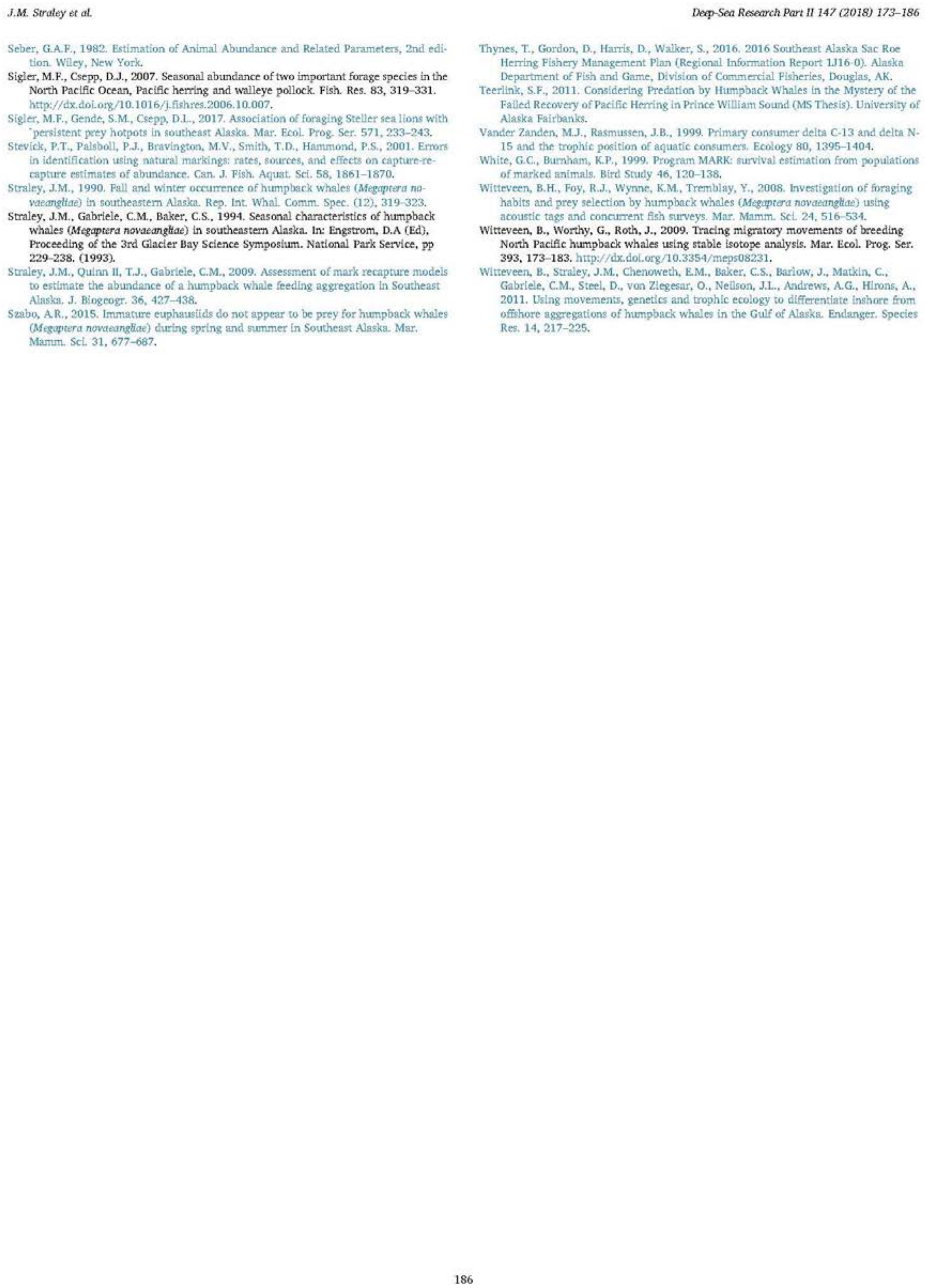

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