

*Exxon Valdez* Oil Spill  
Restoration Project Final Report

Significance of Whale Predation on Natural Mortality Rate of Pacific Herring  
in Prince William Sound

Restoration Project: 100804  
Final Report

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## **Study History:**

In FY 2005, a group of scientific investigators (including Rice and Quinn of this proposal) collaborated to integrate information about the herring population in Prince William Sound and identify factors contributing to its lack of recovery (EVOS TC funded project 050794); Top down control was identified as probably having more influence in Prince William Sound than on other herring stocks. The group concluded that lingering oil exposure does not play a role in limiting recovery. Of the two top 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 population assessment modeling would need to have better quantification on the significance of predation. Predation by marine mammals has been hypothesized as a factor in the failure of the Prince William Sound herring population to rebound. This study assesses the significance of humpback whale predation on herring mortality rates, during the fall and winter months.

## **Abstract:**

By examining humpback whale interactions with three wintering herring population (Prince William Sound, Lynn Canal and Sitka Sound) we determined that humpback whales had the greatest impact on Prince William Sound Herring. The number of whales was greatest in Prince William Sound; they foraged on herring for a longer period of time into the winter, and removed a greater percentage of the available biomass of herring. Whales in Lynn Canal foraging on herring peaked in fall; whale numbers dropped off considerably after October. Whales in Sitka Sound were more abundant than Lynn Canal but they foraged predominately on krill, even though the Sitka herring population is far more robust than the other populations. The herring biomass consumed in Prince William Sound approximated the biomass lost to natural mortality over winter as projected by age structured stock assessments, suggesting they are the dominant top down force in herring removals, at least for the years covered. These data indicate that the focused predation in Prince William Sound can exert top down controlling pressure, but whale populations are not a ubiquitous threat to forage fish populations in other regions at this time.

## **Key Words:**

Abundance, Alaska, *Clupea pallasii*, Humpback whales, Lynn Canal, Mark-recapture, *Megaptera novaeagliae*, Pacific Herring, predation, Prince William Sound, Sitka Sound, schooling behavior.

## **Project Data:**

Data collected for this project included photographs of humpback whale flukes, environment, prey, and effort associate with fluke photographs. *Custodian* - Janice M. Straley University of Alaska Southeast, 1332 Seward Ave, Sitka, Alaska 99835, (work phone: (907) 747-7779, fax: (907) 747-7741). Hydroacoustic data, herring lengths, weights, and chemical analysis of herring

and other prey species were also collected. Herring related data are stored in an Access data base. *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). Modeling data were collected from a variety of reports. *Custodian* - Ron A Heintz, Auke Bay Laboratories, National Marine Fisheries Service, 17109 Point Lena Road, Juneau, AK 99801, (work phone: (907) 789-6058, fax: (907) 789-6094).

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## Executive Summary

In this report we describe the relationship between humpback whales and Pacific herring during the fall/winter months of 2007-8 and 2008-9 for Prince William Sound, Lynn Canal, and Sitka Sound. Each chapter in this report will be submitted to a peer reviewed journal.

The Trustee-funded *Prince William Sound Herring Synthesis* (Restoration Study 050794) associated the failed recovery of Prince William Sound (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 anecdotal evidence indicates humpback whale populations PWS are rising. Increased whale predation is consistent with isotopic analyses indicating PWS whales are primarily piscivores and reports that humpback whale populations in the north Pacific are increasing 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.

Our goal was to determine if humpback whales could be limiting the recovery of PWS herring. We set out four objectives to address this issue: They were to 1) *Estimate humpback whale abundance and distribution during the fall/winter*, 2) *determine the prey composition of humpback whales feeding at this time of year*, 3) *estimate the contribution of herring to humpback whale energy requirements*, and 4) *estimate significance of humpback whale predation on PWS herring*. Our studies focused on fall/winter when herring aggregate into shoals making themselves vulnerable to whale predation. To determine the relevance of whale predation in Prince William Sound we replicated our efforts in two other regions in the Gulf of Alaska with over-wintering herring and humpback whales. Like Prince William Sound, Lynn Canal supports a depressed population of herring, which has failed to recover despite the closure of fisheries in the mid 1980's. In contrast, the Sitka Sound herring fishery is robust and is currently experiencing record breaking commercial harvests. By comparing these three sites, we have identified differences in the interactions between humpback whales and wintering herring shoals and the impact of whale predation on specific herring populations.

### **Chapter I:** *Abundance and seasonal trends of humpback whales associated with wintering Pacific herring.*

Chapter one addresses our first objective, in short, how many whales are present during the fall/winter months and for how long do they remain in Alaskan waters. Using boat-based surveys, photographic identification, and mark-recapture models, we estimated humpback whale abundance at three late-season (mid-September through mid-March) feeding areas (Prince William Sound, Lynn Canal, and Sitka Sound) in the Gulf of Alaska known for large aggregations of wintering Pacific herring. We integrated the observed seasonal trends with the estimates of whale abundance to measure the potential impact of whales in each area. This allowed us to model the number of whales present in each area for each day of the study.

We observed the greatest potential impact was in Prince William Sound. Whale abundance was higher and they were present for a longer time than in Lynn Canal or Sitka Sound. Seasonal trends in whale abundance were similar between Lynn Canal and Sitka Sound peaking earlier in the fall, whereas whale numbers in Prince William Sound remained high into

mid winter. In Prince William Sound and Lynn Canal, presence of whales was strongly associated with large shoals Pacific herring.

**Chapter II:** *A comparison of humpback whale diets on three overwintering herring grounds in the Gulf of Alaska.*

In chapter two we refined our estimates of potential whale impacts by verifying whale diets in each location. It cannot be assumed, based on an overlap of temporal and spatial distribution alone, that whales are feeding on herring. We conducted vessel surveys from September 2007 to March 2009 collecting data on groups of foraging whales. We estimated group size and identified their prey using sonar and direct sampling. Over all years and seasons, there was a significant difference in diet composition observed between the three areas. In Prince William Sound, the greatest proportion of groups fed on herring, while in Sitka Sound the greatest proportion of groups fed on krill. Our observations of the number of groups, group size and group diet indicated the greatest potential impact on PWS herring. A larger number of whales foraged on herring in PWS for a longer time period than in either of the other locations. This prolonged foraging likely resulted from the absence of alternative prey in PWS. Predation from a large predator whose numbers are increasing could impact the recovery of herring.

**Chapter III:** *Humpback whales disrupt the winter schooling behavior of Pacific herring and facilitates predation by multiple predators.*

We conducted hydroacoustic surveys of herring abundance in Lynn Canal and Sitka Sound in order to relate the numbers of foraging whales to herring abundance. The Alaska Department of Fish and Game (ADFG) estimates stock size for PWS and Sitka Sound herring using age-structured stock assessments, but there is no rigorous estimate for Lynn Canal. Instead, ADFG relies on spawn deposition surveys. We conducted hydroacoustic surveys in Lynn Canal and Sitka Sound. Our Sitka Sound estimates were compared with the ADFG stock assessments to verify our survey method. In addition, we are able to examine the behavior of herring in response to whale foraging in Lynn Canal by combining our hydroacoustic data with observations of foraging whale locations and abundance.

Our acoustic survey estimates for Sitka Sound and ADFG's stock assessments agreed within 10%, demonstrating the reliability of our method. In addition, we determined that Lynn Canal is an important overwintering area for herring in southeastern Alaska. In addition, our results demonstrate that the spatial and temporal distribution of humpback whales is strongly associated with herring schooling behavior. Humpback whale foraging activity correlated with dispersed schooling behavior of herring. As winter progressed and humpback whales began migrating out of the region, the spatial and vertical extent of herring decreased as they consolidated into dense schools occupying the deep channel habitats in Lynn Canal. The consolidation of herring schools that coincided with the departure of whales, suggests the feeding methods used by humpback whales disrupt herring school structure. We hypothesize this disruption facilitates commensal predation by other birds and pinnipeds. As evidence for this hypothesis we noted Steller sea lions were most abundant in the survey area when whales were present. Facilitation of commensal foraging by humpback whales could represent a potential indirect impact of humpback whales on herring abundance.

**Chapter IV:** *The impact of humpback whales on wintering herring.*



In chapter four we address the significance of whale predation on herring by relating the potential biomass removed in each location to estimates of herring abundance. To estimate the biomass removed we combined the daily attendance models constructed in chapter 1 with the diets observed in chapter 2 with published data on whale size and metabolic demands. Daily consumption rate models were constructed for each location. Parameter values for the models were varied in order to provide low and high end estimates that bracketed the range of all potential estimates.

Our models indicated that humpback whales consumed more herring in PWS than the other locations and the consumed biomass represented a greater proportion of the herring stock than the other locations. The herring biomass consumed in Prince William Sound approximated the biomass lost to natural mortality over winter as projected by age structured stock assessments. As a proportion of the total herring biomass, removals in PWS approximated the biomass equivalent of a fishery. These data indicate that the humpback whale predation in Prince William Sound can exert top-down controlling pressure. However, the same was not true for the other locations, presumably because there were alternative prey available in the other locations. Thus, while humpback whales are prodigious predators that can exert significant pressure on local forage fish populations their impact of commercially valuable fish populations is not ubiquitous.

### **General Conclusions**

In summary, the ecological impact of humpback whales will increase as their populations continue their remarkable recovery in the North Pacific Ocean. Whales will exert greater control over forage and increased their ability to influence their prey through top-down forcing. The high degree of fidelity whales show for their foraging grounds indicates some local populations of forage fish are more likely to be affected by whales than others, as we observed in Prince William Sound. Currently, humpback whales are statutorily protected. Fishery managers will need to re-evaluate future harvest strategies in order to account for the un-regulated take by whales in some local populations of forage fish. As whale populations continue to increase, they may be consuming an ever increasing take of forage fish.

## **Chapter I: Abundance and Seasonal Trends of Humpback Whales Associated with Wintering Pacific Herring.**

Manuscript title: Late-season abundance and seasonal trends of humpback whales on three important wintering grounds for Pacific herring in the Gulf of Alaska.

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### **ABSTRACT:**

Humpback whale (*Megaptera novaeagliae*) populations in the North Pacific Ocean have made a remarkable recovery from heavy commercial exploitation during the 1900s. As populations rebound, their ecological impact increases, as does their ability to influence their prey through top-down forcing. Using boat-based surveys, photographic identification, and mark-recapture models, we estimated humpback whale abundance at three late-season (mid-September through mid-March) feeding areas (Prince William Sound, Lynn Canal, and Sitka Sound) in the Gulf of Alaska known for large aggregations of wintering Pacific herring (*Clupea pallasii*). Seasonal trends in whale abundance were similar between Lynn Canal and Sitka Sound peaking earlier in the fall, whereas whale numbers in Prince William Sound remained high into mid winter. In Prince William Sound and Lynn Canal, presence of whales was strongly associated with large shoals Pacific herring. In Sitka Sound, whales were not consistently linked to herring during the fall and winter months. During this study we identified four whales in Prince William Sound and two whales from Sitka Sound that skipped the annual migration to lower latitudes (i.e. overwintered in Alaskan waters), but none in Lynn Canal. The trend of late-season whale abundance corresponded with the formation of herring aggregations in PWS and Lynn Canal, and are consistent with the hypothesis that humpback whales could be impacting these struggling herring populations.

**KEY WORDS:** Humpback whales, *Megaptera novaeagliae*, Mark-recapture, Photographic identification, Abundance, Alaska, *Clupea pallasii*, Prince William Sound, Lynn Canal, Sitka Sound.

## INTRODUCTION

Some Pacific herring (*Clupea pallasii*) stocks remain depressed long after commercial fishing has been stopped; giving rise to the hypothesis that humpback whale (*Megaptera novaeangliae*) predation may be limiting recovery of herring populations (Rice and Carls 2007). The biology of herring and humpback whales bring the two species together during the fall months, when herring begin to form their wintering aggregations and whales are building up the energy reserves required for their annual migration to lower latitudes to bear young and breed (Calambokidis et al. 2001). There are many species of fish, birds, marine mammals that feed on herring, but most capture prey one fish at a time, and none have the capacity of humpback whales to take in up to 56,000 liters of seawater and 100s of herring in a single mouthful (Anderson 2000). In spring the herring form large spawning schools, which overwhelm and satiate predators. Following spawning, herring are dispersed in small schools, feeding in the water column, these relatively shallow schools available to many predators. By late fall the herring have replaced their energy stores and are rich in lipid (Vollenweider 2005). They form large dense aggregations at depths that present a challenge for most air breathing predators; however, with their greater diving ability, whales have capacity to effectively forage on these deep schools of wintering herring (Sigler and Csepp 2007).

The potential impact of whale predation on herring has risen considerably in recent decades as humpback whale populations recover from critically low numbers. Humpback whales in the North Pacific have increased from an estimated 1400 whales in the mid 1960's to a population of over 18,000 in 2006, with an annual population growth rate of 4-7% (Calambokidis et al 2008). The prey base for these whales is diverse, ranging from large zooplankton to schooling fish (Nemato 1957, Straley in prep.). Prey selection varies by location, season and possibly individual preference. While the increase in whale abundance is a success story for the extensive conservation effort put forth to protect them, a consequence of their recovery may be that intensive foraging in specific regions is limiting the recovery of struggling herring populations.

Herring become prime targets for foraging whales during the brief spring spawn when adult herring are densely aggregated in shallow water (Wilson et al. 1998). However, predation risk from whales is reduced at this time because relatively few whales have returned from winter breeding grounds. Predation risk for herring is probably greatest in the fall/winter when their lipid content peaks and they form dense aggregations. Whales are still on the feeding grounds at this time and foraging on herring could be a very profitable strategy prior to their southern migration. Predation on herring during the prolonged wintering period has been observed anecdotally for some time, but we do not know how many whales are feeding on wintering herring, or how long foraging persists into the winter months. It has been reported that some whales do not make the winter migration to lower latitudes, and these whales, if targeting herring, could have an even greater impact on winter herring aggregations (Straley 2000).

The goal of this research effort is to understand the significance of humpback whale predation on Pacific herring in the Gulf of Alaska. This is motivated by the collapse of the herring fishery in Prince William Sound (in 1993) and active restoration efforts on the herring are being

contemplated. If whales are limiting the recovery of this stock, then some or all of the restoration activities may be moot. To achieve this goal we estimate whale abundance and describe their seasonal occurrence and persistence on herring wintering grounds over a two year period in three important herring wintering areas in the Gulf of Alaska; (1) Prince William Sound (PWS) and (2) Lynn Canal where herring populations have struggled for the last 2 and 3 decades despite the closure of commercial herring fisheries, and (3) Sitka Sound where herring numbers are robust and recent commercial herring fisheries have yielded record harvest. Specifically, we used boat based surveys to support photographic identification of individual whales in each location throughout the fall and winter. Abundance estimates derived from mark-recapture models were integrated with seasonal attendance patterns to assess the potential impact of whale predation on herring at the three contrasting locations during the fall and winter months. Data collected during these surveys also provided insight into the overwintering of individual whales in Alaskan waters. Information presented here is part of a series of assessment and modeling papers that will address this issue.

## **MATERIALS AND METHODS**

We quantified whale abundance by observing whale attendance patterns in PWS (60° 35' N, 147° 10' W), Lynn Canal (58° 28' N, 134° 55' W) and Sitka Sound (57° 02' N, 135° 25' W) over two winters. We indexed whale abundance by integrating the number of whales present on each day in each location during the study period and refer to the index as “whale-days”. In order to model daily attendance patterns we estimated the number of unique whales present in each location on multiple surveys during each winter and scaled those numbers upward to reflect mark-recapture estimates of whale abundance.

### **Study area and sampling effort.**

We monitored humpback whales at three locations in the Gulf of Alaska where predation on large shoals of Pacific herring (*Clupea pallasii*) occurs during the fall and winter months (Figure 1). PWS is an area of relatively protected waters in the northern Gulf of Alaska, characterized by complex coastlines of glacial fjords and islands. The Lynn Canal study area is a glacial fjord which includes the waters of southern Lynn Canal, Saginaw Channel, Favorite Channel, and northern Stephens Passage. Sitka Sound is a complex network of islands and bays exposed to the Pacific Ocean.

Effort exerted toward identifying whales in the field was quantified as the number of hours spent searching and the distance covered over water. When daylight and weather conditions were limiting during the winter months, an adaptive survey approach was taken and photographic effort was focused on areas with higher concentrations of whales. Aerial surveys and traditional local knowledge were employed to ensure aggregations of whales were not being overlooked during boat based surveys.

### **Estimation of whale abundance.**

Whale attendance records were used to estimate whale abundance by identifying all the individuals present in an area 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. In PWS photographic records were collected on eight boat based surveys (September 2007, November 2007, January 2008, September 2008, December 2008, January 2009, and March 2009). Each survey lasted five days and was conducted aboard the 17.7m vessel *M/V Auklet*. In Lynn Canal and Sitka Sound whales were photographed during day trips from small boats (< 8m). Day trips were conducted during each month of the fall/winter in each year. Combining the number of unique individuals observed in each month we could determine the minimum number of whales present in each location over the course of each winter.

In addition to estimating whale abundance by identifying 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). The closed-capture modeling setting was used in order to directly estimate abundance in each area. 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 for a particular area, 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.

### **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). 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.**

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 (one estimate for the entire study, Table 3). We evaluated these different models using the Akaike's Information Criterion corrected for small sample sizes (AIC<sub>c</sub>) by selecting the model which had the lowest AIC<sub>c</sub> value (Burnham and Anderson 1998).

For all three survey areas, 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.Gary White):

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

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

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

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

### Whale Attendance Patterns.

We determined late-season attendance patterns for the three study areas during the fall/winter months of 2007-8 and 2008-9. 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 and adjusted the pattern to account for the estimated number of whales present.

The data used to establish the attendance patterns include calves and individuals identifiable in poor quality photographs and represent a lower bound to the daily attendance 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 2007-8 because only three surveys were conducted over a limited spatial area. Instead, we relied on the attendance pattern observed in 2008-9.

We used the observed attendance pattern and the Huggins estimate of abundance to establish the upper bound to the whale attendance pattern. The number of whales present on the  $t^{\text{th}}$  day ( $N_t$ ) based on the observed attendance pattern is referred to as  $N_{t \text{ low}}$ . 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 ( $w$ ) ( $N_{aw}$ ) was used to adjust the observed attendance patterns to reflect the expanded number of whales present on any given day ( $N_{t\ high}$ ). These latter estimates were estimated by

$$\sum N_{t\ high} = \sum \alpha N_{t\ low} \quad \text{Equation (3)}$$

where  $\alpha$  is a coefficient that minimizes

$$N_{aw} - \text{Maximum}(N_{t\ high}) \quad \text{Equation (4)}$$

We estimated whale-days to establish the potential humpback whale foraging effort exerted on wintering herring in each location. One whale-day equals one whale being present for one day (i.e. 10 whales present for 10 days would be 100 whale-days).

Identification of overwintering whales.

With minimum migration times to the breeding ground in Hawaii of ~30 days (Gabriele et al. 1996), a whale could theoretically make two transoceanic migrations in 60 days. Our criterion for determining over-wintering (i.e. not making an annual migration to lower latitudes) was a less than 60 day sighting interval. With longer sighting intervals we could not conclude that a migration did not take place.

## RESULTS

Efforts to compare the potential foraging pressure exerted by humpback whales relied on identifying and estimating the number of whales present in each location and then expanding these numbers with modeling since the observations in the field can never accurately count all of the whales in the area. Since closed population models tend to overestimate abundance when applied to open populations (Seber 1982), we consider the Huggins estimate to be an upper limit to whale abundance in each location and the total number of unique individuals to be the lower limit to whale abundance. The herring aggregated at different times in each location making it necessary to construct models describing daily attendance in each location. By summing the daily attendance into a single total (whale-days) we could compare the potential foraging effort exerted by whales at each of the locations and compare the consistency between the two winters of sampling.

### Numbers of unique individuals in each location.

During the course of this study we identified 317 individual humpback whales that had the potential to forage on large shoals of wintering herring in Alaskan waters. In PWS the number of unique individuals observed each month did not decline until after December (Figure 2). The increase in year two was considerably influence by more sampling trips (5 instead of 3), and

greater geographic coverage within PWS. In contrast, the number of unique individuals observed in the other locations was less, and peaked earlier. After accounting for whales seen multiple times, whale abundance was highest in PWS with 81 unique individuals identified in 2007-8 and 147 individuals identified 2008-9 of these whales 45 were seen at least once in both field seasons. Both Lynn Canal and Sitka Sound were considerably lower in number of unique individuals identified when compared to PWS. Late-season surveys of Lynn Canal yielded 42 individual whales in 2007-8 and 24 in 2008-9 with 18 whales being seen in both field seasons. Sitka Sound had 52 whales identified in 2007-8 and 49 in 2008-9 with 21 of these seen both field seasons (Table 2).

### **Huggins closed-capture estimates.**

We examined nine Huggins-closed capture models, three for each location. The models included (1) fixed capture probabilities or capture probabilities that covaried with effort expressed as (2) survey-hours or (3) distance-surveyed (Table 3). In PWS the models with varying capture probabilities were virtually indistinguishable ( $\Delta AIC_c = 1.24$ ) and the fixed capture probability model was also acceptable ( $\Delta AIC_c = 3.11$ ). The best model for Lynn Canal included capture probabilities that co-varied with distance-surveyed ( $\Delta AIC_c > 19.96$ ). In Sitka, the best model had capture probability co-varying with survey-time and the other two models nearly as good ( $\Delta AIC_c < 4.54$ ). Table 2 provides the estimates and 95% confidence intervals from the most parsimonious model for each location and fall/winter. All the models described the same pattern to estimated abundances and were similar in magnitude and error. The relative abundances in the models generally agreed with that of the numbers of unique individuals except that the Huggins model predicted abundance to be highest in Sitka in 2007-8.

### **Whale attendance patterns.**

Humpback whales were generally most abundant across locations in the first half of winter, but the timing of peak abundance depended on both year and location. In PWS whales remained at high abundance throughout the fall of the second winter and only began declining after December (Figure 2). While the attendance pattern for first winter in PWS was not estimated (due to reduced sampling effort) the largest number of whales was observed in December. In Sitka Sound the peak abundance of whales was observed in November during the first winter (2007-8) and in October during the second winter (2008-9) (Figure 2). Peak abundance in Lynn Canal tended earlier, occurring in September in the first winter and October during the second winter, prior to the dense deep aggregations of herring.

### **Cumulative foraging effort on herring.**

Greater numbers of whales and longer attendance patterns in PWS led to much higher estimates of whale days foraging on herring than in either Lynn Canal or Sitka Sounds (Table 3). Using either observed, or expanded through the model, the number of whale days in PWS was much greater, peaking in 2008-9 with an estimated 17,819 whale days foraging on herring, four times the whales days in Sitka Sound and 7 times the number of days in Lynn Canal.



### **Overwintering whales.**

Overwintering on the feeding grounds by humpback whales appears to be an infrequent occurrence in Alaskan waters. During the course of this study we confirmed that four whales in PWS and two whales from Sitka Sound did not make the migration to lower latitudes (This represents less than 2% of the late-season whales we identified during this study). Two of the PWS whales were a mother and her calf the, the other two were adults of unknown sex. The two whales from Sitka Sound were adults of unknown sex. We did not confirm that any whales overwintered in Lynn Canal during the winters of 2007-8 and 2008-9.

## **DISCUSSION**

### **Late-season whales forage on herring.**

We identified over 300 whales (unique ID) during the two winters of study, demonstrating that humpback whales can be abundant in the late fall and early winter in Alaska waters, making it plausible that foraging whales can have a significant impact on local herring populations. Whale populations in the north Pacific have increased steadily for the last several decades (Calambokidis et al. 2008); hence the impact on herring or other forage may be increasing as the whales populations recover. Anecdotal observations support the general increase in the North Pacific, at specific regional locations, and also contributed to the hypothesis that whales are significant predators restricting herring populations in some regions. Although herring populations are struggling in some Alaskan locations, they are booming in others areas, suggesting that whale foraging impact on herring may be very location specific, if at all.

Key to understanding the impact of whales on herring populations is the quantification of whale foraging effort on herring, not just population numbers. We express this in terms of “whale days”. The identification of individual whales provides a minimal estimate of abundance, Counts of whales are typically biased low, there is potential to overlook animals below the surface. Less biased population numbers for analysis were derived from the Huggins Closed Capture models. Although we attempted to meet the assumptions of the Huggins Closed Capture models, our analysis of humpback whale abundance is subject to some bias (White and Burnham1999). Weather, heterogeneity, capture probabilities, migration, and local knowledge of whale distribution all influence mark-recapture estimates. Despite the potential for bias in the mark-recapture estimates, we feel our abundance estimates are sound, given the agreement between estimated population abundance and the number of unique individual whales identified in each stratum (Table 2.).

### **The potential impact of whales on herring was greatest in PWS.**

The greatest number of unique ID whales and the greatest number of “whale days” foraging on herring was in PWS in the winter of 2008-9, and the second highest in the winter 2007-8,

suggesting whales pose the greatest threat to herring in PWS compared to the other locations. The “whale days” in the second winter is more than double the first winter assessment, and is likely the result of increased number of surveys (5 instead of 3) and to greater coverage of PWS during the second field season.

In 2007-8 we failed to survey two areas of major herring and whale aggregations, early fall in Montague Strait and winter in Port Gravina. Thus, we believe that the 2008-9 estimates provide a more thorough and accurate description of seasonal whale trends and abundance in PWS. The numbers of whales is greatest in PWS (relative to Lynn Canal and Sitka), but the attendance pattern is equally important. In PWS, the attendance patterns of whales were better synchronized with the formation of the large shoals of overwintering herring in the late fall /early winter. Thus, it appears that whales in PWS were maximizing the exploitation of wintering herring prior to their southern migration whereas, whale numbers in southeastern Alaska dropped even though herring were still abundant.

### **Attendance patterns of whales on herring were less in Sitka Sound and Lynn Canal.**

The number of whales was less in both Sitka Sound and Lynn Canal, compared to PWS. Coupled with the lower number of whales was the lack of attendance to herring shoals by the whales. In Sitka sound, herring did not form large shoals at depth, apparently lingered on the nearby shelf in their “summer foraging” strategy, and were not condensed into the shoals that might attract substantial whale predation (Straley et al. Chapter 2). Hence the whales present in the early fall were more associated with krill than herring (Straley et al. Chapter 2). In Lynn Canal, the herring shoals appeared in the early fall, on a similar schedule to PWS, but earlier than Sitka Sound. Whereas whale numbers remained high throughout the fall and well into winter in PWS during 2008-9, both locations in southeastern Alaska exhibited an influx of whales in the fall followed by a decline. We attribute the attendance pattern observed in Lynn Canal and Sitka Sound to whales switching to more profitable foraging opportunities. We found no evidence of alternative prey available to whales in PWS. The presence of euphausiids influences whale attendance patterns on herring shoals in both Sitka sound and Lynn Canal mitigating the impacts of whales on local herring populations.

### **Whale attendance pattern may reflect alternative prey resources.**

The availability of alternative prey may explain some of the difference in humpback whale attendance patterns between PWS and southeastern Alaska. Corresponding to the decline in whale numbers in Lynn Canal and Sitka Sound is an increase in whales in nearby Seymour Canal and Fredrick Sound (approximately 150 km south of the Lynn Canal) (Stralely and Moran Unpublished Data). Individual whales from both Lynn Canal and Sitka Sound have been document feeding in Seymour Canal on large swarms of euphausiids in the late fall and winter. We believe that many of the whales in southeastern Alaska use wintering shoals of herring as an intermediate food source until large euphausiid aggregations become available later in the year. In PWS, we consistently found whales near schools of herring, and the lack of abundant alternative prey.

The specific patterns of attendance observed will likely change over time, based on the availability of forage. The mechanisms by which humpback whales select prey are likely a combination of prey density, maternal influences and individual preferences. Their ability to exploit several trophic levels gives them the flexibility to select an optimum foraging strategy that includes many types of prey. When herring populations are down, the effort to capture herring at depth may outweigh the benefits, and whales will move on to other pockets of forage. The recent pattern of whale attendance in Sitka sound is not consistent with past observations by Straley, who observed more of linkage with herring in early previous years. Our observations in PWS and Lynn Canal suggest that whale predation on herring at depth may break up the large continuous shoals into smaller schools, potentially increasing the cost of foraging. Finding and exploiting smaller schools may prompt whales to move to other locations in the hopes of finding denser aggregations of forage.

### **Non-migrating whales are not significant herring predators.**

During two winters of observations six whales out of a potential of 449, (some whales were seen in both years and had two opportunities not to migrate) did not migrate out of their region indicating that the numbers are too small to become a significant factor in herring predation. Only 10 cases of overwintering whales were documented in southeastern Alaska from 1994 – 2000, out of an estimated population of over 900 (Straley 2000). The appearance of year-round humpback whales in Alaskan waters is largely due to staggered migration patterns, with some whales leaving the feeding grounds late and others returning early. (Straley 2000, Straley et al. 2009).

The age, sex, and reproductive condition of non-migrating whales varied and no clear pattern emerged that would allow us to make generalizations about why these whales remained in Alaskan waters throughout the year. It is possible that nutritional stress could be factor in whales skipping a migration. As the North Pacific humpback whale population increases, intraspecific competition for resources may necessitate more time on the feeding grounds to meet the energetic demands of two transoceanic migrations and a fasting period on the breeding grounds. Data on overwintering whales is limited, difficult to collect and trends are generally unknown. However, if overwintering rates can be linked to body condition or prey availability, they may provide index into humpback whale health at the individual and population level as well as insight to the status of their prey. As whale populations continue to increase, non-migrating whales may become more relevant.

### **Conclusions.**

There were more whales in PWS and they were associated with herring for longer period throughout the winter than the two populations in Southeast. Their focus on herring in PWS may have been the result of an absence of exploitable densities of krill. In contrast, in SEAK whale abundance dropped off during fall resulting in a decreased association with herring. Given these observations, it is important for managers seeking to balance commercial harvest levels with

ecosystem demands to recall that the absolute abundance of potential fishery competitors is less important than the temporal pattern over which the abundance is distributed. Our analysis of whale attendance in late fall and winter is consistent with the observation that whales may be exerting significant predation pressure on some herring stocks in Alaska, particularly PWS.

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### Tables

Table 1. Effort in hours of survey time and kilometers traveled during humpback whale surveys in Prince William Sound (PWS), Southern Lynn Canal (LC), and Sitka Sound (SS).

	PWS		LC		SS	
	km	hours	km	hours	km	hours
Sep-07	685	48.0	398	30.5	11	13.7
Oct-07	0	0	100	5.6	37	3.6
Nov-07	357	34.3	378	61.1	119	3.4
Dec-07	0	0	25	14.1	57	5.8
Jan-08	666	36.6	63	4.5	0.0	0.0
Feb-08	0.0	0.0	426	37.6	35	14.6
Mar-08	0.0	0.0	72	2.8	41	4.1
<b>Total</b>	<b>1708</b>	<b>118.9</b>	<b>1462</b>	<b>156.2</b>	<b>300</b>	<b>45.2</b>
Sep-08	763	51.5	89	5.4	26	2.7
Oct-08	587	42.7	187	14.7	124	9.0
Nov-08	0.0	0.0	143	5.7	46	3.4
Dec-08	532	36.5	0	0.0	130	6.0
Jan-09	580	40.4	85	5.0	28	1.7
Feb-09	0	0.0	100	2.3	339	14.6
Mar-09	706	34.6	0	0.0	0	0.0
<b>Total</b>	<b>3168</b>	<b>205.7</b>	<b>604</b>	<b>33.1</b>	<b>693</b>	<b>37.4</b>

Table 2. Late-season humpback whale population estimate with upper and lower 95% confidence intervals for Prince William Sound (PWS), Southern Lynn Canal (LC), and Sitka Sound (SS). Calves were not included in the abundance estimate.

	Winter	Estimate	Lower CI	Upper CI	Unique IDs	Calves
<b>PWS</b>	2007-8	64.2	54.7	76.5	76	5
	2008-9	134.8	128.5	142.1	131	16
<b>LC</b>	2007-8	51.6	47.4	57.5	38	4
	2008-9	35.4	30.7	42.5	22	2
<b>SS</b>	2007-8	95.3	86.5	105.8	44	8
	2008-9	67.8	61.8	75.4	45	4

Table 3. Huggins closed-capture modeling results for each field season and location Prince William Sound (PWS), Southern Lynn Canal (LC), and Sitka Sound (SS). Standard errors abundance estimates are in parenthesis. Models are ranked best to worse for each region.

	Model	AICc	$\Delta$ AICc	Parameters	2007-8 Estimate	2008-9 Estimate
<b>PWS</b>	Effort (time)	598.43	--	3	64.2 (30.6)	134.8 (11.9)
	Effort (distance)	599.67	1.24	3	64.8 (31.0)	134.8 (11.9)
	Null	601.54	3.11	2	66.5 (32.1)	135.2 (12.0)
<b>LC</b>	Effort (time)	411.70	--	4	51.6 (6.4)	35.4 (8.7)
	Effort (distance)	431.66	19.96	4	52.7 (6.8)	35.7 (8.8)
	Null	445.50	33.80	3	54.3 (7.3)	35.8 (8.9)
<b>SS</b>	Effort (time)	491.75	--	4	95.3 (24.2)	67.8 (11.9)
	Effort (distance)	495.75	4.00	4	96.4 (24.6)	67.8 (11.9)
	Null	496.29	4.54	3	96.5 (24.6)	68.2 (12.1)



Table 4. Whale foraging effort (whale days) for each field season and location Prince William Sound (PWS), Southern Lynn Canal (LC), and Sitka Sound (SS). Values for  $\alpha$  show the scalar used to adjust  $N_{t\text{ observed}}$  to account the mark recapture estimates of whale abundance. See equations 4 and 5. The attendance pattern for Prince William Sound in 2007-8 was not modeled because only three surveys were conducted over a limited spatial area.

	Winter	$N_{t\text{ observed}}$	$N_{t\text{ expanded}}$	$\alpha$
<b>PWS</b>	2007-8	-	8916	-
	2008-9	8195	18719	1.1
<b>LC</b>	2007-8	1711	2940	1.7
	2008-9	1140	2019	1.8
<b>SS</b>	2007-8	2348	7190	1.7
	2008-9	2188	5144	2.3

## Figures

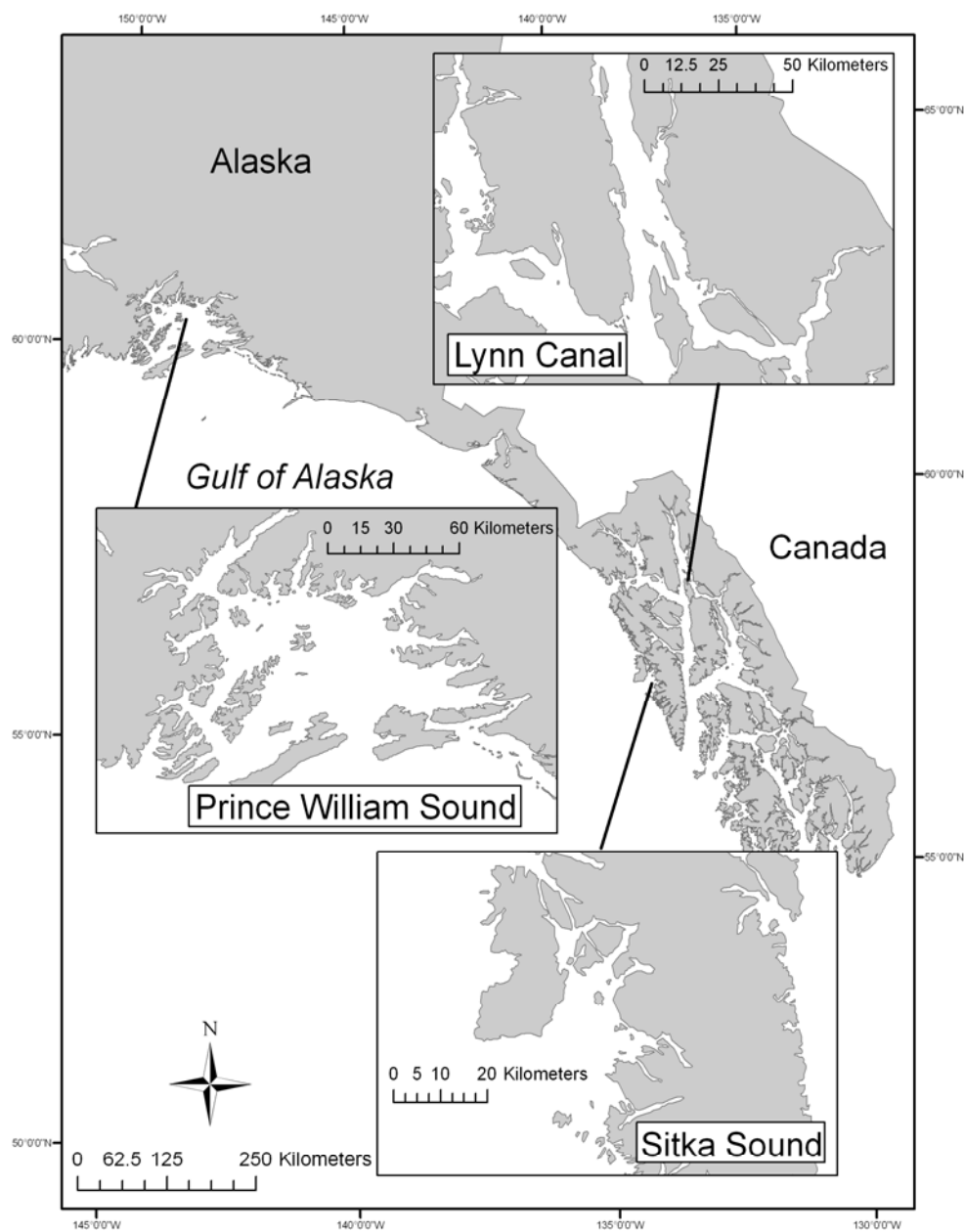


Fig. 1. Locations of the Prince William Sound, Lynn Canal, and Sitka Sound study areas.

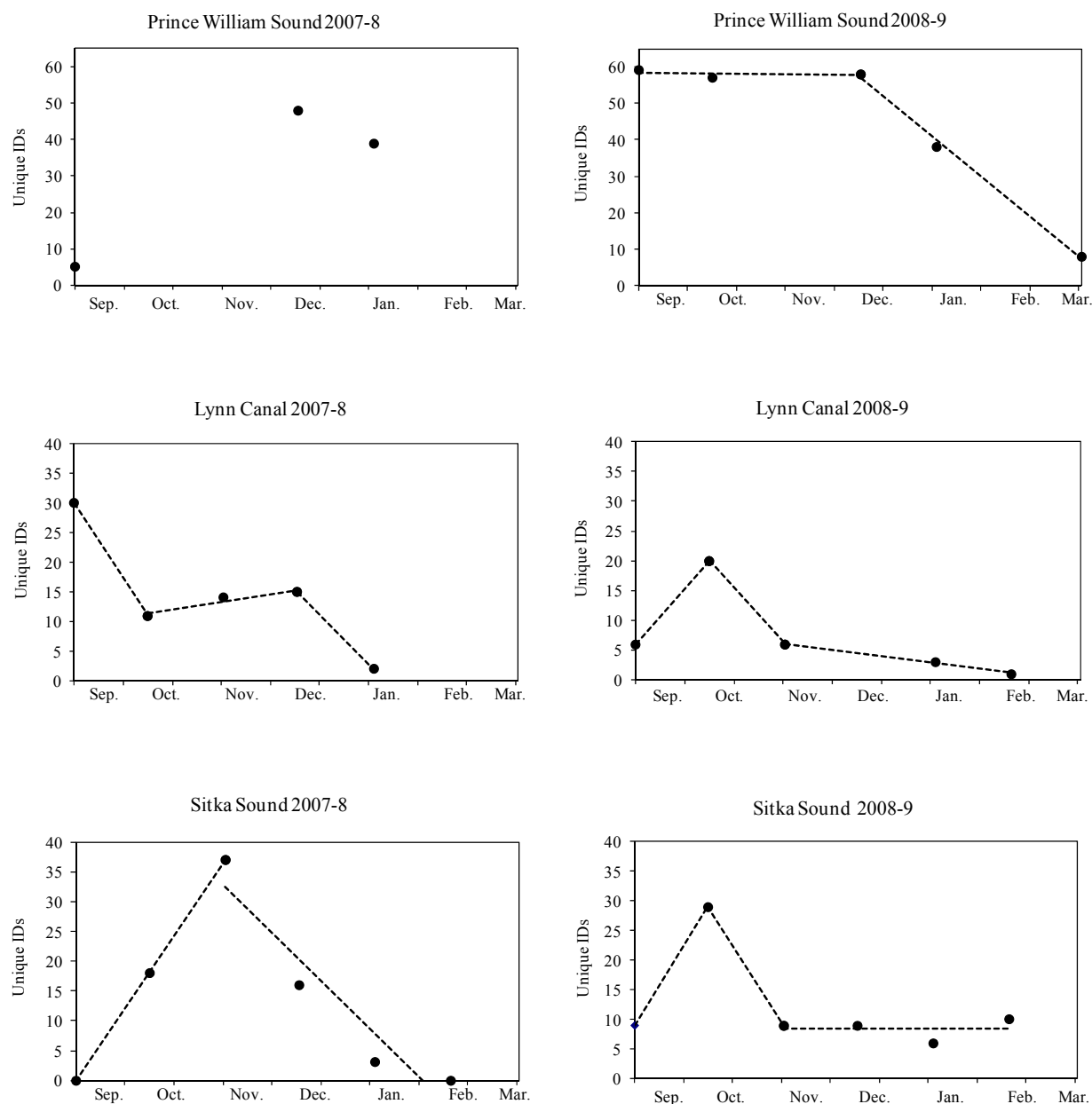


Fig.2. Late season attendance patterns of humpback whales in Prince William Sounds, Lynn Canal and Sitka Sound. Points show the number of unique whales identified in each location during each month. The attendance pattern for Prince William Sound in 2007-2008 was not modeled because only three surveys were conducted over a limited spatial area.

### Appendices

Appendix 1. Capture histories for humpback whales in Prince William Sound.

2007-8							
Occasion	R(i) j= 2		3	4	5	Total	
1	3	1	0	0	0	1	
2	14		2	0	0	2	
3	8			0	0	0	
4	0				0	0	
2008-9							
Occasion	R(i) j= 2		3	4	5	Total	
1	41	20	3	1	0	24	
2	46		11	2	0	13	
3	30			9	0	9	
4	22				3	3	

## Appendix 2. Capture histories for humpback whales in Lynn Canal.

2006/2007									
Occasion	R(i)	j= 2	3	4	5	6	7	Total	
1	0	0	0	0	0	0	0	0	0
2	8		1	0	0	0	0	1	
3	3			1	1	0	0	2	
4	1				0	0	0	0	
5	3					2	0	2	
6	2						0	0	
2007-8									
Occasion	R(i)	j= 2	3	4	5	6	7	Total	
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	
2008-9									
Occasion	R(i)	j= 2	3	4	5	6	7	Total	
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 3. Capture histories for humpback whales in Sitka Sound.

2006/2007								
Occasion	R(i)	j= 2	3	4	5	6	7	Total
Oct	5	2	0	0	0	0	0	2
Nov	10		0	0	0	0	0	0
Dec	0			0	0	0	0	0
Jan	0				0	0	0	0
Feb	0					0	0	0
Mar	1						0	0
2007-8								
Occasion	R(i)	j= 2	3	4	5	6	7	Total
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
2008-9								
Occasion	R(i)	j= 2	3	4	5	6	7	Total
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

**Chapter II: A Comparison of Humpback Whale Diets on Three Overwintering Herring Grounds in the Gulf of Alaska.**

Manuscript title: 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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## ABSTRACT

The seasonal presence and diet for late migrating humpback whales (*Megaptera novaeangliae*) were investigated to assess the impact of predation upon three Pacific herring (*Clupea pallasii*) populations in the Gulf of Alaska (133°W-147°W; 57°N-61°N). Areas were known for 1) fall and winter herring aggregations and 2) humpback whale predation. Herring population status differed; one was robust (Sitka Sound) and two were recovering (Lynn Canal and Prince William Sound). Vessel surveys from September 2007 to March 2009 collected data on whale observations and prey. Using sonar and capture methods, prey was identified for groups of feeding whales. Hydroacoustic estimates of prey availability in Sitka Sound and Lynn Canal were used to estimate the functional response of whales to increasing herring abundance. Over all years and seasons, there was a significant difference in diet composition observed between the three areas (Pearson  $\chi^2 = 83.979$ ,  $df = 6$ ,  $p < 0.0001$ ). In Prince William Sound, the greatest proportion of groups was feeding on herring, and Sitka Sound had the greatest proportion of groups feeding on krill. Prolonged foraging on herring in Prince William Sound is due to the absence of alternative prey or a preference for herring. Consequently, whale predation likely has the greatest impact on herring in PWS.



### INTRODUCTION

As seasonal migrants, humpback whales (*Megaptera novaeangliae*) are found in higher latitudes feeding on schooling fish and zooplankton during the summer and traveling to breeding areas in the lower latitudes of the world's oceans in winter. The Hawaiian Islands are the primary migratory destination for humpback whales from genetically distinct feeding aggregations located across the North Pacific, including in the Gulf of Alaska: Prince William Sound (PWS) and Southeast Alaska (SEAK) (Baker et al. 1996, 1998; Witteveen et al. in press). The migration pattern is complex with some humpback whales still present on the Alaskan feeding grounds in the fall and winter (Straley 1990, 1994). However, because the transit to Hawaii takes about a month (Gabriele et al. 1996), whales can be present on the feeding grounds until early February and still travel to Hawaii and to be present for the peak of the breeding season in March (Gabriele 1992). Therefore the timing of the southbound migration is staggered, with some whales leaving earlier in the fall for the breeding grounds, some leaving later and only a few whales seen often enough in winter to have forgone migration that year (Straley 1990, 1994).

During the winter in PWS and SEAK, Pacific herring (*Clupea pallasii*) overwinter in dense aggregations in deep fjords and troughs prior to spawning in the spring. The three areas compared in this study are divergent in the trajectory of their respective herring populations. In PWS the spawning population of herring collapsed in 1992-93 and has not recovered sufficiently to sustain a fishery. In SEAK, Sitka Sound's (SS) large robust herring fishery has existed in for several decades (Collie 1990). In years prior to the PWS oil spill, SS and PWS herring recruitment were correlated (Williams and Quinn 2000) likely due to the influence of broad-based environmental and oceanographic forces. In LC (LC), there are known concentrations of over wintering herring (Sigler and Csepp 2007), however, the local spawning stock has not been commercially fished since the 1980s and is not recovering.

Humpback whales have been observed feeding on these densely aggregated herring in winter, however, the information available regarding humpback whale distribution, numbers and target prey was varied for the three study areas. In PWS, McLaughlin Environmental Services (MCES) recorded counts of humpback whales present in Sawmill Bay feeding upon herring from late November to January, during the mid-2000s (MCES, unpublished data). In other areas of PWS, humpback whales have been reported associating with herring in fall and winter (from Matkin and Hobbs as reported in Okey and Pauly 1999), but the numbers of whales, geographic distribution and seasonal presence were unknown outside of Sawmill Bay. In SS, year round studies on humpback whales have occurred since the early 1980s and have documented whales feeding upon herring and euphausiids (termed krill for this study) during the fall and winter (Straley 1990, 1994). However, the proportion of herring in the diet was unknown. LC has a year-round presence of humpback whales documented from shore based monitoring (T. Quinn, unpublished data) but the numbers of whales using this entire area during the fall and winter and the target prey was unknown. Whales foraging on aggregated herring and euphausiids in winter are consuming an energy rich prey (Anthony et al., 2000; Falk-Petersen et al. 2000;

Vollenweider 2005) and are likely maximizing their reproductive fitness by spending more time provisioning themselves for two oceanic migrations and other activities associated with mating and calving because little or no feeding occurs on the breeding grounds.

Various hypotheses have been proposed to account for the collapse and lack of recovery of herring in PWS (Pearson et al. 1999). Intensive foraging by humpback whales on aggregated winter herring is one hypothesis that may be impacting the recovery of herring. This population of humpbacks is increasing at an annual rate of 5.5% to 6%; derived by comparing abundance estimates from two studies conducted in 1991 to 1993 and 2004 to 2006 (Calambokidis et al. 2008). Therefore, humpback whale predation may represent a significant source of mortality to herring; particularly if feeding on herring occurs for a number of months or targets a specific age class of herring.

The overall goal of this study was to compare the impact of whale predation upon herring in three geographically distinct areas where humpback whales and herring are present in the fall and winter. These areas differed in the status of herring with SS hosting a large robust population and the other two struggling. The specific objective for this paper was to determine the proportion of herring in the whales' diet using counts of whales foraging upon herring each month across the fall and winters of 2007/08 and 2008/09 and to relate the proportion to the availability of herring. Heintz et al. (Chapter 4) incorporated the data from this aspect of the study and overall estimates of the population of humpbacks in each area (Moran et al. Chapter 1) to assess the impact of whale predation upon Pacific herring in three areas of Alaska using a bioenergetics model. In addition we estimated the abundance of herring present in SS and LC to characterize the functional response between the number of whales foraging on herring and the abundance of herring.

## METHODS

### **Study Areas**

All three study sites are located around the perimeter of the Gulf of Alaska (Figure 1). Prince William Sound (PWS) is an area of relatively protected waters in the northern Gulf of Alaska (60.5 N 147.0 W), characterized by complex coastline of glacial fjords and islands and approximately 4500km<sup>2</sup> in area. Within PWS, we surveyed Sawmill Bay (60.2 N 148.1 W) extensively. This is a very small bay located in the southwestern portion of PWS. Sitka Sound (SS) is located on the eastern edge of the Gulf of Alaska (57.0 N 135.5 W) on Baranof Island in southeastern Alaska. It comprises a complex network of islands and bays, encompassing approximately 450km<sup>2</sup>. Southeastern Alaska itself is a mosaic of islands and mainland deeply incised with glacial fjords with many passage ways and bays protected from the Gulf of Alaska. Lynn Canal (LC) is located to the north and east of Sitka Sound (58.4 N 134.8 W) in a large

north-south oriented fjord. This area encompasses approximately 500km<sup>2</sup> and includes the waters of southern LC and northern Stephens Passage.

<FIGURE 1>

### **Effort**

Effort in hours of survey time and kilometers traveled was recorded during humpback whale surveys across the fall and winter months in PWS, LC and SS from mid-September 2007 to mid-March 2009.

In PWS, eight 5-day surveys were conducted aboard the 17.7m vessel *M/V Auklet* starting and ending in Cordova. Additionally, in PWS, surveys were conducted from a small boat (<7m) in Sawmill Bay by MCES in 2007/08 and 2008/0, Distance traveled was not recorded for all of 2007/08 and half of the 2008/09 Sawmill Bay surveys. In February 2007, JMS visited MCES and a handheld GPS was used to determine an average trackline of 9km for the survey route which was used as the estimated distance traveled for surveys in the absence of a trackline.

In LC and SS, surveys were conducted during day trips from small boats (< 8m). When daylight and weather conditions were limiting during the winter months effort was focused on areas with higher concentrations of whales. Prior knowledge of whale distribution was used to ensure aggregations of whales were not being overlooked during boat based surveys.

To maintain consistency in comparing data collected for analysis of target prey among the three study areas, three seasons were defined: 1) fall encompassed the months from to mid-October to mid-November, 2) winter from mid-November to mid-February and 3) spring from mid-February to mid-March. Although technically these grouping of months for winter and spring are not accurate for the calendar year, they do define the whale and prey behavior. In winter (November to February) daylight is limited and herring have moved into the deep fjords for overwintering. In spring (February and March) a transition occurs during this time period from winter to spring with a few whales beginning to return from the breeding grounds, a few whales may have lingered and forgone migration and herring become active, preparing for spawning during these months.

### **Whale Observations**

#### ***Groups and Counts of Whales***

Whales were considered to be part of a group if they dove and surfaced in synchrony and were in close association, within a whale body length of each other. When a group of humpback whales was located the number of whales were counted, behavioral role and age class determined (calf, adult, mother). If whale numbers were over 10, associations were brief and the group dynamics were fluid the group was called a shoal, however every effort was made to record group

association data the whales within a shoal. In Sawmill Bay, PWS, each survey was considered a shoal and group associations were not recorded.

In each study area, the number of groups of whales observed, the sum of all whales counted in each group, the average group size and the sum of whales photo-identified each month (mid-month to mid-month) was tallied. In PWS, the vessel surveys and MCES Sawmill Bay data resulted in three tables to present the whale count data represented in three datasets:

- 1) All whales seen during all surveys
- 2) Whales from the MCES surveys occurring during or within two days of the dates of the large vessel surveys and these data were used to determine the proportion of prey in the whales' diet. It was necessary to constrain data collected from Sawmill Bay in this manner because the MCES surveys were conducted in one small area and the vessel surveys covered the entire PWS. Hence, using all the MCES data could over represent the percentage of herring in the whale's diet each month. Therefore, to minimize this bias, the MCES surveys dates used were those which occurred during or within 2 days of the eight PWS-wide vessel surveys.
- 3) All whales seen during MCES surveys in Sawmill Bay only. All Sawmill Bay data were included in the overall number of whales, length of stay and movements across the fall and winters of 2007/08 and 2008/09.

### ***Unique Individual Whales***

If daylight and sea conditions allowed, whales were approached for a digital photograph to capture the ventral surface of the flukes when the whale dives and the flukes are perpendicular to the surface of the water. The black and white pattern on the ventral surface is used to identify each whale. Photographs of unique individual whales were tallied to determine the composition of each group of whales, the overall number of unique whales present each month, year and across both years of the study. Identifying the whales in each group provided a means to only use a group of whales once each day for determining the diet of a group of whales.

### ***Behavior of Groups of Whales***

Groups of whales were determined to be feeding if prey was observed directly being consumed or inferred by repeated diving in the same location or along a trajectory (shoreline or other barrier), and prey was observed on the sonar or visually or other predators were present. All whales in groups were presumed to be feeding on the same prey. Other behaviors observed were resting, where a whale is not moving at the surface and motionless; traveling, if the whale was moving in a steady direction with shorter dive times than a foraging dive; and milling, if a specific behavior could not be determined. Feeding was the only behavior analyzed for the purposes of this paper.

### **Prey Observations**

#### ***Target Prey Identification***

When groups of whales were located and determined to be feeding, effort was made to determine what the whales were eating. Direct observations of prey being consumed, remains after feeding, and sonar mapping of the prey fields observed on a dual 50/200kHz frequency echosounder were used to determine target prey of humpback whales. 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 of target prey was accomplished using herring jigs, zooplankton tows, cast nets and skim nets (used to clean swimming pools) to collect surface fish near feeding whales. Scales and zooplankton were collected behind whales feeding at the surface with the skim net. Fecal samples were collected when possible. Size distributions of herring captured was assumed to be consistent with the size distribution observed in samples collected from locations where whales were foraging. Certainty of identification of the target prey was recorded as certain, probable or undetermined. Only cases where the identification was certain or probable were used to identify specific prey.

### ***Proportion of Prey Type in the Groups of Whale's Diet***

The proportion of prey type in the diet of observed feeding groups of whales was determined across months from mid-September to mid-February each year. Groups were used as the unit of measure for determining the proportion of prey in the diet. The group was used rather than individual whales because the whales were feeding upon the same prey (Table 1). Therefore, each group of whales associating together each day was tallied across the season to determine the number of groups observed each month. For each month the groups of whales feeding on herring, euphausiids (krill), both or undetermined was calculated as a percentage of the total prey observed for all groups each month.

### ***Availability and Abundance of Herring in Sitka Sound and Lynn Canal***

Herring biomass was measured via monthly hydroacoustic surveys in SS and LC according to methods detailed by Boswell et al. (Chapter 3). Results and methods for the LC surveys are reported by Boswell et al. (Chapter 3), here we present data for SS and draw on the LC data to describe the functional response of whales to increased herring abundance. Acoustic surveys of herring in SS were conducted 3 - 5 days each month from December 2007 through March 2008 and November 2008 through March 2009. Briefly, monthly hydroacoustic transect-based surveys were conducted in December 2007 and March 2008 and over the course of ten days from November 2008 to March 2009. In SS herring surveys followed a 155 km transect line covering an area of 115 km<sup>2</sup>. Figure 2 shows the track lines followed during each survey.

<Figure 2>

Herring biomass was measured during daylight hours with a georeferenced Simrad EK60 split-beam echosounder interfaced with a 38 kHz 12° circular-beam transducer towed beside the vessel at 5-10 km hr<sup>-1</sup>. Acoustic collection and calibration parameters followed those of Sigler and Csepp (2007). Acoustic data in SS were subdivided into 7 strata where each stratum was generally characterized by homogenous bathymetry and herring schooling behavior. Herring

schools were manually identified in Echoview (4.3; Myriax, Pty. Ltd.) and the Nautical Area Scattering Coefficient (NASC;  $\text{m}^2 \text{nmi}^2$ ), the aerial acoustic measure proportional to fish density, was exported for each 10 m-deep by 0.18 km-long cell containing herring (Simmonds and MacLennan 2005). The NASC values for each 0.18 km segment were summed over each 10 m depth interval and corrected for the effects of shadowing and acoustic extinction introduced by herring's dense schooling behavior (Zhao and Ona; Sigler and Csepp 2007).

Fish length and weight measurements are required to convert NASC values to biomass estimates. Opportunistic herring collections were made from acoustic targets using jigging, variable-mesh gillnets and mid-water trawl. Measurements of fish lengths (L in cm) from direct capture samples were used to calculate depth-dependent target strengths (TS) for individual fish to scale NASC values (Ona 2003), where:

$$\text{TS} = 20 \log_{10} L - 2.3 \log_{10} (1 + Z/10) - 65.4, \text{ and} \quad (1)$$

Z = mean water depth (m) occupied by herring school

TS were then used to scale NASC values and derive aerial estimates of fish density (fish  $\text{nmi}^{-2}$ ) (MacLennan et al. 2002), where:

$$\text{Fish density} = \text{Corrected NASC} / 10^{(\text{TS}/10)} \quad (2)$$

Aerial biomass ( $\text{g nmi}^{-2}$ ) was calculated by applying a length-weight relationship derived from herring captured during the study period, where:

$$\text{Weight (g)} = 8.0\text{e}^{-7} * L^{3.4798} \quad (3)$$

Total biomass per stratum was extrapolated as the product of aerial biomass and stratum area.

### ***Statistics***

A Pearson Chi-square test (JMP 9 software) was used to test the differences among the diets of groups of humpback whales observed both years 1) between the three study areas and 2) across seasons within each study area. We examined the functional response of whales to herring by estimating the number of whales foraging on herring in each month. The number of whales foraging on herring was estimated as the product of the number of whales counted in a given month and location, the proportion of groups observed foraging and the proportion of those fish that foraged on herring. The numbers of whales foraging on herring on each date were plotted along to herring biomass to visually ascertain if any relationship existed between the two.

## RESULTS

### **Effort**

Effort in survey days, distance traveled and hours are presented in Table 1 for all areas.

In PWS, three surveys occurred in September, October and January 2007/08 and five surveys occurred in September, October, November, January and March 2008/09. No large vessel surveys occurred in December of either year. Additionally, 28 and 21 surveys were conducted in

2007/08 and 2008/09, respectively, in Sawmill Bay. In LC, 18 and 7 surveys occurred; and in SS, 13 and 19 surveys occurred in 2007/08 and 2008/09, respectively

In PWS, the overall effort from the combined surveys was greater in 2008/09 than 2007/08 (Table 1a). In particular, the addition of two large vessel surveys nearly doubled the distance traveled in 2008/09. In Sawmill Bay, MCES survey effort was lower in 2008/09 but the days of effort were consistent across the fall and winters within each year (Table 1c). In LC, overall effort was greatly reduced in 2008/09 (Table 1d). In SS, in 2008/09 distance traveled searching for whales increased twofold but the hours on the water were nearly identical to effort in 2007/08 (Table 1e).

<TABLE 1>

#### Whale Foraging Behavior and Diets

##### **PWS**

In PWS large numbers of whales actively foraged on herring throughout most of the survey period (Table 2, Figure 3). Whale numbers remained relatively constant between September and December in both years (Table 1a) and only decreased in number after February. Peak abundance was noted in December in 2007 and November in 2008. In addition, a high proportion of the whales were foraging. Between September 2007 and February 2008, 68%-80% of the groups we observed were foraging (Table 2). During the same period in 2008/09, we observed between 60% and 88% of the groups foraging. There was no seasonal trend to the percentage of groups observed foraging. In 2007/08 the lowest proportion of groups foraging was observed in December (68%), while in 2008/09 the proportion observed foraging in December was among the highest (79%). Herring was an important dietary item for these whales and the proportion of herring did not differ among months ( $\chi^2 = 2.38$ ,  $df = 2$ ,  $P = 0.305$ ). In 2007/08 between 16% and 81% of the foraging groups were observed eating herring (Table 3), however we were unable to positively identify the prey for many of the groups. Of those groups with positively identified diets, herring were consumed by 71% to 100%. In 2008-2009, when we had greater survey effort, foraging groups were consuming herring between 67% and 100% of the time.

<Table 2>

<Figure 3>

##### **LC**

Whales in LC were less abundant and foraged less than those in PWS but still consumed herring (Table 3, Figure 4). There was a seasonal component to whale abundance in LC (Table 1d). Whales were most abundant in the early part of the survey period in both years and had largely vacated the area by late December. When whales were abundant they exerted relatively little foraging effort and there was no apparent seasonal effect on the proportion observed foraging. In September of 2007 50% of the groups observed were foraging and 63% were foraging in October of 2007. In September 2008, 75% of the observed groups were foraging, and 67% were

observed foraging in November 2008. There was no survey conducted in October 2008. Despite the relatively low foraging levels, foraging whales were focused on herring. Herring were identified as the prey for 100% of the groups with positively identified prey types in seven of the eleven months surveyed and the proportion of herring consumed did not differ among months ( $\chi^2 = 3.11$ ,  $df = 3$ ,  $P = 0.375$ ).

<Table 3>

<Figure 4>

### SS

Foraging was most intense in SS, but there were fewer whales than PWS and they preferred krill when they were most abundant (Table 4, Figure 5). There was a seasonal pattern to whale abundance in SS similar to the pattern observed in LC; whales peaked in abundance in October in 2007 and September in 2008 (Table 1e). Whales were mostly gone from SS in after mid-December in 2007 while small but consistent numbers of individuals lingered in the area throughout the entire winter of 2008/09. Whales in SS were actively foraging throughout the survey period. In October 2007, 94% of the groups we saw were actively foraging (Table 4). Throughout the rest of the winter all observed groups were foraging. Similarly in 2008, the lowest proportion of groups observed foraging was 77% in December and 79% in September. Otherwise all groups were observed to be foraging. Herring were much less important as prey in SS compared with LC or PWS. In both years herring were not important prey until whale abundance had declined. However, late in the year herring was the only prey consumed (Table 7, Figure 5).

<Table 4>

<Figure 5>

## **Relationship between Whale diet and Herring Abundance**

### LC

Whales foraged progressively less on herring as herring abundance increased in Lynn Canal (Figure 6). Reductions in herring predation related to reductions in the number of whales. Despite large increases in the abundance of herring in winter, most whales departed so that the overall number of whales eating herring decreased. This resulted in an apparent inverse relationship between the numbers of whales foraging on herring the biomass of herring present.

### SS

In SS whale foraging effort on herring increased as herring abundance increased (Figure 7). As in LC the number of whales decreased during winter. However there was a distinct increase in the number of whales foraging on herring. This increase was due to either the remaining whales



switching to herring from krill or from the departure of krill-eating whales. Note that hydroacoustic surveys were conducted monthly in SS during 2007/08 but no herring were detected except in December and March. Nevertheless we observed some groups foraging on herring as early as October in 2007. Herring arrived just before the spawning event in March 2008. We estimated a biomass of 82,500 tonnes. Herring arrived in SS earlier during the winter of 2008/2009 and some whales may have followed them. (Figure 7). Between December and January the herring biomass increased from 7.3 to 18.6 tonnes. Similarly, between early December and mid-January the number of whales present increased from 5 to 18. Our survey in March was conducted while herring was spawning near the beaches of SS hence our estimates likely underestimate the true biomass present.

<Figure 6>

< Figure 7>

## DISCUSSION

In the winter, humpback whale diets and timing of foraging patterns varied considerably between locations. In PWS whales foraged predominately on herring for a prolonged period late into winter, but in LC and SS the whales departed the study areas earlier in the winter as herring density was on the rise. Similar general trends of whales concentrating early in the fall and departing for breeding grounds in January have been previously reported for SEAK (Straley 1990, 1994). Although whales in both SEAK locations departed prior to peak of the herring presence, there were differences between locations. Whales foraged on krill early in fall in Sitka Sound and those whales that remained in SS later into winter took advantage of the increasing herring abundance. In contrast, LC was the earliest area to have a peak in numbers of whales and the earliest to have most of the whales depart, despite increases in prey abundance. Foraging groups in LC focused almost exclusively on herring in fall, but reductions in whale numbers meant that the number of whales foraging on herring decreased throughout the winter.

The departure of whales from the SEAK study areas could be attributed to some whales departing for Hawaii, the breeding grounds for most of SEAK's humpback whales. It is evident that some whales do depart the feeding area earlier because whales are sighted around the Hawaiian Island waters in the late fall. However, not all whales leave the feeding area at this time because peak abundance for whales in Hawaii is mid-February to mid-March (Gabriele 1992). The minimum amount of time for migration to Hawaii is approximately 39 d (Straley and Gabriele 1993) indicating the modal departure period likely occurs after mid-December, at least 30 days after whales began leaving LC and SS. It is possible these whales left on an extended migration to Hawaii, but this would entail prolonging their migratory purposes for at least 30 additional days. It is more likely that they were moving to alternative foraging locations prior to migrating. The fact that herring abundance was increasing in the locations they were vacating suggests these alternative locations probably harbor a preferred alternative prey.

Humpback whales in Southeast Alaska may prefer a diet of krill over herring when available, or when the caloric content of krill is maximized. Whales identified in Sitka Sound in the early fall have been sighted later that same year in Seymour Canal, a 65 km long narrow canal, located south of LC and east of SS, feeding on krill (Straley unpublished data) and then returning to Sitka Sound for herring in early winter, presumably when krill supplies become diminished in Seymour Canal. Depletion of dense prey patches (attributed to euphausiids) has been demonstrated by foraging humpback whales in SEAK in the summer (Szabo pers. comm). The movement of whales from LC and SS despite large increases in prey availability suggests the nutritional benefit of foraging in alternative locations or on alternative prey must have outweighed the benefit of remaining in place.

In polar regions in the fall and early winter, krill of all species are at a lipid maximum. Krill store energy as lipids or waxes to not risk missing reproduction in the spring (Falk-Petersen 2000). These lipid rich zooplankton are an efficient calorie source for pelagic marine species and higher trophic levels, specifically humpback whales in the fall and winter. Although herring, as well, are at a caloric high in the fall and winter they may be more difficult to capture at this time of year. The behavior of herring may not be as constant and predictable as krill and herring may be more easily disturbed. Herring in fall and winter occur in a deep dense layer at the bottom of the ocean during the day, which may preclude or make capture challenging because of the depth and association with the bottom during the day. At night both krill and herring rise towards the surface and become diffuse and more available for predators.

Alternatively, the explanation for why whales in SEAK abandon abundant herring areas to forage on krill (or alternate prey) may be more complex than prey abundance and density alone. The breaking up of large herring shoals by foraging whales may increase foraging cost (Boswell et al. Chapter 3). Variation in individual foraging strategies which may be culturally inherited from maternally derived preferences (Weinrich et al, 1992, Estes et al. 2003) for specific prey types or specific feeding areas could influence a whale's decision to move. As the breeding season approaches, social interactions should be considered. The transition from a feeding to a breeding focus occurs prior to migration. Whales begin to exhibit behaviors such as singing and forming surface active groups (thought to compete for access to females) associated with mating and are frequently observed in Alaskan waters during late fall and winter (Baker et al. 1986; Straley 1990). The presence of a large aggregation of over 150 whales in Seymour Canal, a narrow 65km long canal south of LC and east of SS, may be influenced by the transition from feeding to breeding behaviors and perhaps other complexities of social behavior not yet understood by human observers.

The whales in PWS did not follow the pattern of early departure observed in SS and LC. Whale abundance remained relatively constant in PWS until mid-February, leaving sufficient time to reach Hawaii for breeding. Their prolonged foraging effort on herring suggests the PWS whales did not have the option of foraging in alternative locations or on alternative prey or even perhaps

gathering with a larger group of whales to reestablish non-feeding behaviors associated with mating. Another possible explanation is that PWS whales prefer to forage on herring and were unwilling to seek alternative prey. Herring in PWS would bear the burden of whale predation in any of these cases. These alternatives are consistent with the results of the isotopic analysis of whale blubbers collected from around the Gulf of Alaska during the summer (Witteveen et al. in press). Whales near PWS had a trophic position higher than that of whales sampled near SEAK, indicating PWS whales consume more fish than SEAK whales.

The conclusion that whales primarily consumed herring in PWS for an extended time period is unaffected by the differences in survey effort between the two winters. Initially the PWS survey was designed to focus on western PWS and specifically the known aggregation of whales and herring present in late fall and early winter in Sawmill Bay. However, large vessel surveys in 2007/08 found more whales dispersed throughout PWS and, as a result, two large vessel surveys were added the next year. Although the survey effort was inconsistent among the two years in PWS, the increase in large vessel surveys enhanced and greatly improved the data the second year. By adding the two additional surveys in 2008/09 we documented over 100 unique whales seen outside of Sawmill Bay and observed multiple feeding aggregations of humpback whales in the fall and winter in PWS. Moreover, the whales primarily foraged on herring in both years.

In conclusion, a comparison of abundance, seasonal presence, behavior and diet for humpback whales during the fall and winter in three areas of Alaska followed trends found in previous studies of late migrating whales (Straley 1994). However, differences in their attendance and prey choice meant that whales in the different locations varied in their impact on local herring populations. In SS whale abundance declined as their preference for herring increased. They exerted the greatest foraging effort on herring when herring abundance was at its maximum and whale abundance was low. This is consistent with the observation that SS herring stocks are healthy. In LC whale abundance declined at the same time as herring abundance increased. This suggests LC may be a good place to forage on herring, but that adjacent areas with preferred prey were available and preferred by whales. In contrast to the SEAK locations, whales in PWS had a prolonged winter attendance and preference for herring. This may be a result of reduced availability of alternative prey coupled with a possible prey preference for herring. The herring population in PWS is struggling. The absence of alternative prey for whales, or preference for herring, combined with a prolonged predation could be limiting the recovery of this population.

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## Tables

Table 1. Survey effort and whale observations for humpback whales in Prince William Sound (PWS), LC (LC) and Sitka Sound (SS) during the fall and winters of 2007/08 and 2008/09.

a. All PWS Surveys were used to document whale movement patterns and seasonal presence. Bold numbers represent estimated distances in Sawmill Bay.

2007/08	Effort			Whales						Number unique across years		
month	Day s	km	Hrs	groups	counted	average group size	photo- identified	unique	unique year			
15 Sep-14 Oct	7	579	51.3	24	25	1	8	7	94	199		
15 Oct-14 Nov	3	27	3.6	3	4	1	4	2				
15 Nov-14 Dec	11	430	76.6	46	200	4	99	51				
15 Dec-14 Jan	6	54	10.0	6	81	14	58	29				
15 Jan-14 Feb	10	580	44.7	28	96	3	65	44				
15 Feb-14 Mar	5	45	4.4	3	5	2	3	2				
Total	42	1715	190.5	110	411	Average =4	237	135				
2008/09	Effort			Whales								
month	Days	km	Hrs	groups	counted	average group size	photo- identified	unique	unique year			
15 Sep-14 Oct	8	819	54.9	26	115	4	79	59	160			
15 Oct-14 Nov	11	624	47.2	40	137	3	69	62				
15 Nov-14 Dec	10	578	47.1	44	171	4	101	67				
15 Dec-14 Jan	4	72	7.8	5	72	14	57	36				
15 Jan-14 Feb	9	641	47.4	22	102	5	74	43				
15 Feb-14 Mar	8	648	33.1	7	14	2	12	10				
Total	50	3382	237.5	144	611	Average =4	392	277				



## Chapter 2

b. PWS surveys used to determine proportion of prey in whale diet. These data are a subset of table 1a and includes all the large vessel surveys and a subset of MCES surveys which were concurrent or within 2 days of vessel surveys.

2007/08	Effort			Whales						Number unique across years		
month	Days	km	hrs	groups	counted	Average group size	photo- identified	unique	unique year			
15 Sep-14 Oct	5	559	48.8	24	31	1	5	5	81	183		
15 Oct-14 Nov	0	-	-	-	-	-	-	-				
15 Nov-14 Dec	8	376	68.0	44	106	2	63	48				
15 Dec-14 Jan	0	-	-	-	-	-	-	-				
15 Jan-14 Feb	5	535	32.3	26	64	2	42	40				
15 Feb-14 Mar	0	-	-	-	-	-	-	-				
Total	18	1470	149.1	94	201	Average =2	110	93				
2008/09	Effort			Whales								
month	Days	km	hrs	groups	counted	Average group size	photo- identifi ed	Unique	unique year			
15 Sep-14 Oct	6	763	54.9	26	71	3	79	59	147			
15 Oct-14 Nov	5	596	42.7	32	143	4	58	57				
15 Nov-14 Dec	7	550	43.2	38	95	3	81	63				
15 Dec-14 Jan	0	-	-	-	-	-	-	-				
15 Jan-14 Feb	5	598	42.3	20	58	3	51	38				
15 Feb-14 Mar	5	618	30.0	5	8	2	8	8				
Total	28	3117	213.0	121	375	Average =3	277	225				

## Chapter 2

c. PWS surveys in Sawmill Bay only conducted by MCES. All Sawmill Bay data were used to describe whale movement and seasonal presence.

2007/08	Effort			Whales						Number unique across years		
month	days	Km	hrs	groups	counted	average group size	photo- identified	unique	unique year			
15 Sep-14 Oct	3	27	3.50	2	8	4	3	2	55	101		
15 Oct-14 Nov	3	27	3.58	3	4	1	4	2				
15 Nov-14 Dec	6	54	8.55	5	74	15	36	26				
15 Dec-14 Jan	6	54	10.00	6	81	14	58	29				
15 Jan-14 Feb	5	45	12.33	5	32	6	23	16				
15 Feb-14 Mar	5	45	4.42	3	5	2	3	2				
Total	28	252	42.38	24	204	Average =9	127	77				
2008/09	Effort			Whales								
month	days	Km	hrs	groups	counted	average group size	photo- identified	unique	unique year			
15 Sep-14 Oct	2	18	1.33	0	0	0	0	0	72			
15 Oct-14 Nov	4	36	4.82	1	2	2	2	2				
15 Nov-14 Dec	4	46	7.95	4	70	18	52	38				
15 Dec-14 Jan	4	72	7.78	4	72	18	57	36				
15 Jan-14 Feb	4	61	7.00	4	47	12	37	37				
15 Feb-14 Mar	3	30	3.16	2	6	3	5	5				
Total	21	263	32.04	15	197	Average =13	153	118				

## Chapter 2

d. LC surveys used for all analyses.

2007/08	Effort			Whales						Number unique across years	
Month	days	km	hrs	groups	counted	average group size	photo- identified	unique	unique year		
15 Sep-14 Oct	3	398.2	26.3	2	55	28	44	30	42	48	
15 Oct-14 Nov	4	333.4	35.4	11	92	8	17	13			
15 Nov-14 Dec	3	259.3	15.8	17	50	5	32	19			
15 Dec-14 Jan	2	179.6	9.3	4	10	10	8	6			
15 Jan-14 Feb	0	-	-	-	-	-	-	-			
15 Feb-14 Mar	6	498.2	40.4	1	2	1	0				
Total	18	1668.7	127.2	35	208	Average =6	101	68			
2008/09	Effort			Whales							
Month	days	km	hrs	groups	counted	average group size	photo- identified	unique	unique year		
15 Sep-14 Oct	3	275.9	20.1	4	55	14	34	22	24		
15 Oct-14 Nov	0	-	-	-	-	-	-	-			
15 Nov-14 Dec	1	142.6	5.7	3	7	2	6	6			
15 Dec-14 Jan	1	85.2	5.0	2	3	2	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	10	66	Average =7	44	32			

## Chapter 2

e. Sitka Sound surveys used for all analyses.

2007/08	Effort			Whales						Number unique
month	days	km	hrs	groups	counted	average group size	photo- identified	unique	unique year	across years
15 Sep-14 Oct	2	64.8	5.5	1	20	20	13	13	52	80
15 Oct-14 Nov	5	122.2	13.7	33	83	3	64	38		
15 Nov-14 Dec	3	72.2	7.7	16	43	3	22	16		
15 Dec-14 Jan	0	-	-	-	-	-	-	-		
15 Jan-14 Feb	2	53.7	2.7	2	2	1	0	0		
15 Feb-14 Mar	1	40.7	4.1	3	6	2	3	3		
Total	13	353.7	33.7	55	154	Average =5	102	70		
2008/09	Effort			Whales						
month	days	km	hrs	groups	counted	average group size	photo- identified	unique	unique year	
15 Sep-14 Oct	3	124.1	13.1	19	60	3	46	28	49	
15 Oct-14 Nov	3	66.7	9.9	10	19	2	18	13		
15 Nov-14 Dec	1	24.1	2.2	4	5	1	5	5		
15 Dec-14 Jan	5	174.1	13.6	9	18	2	9	9		
15 Jan-14 Feb	4	200.0	8.8	12	22	2	21	10		
15 Feb-14 Mar	3	166.7	8.9	7	11	2	7	6		
Total	19	755.6	56.4	61	135	Average =2	106	71		

## Chapter 2

Table 2. Behavior of groups of whales observed in PWS, 2007/08 and 2008/09. These data include all the large vessel surveys and a subset of MCES surveys which were concurrent or occurred within 2 days of vessel surveys.

Group Behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	19	0	30	0	22	0	71
	2008/09	23	23	30	0	13	3	92
	Totals	42	23	60	0	35	3	163
Other	2007/08	5	0	14	0	4	0	23
	2008/09	3	9	8	0	7	2	29
	Totals	8	9	22	0	11	2	52

Table 3. Behavior of groups of whales observed in LC, 2007/08 and 2008/09.

Group Behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	1	7	9	3	0	0	20
	2008/09	3	0	2	2	1	0	8
	Totals	4	7	11	5	1	0	28
Other	2007/08	1	4	8	1	0	1	15
	2008/09	1	0	1	0	0	0	2
	Totals	2	4	9	1	0	1	17

Table 4. Behavior of groups of whales observed in Sitka Sound, 2007/08 and 2008/09.

Group Behavior	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Feed	2007/08	1	31	16	0	2	3	53
	2008/09	15	10	4	7	12	7	55
	Totals	16	41	20	7	14	10	108
Other	2007/08	0	2	0	0	0	0	2
	2008/09	4	0	0	2	0	0	6
	Totals	4	2	0	2	0	0	8

Table 5. Prey type for groups of whales feeding in PWS, 2007/08 and 2008/09.

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

Table 6. Prey type for groups of whales feeding in LC, 2007/08 and 2008/09.

Prey	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Herring	2007/08	1	6	5	1	0	0	13
	2008/09	2	0	1	2	1	0	6
Krill	2007/08	0	0	2	0	0	0	2
	2008/09	0	0	0	0	0	0	0
Both	2007/08	0	0	1	0	0	0	1
	2008/09	0	0	1	0	0	0	1
Unknown	2007/08	0	1	1	2	0	0	4
	2008/09	1	0	0	0	0	0	1
	Totals	4	7	11	5	1	0	28

Table 7. Prey type for groups of whales feeding in SS, 2007/08 and 2008/09.

Prey	Year	15-Sep	15-Oct	15-Nov	15-Dec	15-Jan	15-Feb	Totals
Herring	2007/08	0	2	7	0	2	3	14
	2008/09	0	4	4	4	12	7	31
Krill	2007/08	0	24	8	0	0	0	32
	2008/09	15	6	0	0	0	0	21
Both	2007/08	0	0	0	0	0	0	0
	2008/09	0	0	0	3	0	0	3
Unknown	2007/08	1	5	1	0	0	0	7
	2008/09	0	0	0	0	0	0	0
	Totals	16	41	20	7	14	10	108

## Figures

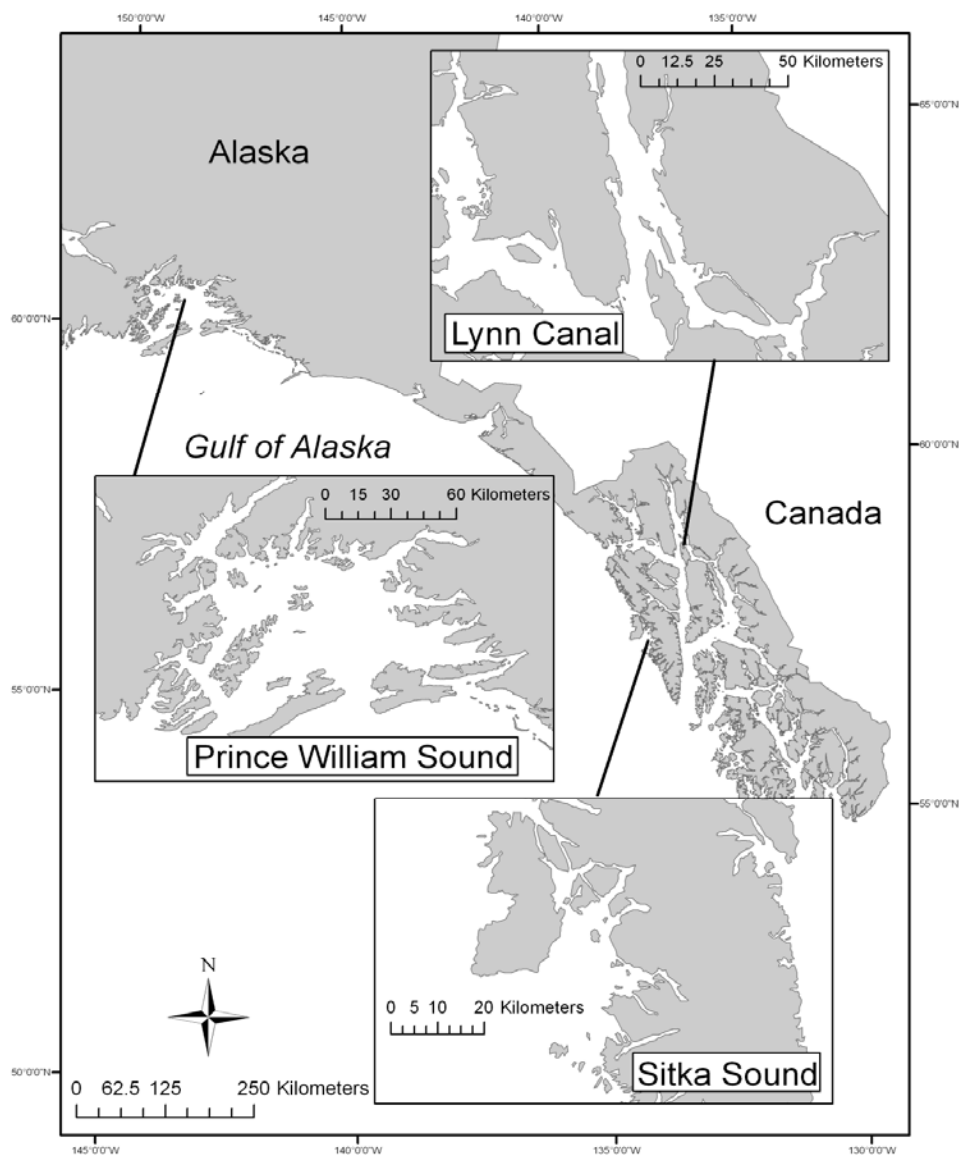


Figure 1. Locations of the Prince William Sound, LC, and Sitka Sound study areas.



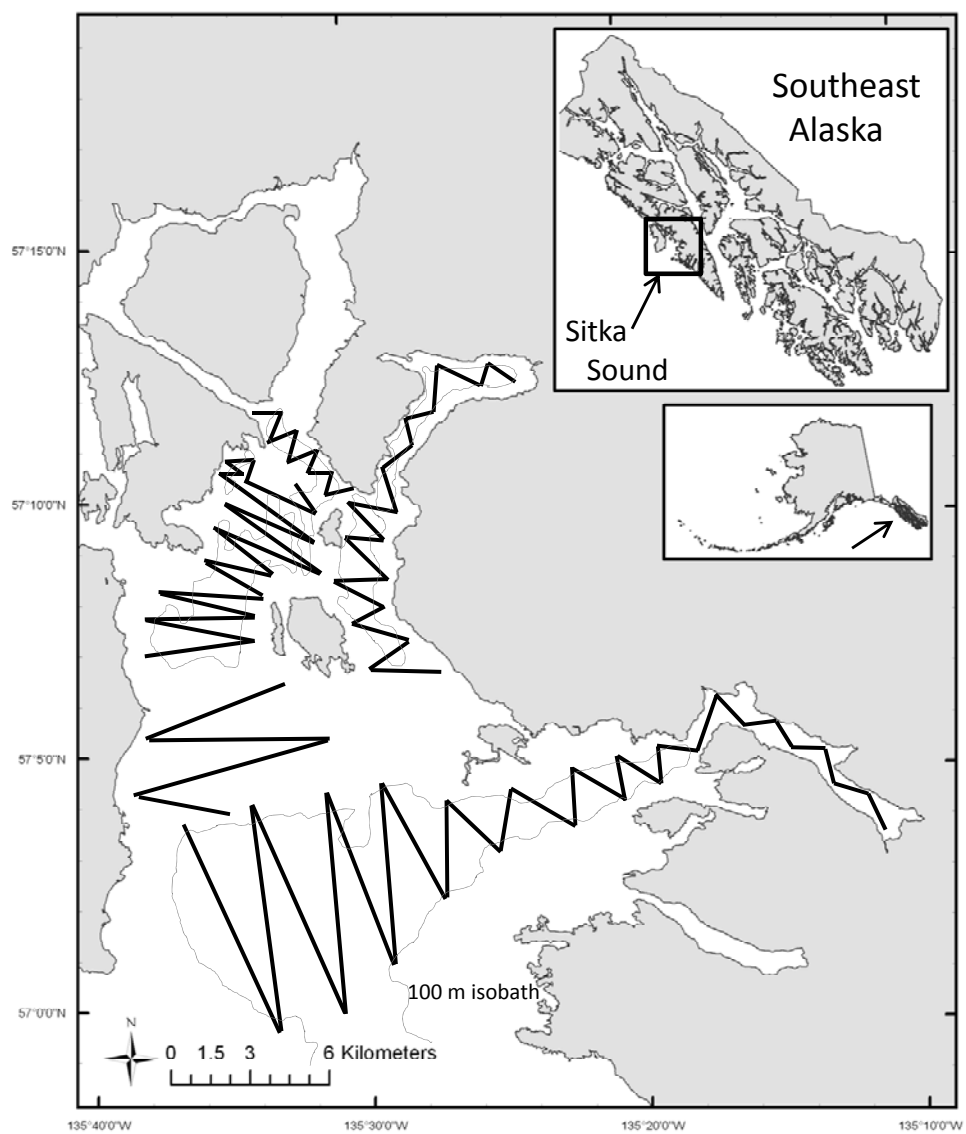


Figure 2. Sitka Sound acoustic survey track with 100 m isobaths of surveyed trenches, fall and winter 2007/2008 and 2008/209.

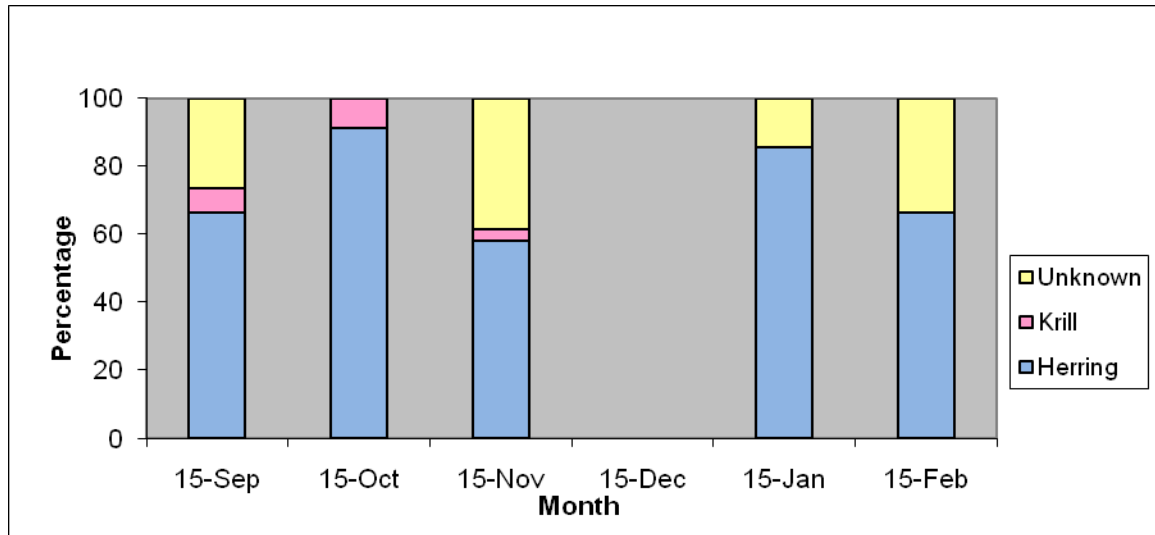


Figure 3. Proportion of prey type observed by groups (N=163) of feeding humpback whales in Prince William Sound each month during the fall and winters, 2007/08 and 2008/09.

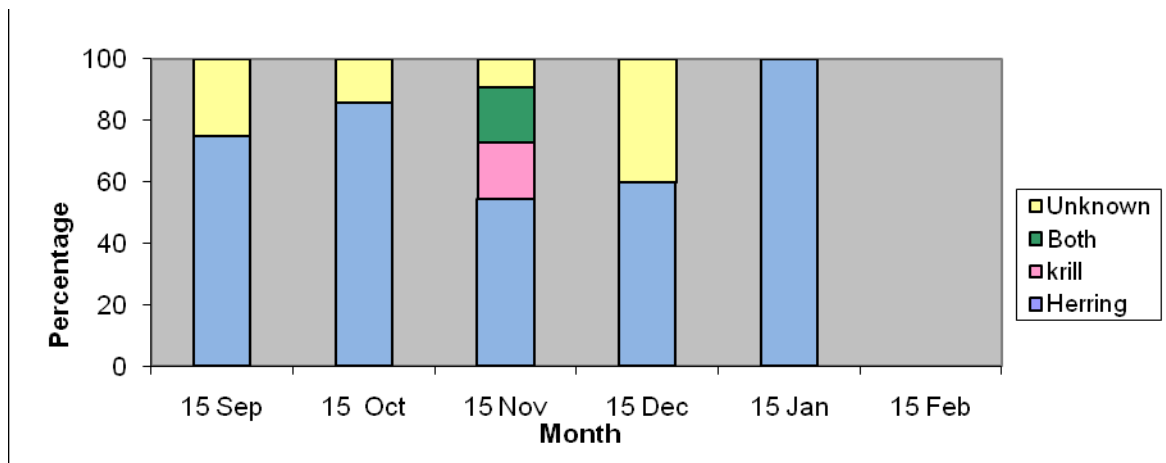


Figure 4. Proportion of prey type observed by groups (N=28) of feeding humpback whales in LC each month during the fall and winters, 2007/08 and 2008/09.

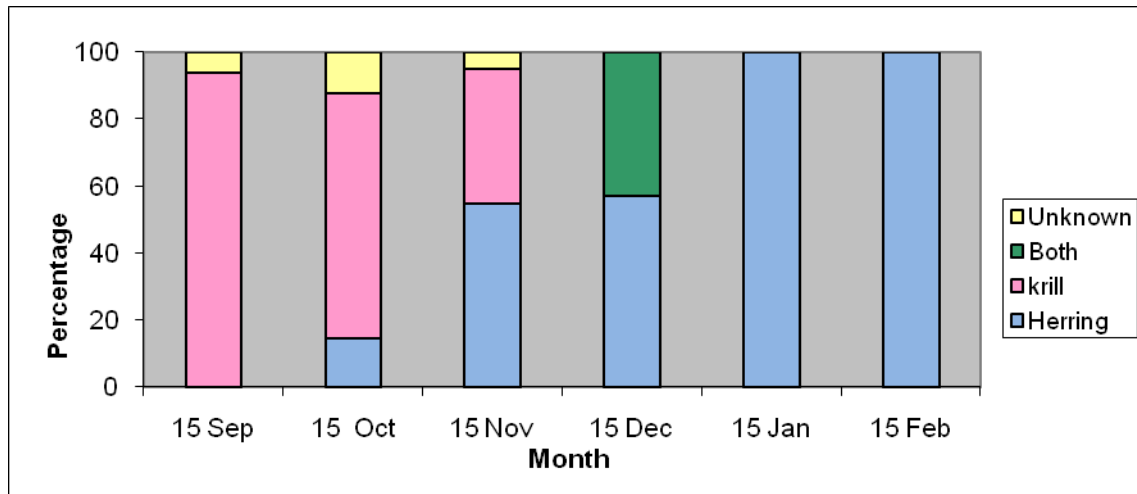


Figure 5. Proportion of prey type observed by groups (N=108) of feeding humpback whales in Sitka Sound each month during the fall and winters, 2007/08 and 2008/09.

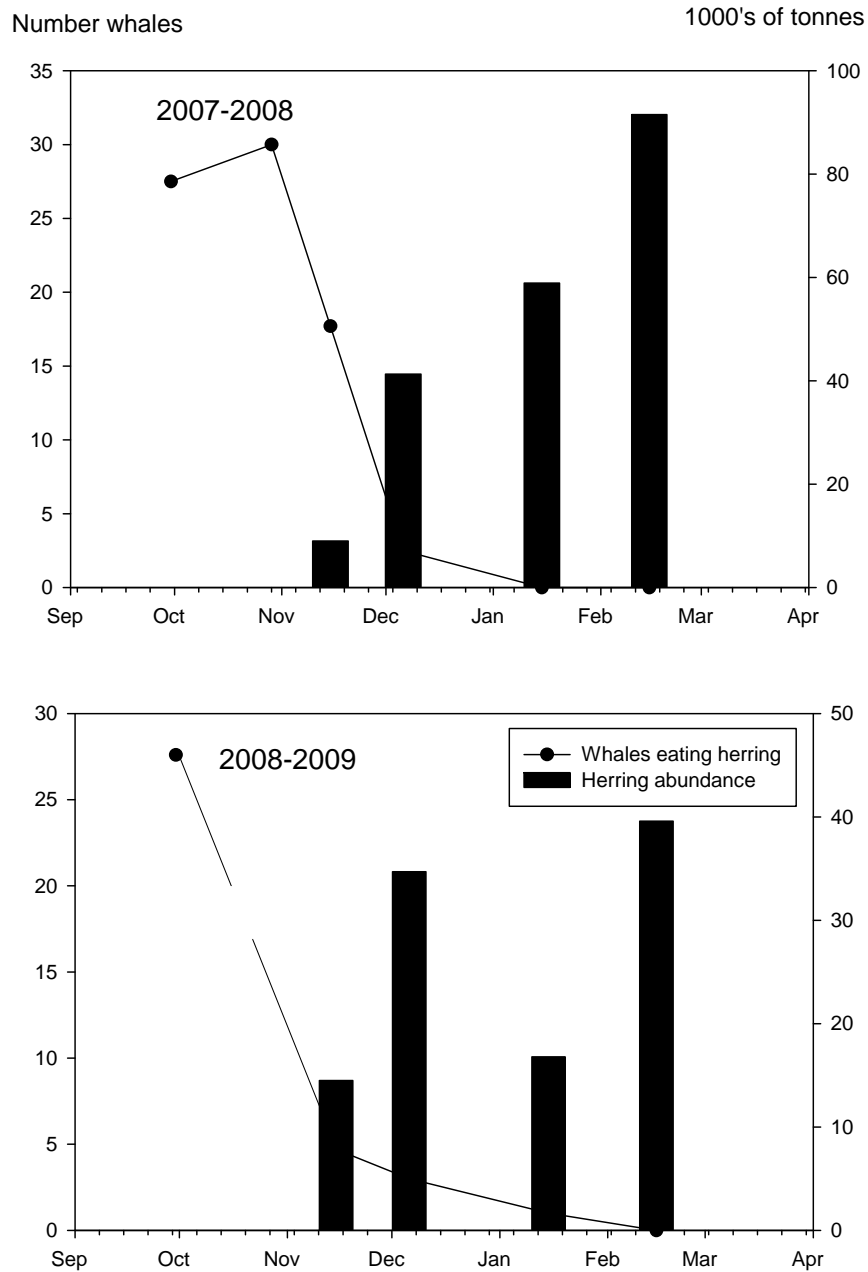


Figure 6. Estimated number of whales foraging on herring and the biomass of herring in Lynn Canal from fall to early spring 2007/2008 and 2008/2009. No whale surveys were conducted in October of 2008. No herring surveys were conducted in September or October of either year.

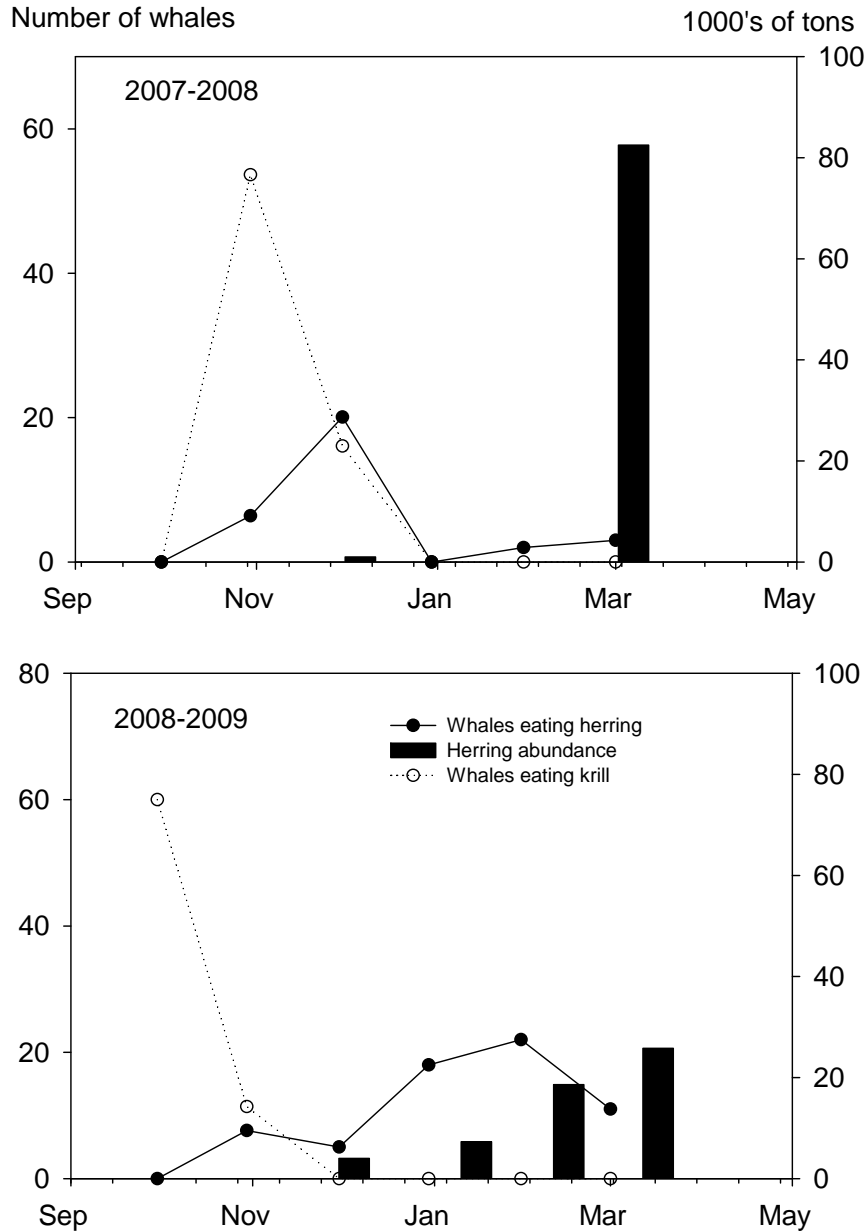


Figure 7. Estimated number of whales foraging on herring and the biomass of herring in Sitka Sound from fall to early spring 2007/2008 and 2008/2009. No herring surveys were conducted in September or October of either year.

**Chapter III: Humpback Whales Disrupt Winter Schooling Behavior of Pacific Herring and Facilitates Predation by Multiple Predators.**

Manuscript title: Humpback whale foraging structures winter schooling behavior of Pacific herring and facilitates commensal predation by multiple predators

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### Abstract

As humpback whale populations recover from the large-scale harvests of the twentieth century, they play an uncertain role in structuring of marine ecosystems. Understanding the impact of whales on their forage base will be an important component of ecosystem management. We examined the association between humpback whales and the winter schooling behavior of Pacific herring in Lynn Canal, Alaska. We measured herring abundance, distribution and school structure through monthly hydroacoustic surveys between November and February during the winters of 2007-2008 and 2008-2009. We simultaneously estimated the number of whales present in the area for each month. The spatial and temporal distribution of humpback whales was strongly associated with herring schools during the early stages of the winter in both years. Humpback whale foraging correlated with dispersed schooling behavior of herring. When whales were most numerous, herring were spread over a larger area and broadly distributed throughout the water column. As winter progressed, humpback whales departed the area, and the spatial and vertical extent of herring decreased as they consolidated into dense schools in deep channel habitats. The late winter behavior is presumed to be a metabolically beneficial strategy during winter months when prey is scarce and fish are maturing. We have observed seabirds and pinnipeds associating with whales and capitalizing on whale foraging efforts during the winter months. The disruption of herring schools by foraging whales apparently makes herring available to other predators with limited diving abilities. These associations are persistent (months) and predictable (spatially and temporally) which likely facilitates a predictable long-term foraging strategy for multiple species during winter months when herring are enriched with lipid. We hypothesize humpback whale foraging facilitates commensal predation which may have profound effects on winter survival of other herring predators. As humpback whale numbers increase, this may represent a mechanism of top-down control on herring populations that adds to the direct effects of whale predation.

### Introduction

Ecosystem management depends on a comprehensive understanding of the ecological relationship between predators and their prey, which is often more complicated than a simple calculation of the quantity of prey a predator requires to meet their energetic demands. Seasonal behavioral changes of prey, availability of alternate prey resources, competition, and a multitude of other variables may influence the net energetic acquisition per foraging effort and thus the type of prey pursued by a predator at any given time. Here we examine the ecological relationship between humpback whales (*Megaptera novaeangliae*) and their prey Pacific herring (*Clupea pallasii*) in southeastern Alaska in the winter, as they are two of the most conspicuous species present during this depauperate time of year.

Humpback whales are significant predators, consuming 0.4 tons of prey per whale per day (Witteveen 2003). Following the cessation of whaling when humpback whales were nearly exploited to extinction, their populations in the Pacific Ocean have increased at a rate of approximately 5% per year (Calambokidis et al. 2008). This has resulted in an abundance of

large baleen whales that has not been seen for nearly a century and it may have a dramatic impact on their prey base. The 2004-2006 population estimate for the North Pacific humpback whale population was approximately 20,000 individuals (Calambokidis et al. 2008). At this level they may remove a significant biomass of prey, which in some locations, can be of the same magnitude as a commercial fishery (Heintz et al. Chapter 4). Humpback whales consume many types of prey, including herring, krill, capelin (*Mallotus villosus*) and walleye pollock (*Theragra chalcogramma*). As whale numbers increase, their impact on forage species, which are also prey for a host of other marine mammals, sea birds, and piscivorous fish, is of considerable interest and may have ecosystem-level effects (Overholtz and Link 2007).

Pacific herring are one of the primary prey species for humpback whales in southeast Alaska (Straley et al. Chapter 2). Herring inhabit the inside waters of southeast Alaska year round, though their distribution changes seasonally. In the spring, herring aggregate at their numerous spawning grounds, which are used to define management 'stocks'. Following the spawn, herring disperse over larger areas to feed. With the onset of fall, herring coalesce at habitual overwintering grounds into large schools at depth, some of which consist of multiple spawning stocks. These seasonal migrations are common to both Atlantic (*Clupea harengus*) and Pacific herring. For example, the entire adult stock of spring-spawning Norwegian herring is known to overwinter in several fjords in massive schools at depths of 100-400 m during the day (Huse and Ona 1996; Misund 1993, Nottestad 2001). We hypothesize that such an overwintering aggregation of Pacific herring occurs in Lynn Canal in southeast Alaska, though on a much smaller scale.

In the fall, herring biomass in Lynn Canal steadily increases to form large schools in 100 m water depth which can extend up to 1 km wide by 5 km long and be composed of 20,000 – 30,000 tons (Sigler and Csepp 2007). Overwinter herring biomass generally peaks around February before declining again in the spring as herring move to spawning grounds. This winter biomass is significantly greater than the local spring spawning stock biomass of less than 2,500 tons (Pritchett et al. 2007).

Formation of these large, overwintering schools at depth are attributed partially to energy conservation strategies. Herring are zooplanktivores and significantly reduce feeding in the winter as a result of decreased food availability (Wing and Reid 1964). Concurrently, herring provision their gonads in preparation for spawning in the spring. Maturation in the absence of food results in energetic losses of two-thirds of their lipid content and half their energy content over winter (Vollenweider et al. 2011). Formation of large schools bestows hydrodynamic benefits and thus decreases swimming costs (Landa 1998). Additionally, herring may seek habitats that confer an energetic advantage. In the winter, oceanographic characteristics of the water column such as temperature tend to be homogenous, thus herring likely do not seek colder pockets to reduce metabolic costs (Clarke and Johnston 1999; Rottingen et al. 1994). Rather, depth selection may be more of a strategy to reduce or optimize swimming speeds. Herring are physostomous and must therefore regulate buoyancy either by surfacing to refill their swim bladder or alter their water depth. Though the depth at which fatty herring reach neutral buoyancy is controversial, 100 m has been suggested for overwintering Norwegian spring spawning herring (Huse and Ona 1996; Radakov and Solovjev 1959). Thus, the formation of



large overwintering schools at depth may reduce metabolic demand that would favor overwinter survival and maximize the reproductive investment.

Formation of large, vertically compressed overwintering schools at depth are also thought to be a strategy for predator avoidance (Nottestad and Axelsen 1999; Rottingen et al. 1994). Large school formations confer safety by diminishing the probability of an individual being consumed as school size increases (Landa 1998). By inhabiting deep water, herring may avoid surface-oriented predators such as sea birds and pinnipeds. Steller sea lions are abundant in Lynn Canal, their numbers peaking at nearly 800 animals in winter months (Womble and Sigler 2006). At the same time, predation pressure at depth by piscivorous fish may diminish as walleye pollock (*Theragra chalcogramma*), Pacific hake (*Merluccius productus*) and arrowtooth flounder (*Atheresthes stomias*) move out of the area presumably to spawn (Csepp et al. 2011). Of the predatory fish that remain or move into the area in the winter such as Pacific halibut (*Hippoglossus stenolepis*) and Pacific cod (*Gadus macrocephalus*), lack of illumination at depth may aid in predator avoidance.

Given the benefits of these overwintering schools, it is not clear why schools do not coalesce until late winter in Lynn Canal. During the early part of winter herring biomass accumulates and the schools occupy shallower water (Sigler and Csepp 2007). Delayed formation is not likely due to feeding and appears contrary to the need to avoid predators and minimize energy loss. The presence of piscivorous humpback whales may be responsible for the delay in school formation. Humpback whales routinely forage at depths of more than 100 m (Witteveen et al. 2008) and consume large numbers of herring in a single event. Humpback whales may also be attracted to large schools within their diving range because such schools would reduce the energy spent searching for prey. Nottestad et al. (2002) reported fin whales having a significant impact on school structure and observed several occurrences of school disturbance as a result of predation efforts. If humpback whales are responsible for delaying school formation then increases in humpback whale populations may result in a change in herring behavior with unknown consequences for population productivity.

The objective of this study was to examine the association between humpback whales and the winter schooling behavior of herring in Lynn Canal, Alaska. We examined herring abundance, distribution and school structure using monthly hydroacoustic surveys between November and February during the winters of 2007-2008 and 2008-2009. We simultaneously estimated the number of whales present in the area each month. By comparing the herring behavior with whale abundance we were able to test the hypothesis that herring do not form deep large schools when whales are present.

## Methods

### *Study Area*

A 1000 km<sup>2</sup> area of Lynn Canal, southeastern Alaska was selected as the study region (Fig. 1). Large schools of herring (Sigler and Csepp 2007; Gende and Sigler 2006; Carlson 1980) and humpback whales (T. Quinn, pers. comm.) are known to inhabit the area. Winter months (November through February) were the focal period for the study based on known herring migrations to their overwintering areas in Lynn Canal (Sigler and Csepp 2007; Gende and Sigler

2006) and the corresponding movement of whales associated with the herring shoals (Moran et al. Chapter 1). Furthermore, the study area is readily accessible for small vessel surveys to exploit weather windows during winter months when weather conditions are generally adverse. Monthly herring and whale surveys were conducted between November and February during two consecutive winters, 2007-2008 and 2008-2009.

During each survey water temperature and conductivity were collected to characterize water chemistry and vertical water column structure using a Seabird 19+.

### *Acoustic Surveys*

To estimate herring biomass (t, tonnes), monthly hydroacoustic transect-based surveys were conducted over the course of three days within a one-week period from November to February during the 2007-2008 and 2008-2009 winters. Herring surveys followed a standard 200 km transect line covering an area of 161 km<sup>2</sup> (Fig. 2). Herring biomass was measured with a Simrad EK60 split-beam echosounder interfaced with a 38 kHz 12° circular-beam transducer towed beside the vessel at 5-10 km hr<sup>-1</sup>. Collection parameters applied in this study followed those of Sigler and Csepp (2007). Position data was collected for each acoustic transmission with a Garmin Global Positioning System with an accuracy of 10 m. All surveys were conducted during daylight hours to account for potential variation due to vertical migration behavior and acoustic intensity (Huse and Korneliussen 2000). Echosounders were calibrated before and after the study following the standard sphere method (Foote et al. 1997).

Scattering intensity data were processed in Echoview (4.3; Myriax, Pty. Ltd.). Prior to echo integration techniques, a 10 m depth by 0.18 km distance where 0.18 km corresponds to one elementary sampling distance unit (EDSU) grid was applied to the echogram, effectively generating cells to calculate the echo integral of scattering intensity. Sound speed and absorption coefficients were applied to account for the effects of temperature and salinity on the acoustic transmissions. The nomenclature for the acoustic variables follows MacLennan et al. (2002).

Briefly, monthly surveys were subdivided into 13 strata (Table 1), where each strata was generally characterized by homogenous bathymetry and herring schooling behavior. Herring schools were manually identified and selected for analysis, where the Nautical Area Scattering Coefficient (NASC; m<sup>2</sup> nmi<sup>2</sup>), the areal acoustic measure proportional to fish density, was exported for each cell containing herring following standard echo integration techniques (Simmonds and MacLennan 2005). Processed output from Echoview were compensated for the effects of shadowing and acoustic extinction due to highly-dense fish schools (Zhao and Ona 2003; Sigler and Csepp 2007). To generate an areal estimate of herring biomass, NASC values were summed across over each 10 m depth interval within each EDSU. Herring school metrics were also exported from Echoview to facilitate analysis of temporal variability in mean school depth and shape.

Processed echo integration data output from Echoview were imported into SAS (v9.1.3) to compensate for effects of acoustic shadowing and extinction on the estimates of herring school biomass (Foote 1990; Sigler and Csepp 2007; Zhao and Ona 2003). Although Sigler and Csepp (2007) extensively characterized the effects of acoustic shadowing on their estimates of herring biomass within their study, we reapplied their method given the differences in areas surveyed

and the temporal differences between studies. As with the previous study conducted in Lynn Canal, we selected data within the acoustic record with near-flat homogeneous bottom both in the presence of schooling herring and without herring to calculate the extinction coefficients. We calculated extinction values from 11 different strata with a total of 1161 20 m transects, as defined in Sigler and Csepp (2007), where the shadowing coefficient reported by Sigler and Csepp (2007)  $0.94 \pm 0.16$  was similar to our calculated value ( $0.972 \pm 0.269$ ). Similarly, the mean correction factor applied to correct NASC values for acoustic extinction was comparable ( $1.78 \pm 0.31$ ), relative to 1.21 and 1.07 for Ona (2003) and Sigler and Csepp (2007), respectively.

Given the densely packed herring schools, individual targets were not resolvable, and therefore, in situ size estimates were not available for scaling NASC to generate fish density estimates. Therefore, we applied the mean length from direct capture methods (see below) as input into a target strength-fish length relationship, where target strength (TS) represents the acoustic scattering intensity from an individual, and is proportional to fish length. Others have reported a significant depth effect on the measured TS of herring (Thomas et al. 2002; Ona 2003; Sigler and Csepp 2007), thus we adopted the depth dependent TS relationship developed by Ona (2003) as it allowed for greater variation in fish school depth;

$$TS = 20 \log_{10} L - 2.3 \log_{10} (1 + Z/10) - 65.4, \quad (1)$$

where L is mean fish length (cm) and Z is mean water depth (m) of the herring school. By solving for TS, we were able to use the measured mean fish lengths from direct capture to scale the corrected NASC values from extinction calculations and derive areal estimates of fish density (fish  $\text{nmi}^{-2}$ ) (MacIennan et al. 2002);

$$\text{Fish density} = \text{Corrected NASC} / 10^{(TS/10)} \quad (2)$$

Areal biomass ( $\text{g nmi}^{-2}$ ) was calculated by applying a length-weight relationship derived from herring captured during the study period;

$$\text{Weight (g)} = 8.0e^{-7} * L^{3.4798} \quad (3)$$

where L is fish length (cm), and weight is expressed in g; and total biomass per strata was extrapolated through the product of areal biomass and strata area (Table 1). Finally, biomass was extended to metric tons and was used for all analyses reported herein.

We independently verified our methods by conducting a similar set of surveys in Sitka Sound, Alaska during the same winters. Our estimates of herring biomass were compared with estimates of stock biomass derived from spawn deposition surveys and age-structured stock assessments conducted by the Alaska Department of Fish and Game (ADFG). Our survey methods were the same as those described here except that we divided the  $115 \text{ km}^2$  survey area into seven strata. See Straley et al. (Chapter 2) for more details.

### *Trawl collections*

Herring were collected approximately every 4 weeks (Sept, Nov, Feb, April, May in 2007-2008, and Dec, Feb, Mar, May 2008-2009) to identify species observed on the hydroacoustics and to obtain length frequency distributions and length-weight regressions for conversion of NASC to biomass. Fish collections were made using variable-mesh gillnets deployed from a gillnetter and a mid-water trawl was used when larger vessels were available. Variable-mesh monofilament gillnets consisted of 3 panels stacked vertically, each measuring

2.7m deep by 91m long. Stretched-mesh sizes of the panels were 2.5cm, 3.8cm, and 5.1cm, from the bottom to top panels, respectively. The midwater trawl was a herring rope trawl constructed by Research Nets Inc. (Redmond, WA), with an opening 3.0m deep by 6.1m wide, with a 0.6cm mesh codend liner and 1.5m<sup>2</sup> alloy doors. Tow duration was adjusted as necessary to ensure adequate catches for species identification and length frequency samples.

### *Whale Surveys*

Monthly humpback whale abundance was estimated during day-long surveys in a small vessel (<8m) in the Lynn Canal region (Fig. 2). When daylight and weather conditions were limiting during the winter months, an adaptive survey approach was taken and effort was focused on areas with higher concentrations of whales. Aerial surveys and traditional local knowledge were employed to ensure aggregations of whales were not being overlooked during boat-based surveys. To correlate whales with the presence of herring schools we recorded whale position data in addition to group size, whale activity, estimated prey type and prey depth for each group of whales encountered during a survey. Photographic mark-recapture methods were used to estimate seasonal whale abundance with Nikon D-300, D-200, and D-70 cameras equipped with 80-200 mm lenses. Digital images of the markings on the ventral side of humpback whale flukes were captured to identify individual animals (Katona et al. 1979). We used Huggins Closed-Capture Models in Program MARK to generate estimates of humpback whale abundance following mark-recapture techniques (White and Burnham 1999); survey details are fully described in Moran et al. (Chapter 1). Estimates of the number of unique whales generated from mark-recapture techniques were used to calculate ‘whale days’, which is the cumulative number of whales present on each day summed over each month. Rather than reporting winter trends in whale abundance, we report ‘whale days’ which is more illustrative of the monthly predation pressure on Pacific herring. Monthly visual surveys were conducted throughout Lynn Canal in an effort to locate natural centers of abundance. Search effort was determined by summing the amount of time (0.5 min intervals) spent in each 2 km x 2 km cell in the Lynn Canal area. Point density was summarized with the Point Enumeration Tool (Hawth’s Tools extension; Beyer 2004) in ArcMap (9.3; ESRI) to calculate the maximum search effort distributed within each cell (Fig. 2). The result is a sum of the amount of time (log minutes) spent within each 2 km<sup>2</sup> cell during whale survey efforts.

### *Statistics*

We interpolated the spatial distribution of the herring biomass from the acoustically-determined biomass estimates using the inverse distance weighted (IDW) routine from Spatial Analyst toolbox in ArcMap (version 9.3.1; ESRI, Redlands CA). IDW interpolation can be calculated with a fixed Euclidian distance or with a variable search radius that is set by a number of neighbors. In all IDW routines, we used a variable radius set to 20 nearest neighbors and an output grid cell size of 250 m<sup>2</sup>. Spatially interpolated herring densities were binned into quantiles, and represent the areal extent over which each quantile extended within each month. Contour polygons were applied to interpolated densities to measure the area corresponding to

each quantile. Quantiles were assigned a color and mapped to illustrate the spatial distribution of herring densities (Simpfendorfer and Heupel, 2004).

As a secondary means to examine spatial extent occupied by herring schools, we calculated a ‘normalized school area’, defined as the area occupied by the 4<sup>th</sup> quartile of herring divided by the area occupied by those falling within the first. This indexes the area occupied by the most densely occupied EDSUs relative to the area occupied by the least densely occupied EDSUs. If whales disrupt the formation of dense schools we expect the normalized school area to be low because herring would be diffusely distributed.

Variation in herring length distributions from trawl collections was evaluated among strata and months with an analysis of variance (ANOVA; Proc Mixed; SAS, 9.2). To test the null hypothesis that herring school depths were not variable across winter months and by extension a function of decreasing whale abundance, we conducted an ANOVA (Proc GLM; SAS, 9.2) with year, month, and strata as main effects in the model (Table 2). Tukey’s honestly significant difference post hoc test was used to identify differences in means among interactions and main effects. All means and standard errors are reported as least-squares means. All statistical tests were considered significant at  $\alpha = 0.05$ .

To determine if whale positions exhibited affinity for the areas of high fish concentrations (from the IDW analysis), we calculated the spatial mean of whale sighting locations (latitude/longitude coordinate pairs) weighted by the number of whales observed at each geographic location during November and December of 2007 (when sighting sample sizes were adequate for spatial analysis). Additionally we wanted to test if humpback whale locations were clustered within the study area. Thus, we used the Ripley’s K function, a global measure of spatial dependence based on the pattern of spatial point data, to test whether whale sightings were spatially clustered in each of the two months (O’Brien et al. 1999). Following O’Brien et al. (1999), the statistic can be written as:

$$K(d) = \lambda^{-1} E \quad (4)$$

where,  $K(d)$  is the number of whale citing locations within distance  $d$  of an arbitrary event;  $\lambda$  is the intensity (here the mean number of observed whales per unit area) and  $E$  denotes the expected number of whales within a given distance interval.  $K(d)$  relates the abundance of the observed whales within the search radius  $d$  to the number of whales expected to fall within  $d$  of each other under the assumption of complete spatial randomness.

Following the common transformation of the K-function (O’Brien et al. 1999) we apply  $L(d)$  to examine spatial clustering of whale distributions;

$$L(d) = \left[ \frac{A E N_i E N_j k_{ij}}{\pi N(N-1)} \right]^{1/2} \quad \text{for } i \neq j \quad (5)$$

where  $L(d)$  is a linear expression of the expected number of whales  $j$  occurring within distance  $d$  of all  $i$  cases,  $A$  is the area of the study region (here defined as the maximum extent of whale observations in the two months),  $k$  is the K function,  $\pi = 3.1415926$ , and  $N$  is the total number of whale sightings for each month. The expectation of  $L(d)$  is  $d$  when the null hypothesis of complete spatial randomness holds, which is that whale sightings are not clustered.

## Results

### *Herring*

Over the course of winter, Pacific herring biomass increased as did the density of schools, resulting in progressively smaller areas occupied by fish. Biomass varied widely among months, with biomass generally increasing throughout the winter (Tables 3 and 4; the lowest biomass found during November (2007:  $9,043.3 \pm 1,268.4$  t; 2008:  $14,559.6 \pm 513.2$  t) and the greatest during February (2007:  $91,459.6 \pm 14,286.1$  t; 2008:  $39,599.4 \pm 3,329.1$  t) for both winters. Biomass estimates based on our survey methods agreed with biomass estimates derived from age-structured stock assessments. In March 2008 we estimated 82,499 tonnes of herring in Sitka Sound while the ADFG estimate of post-fishery mature biomass was 90,102 tons with a harvest of 14,386 tons. Our survey was conducted approximately 3 weeks before the fishery commenced (Straley et al. Chapter 2) suggesting there was time for more fish to arrive in the staging areas prior to spawning. In contrast, our estimate for March 2009 was significantly lower (25,845 tonnes) than the ADFG estimate of 79,862 tonnes, however the survey was conducted while the fishery was underway. As this is a roe fishery, a significant proportion of the biomass was likely in shallow water outside our survey area.

As herring biomass in Lynn Canal grew over winter, herring coalesced into increasingly dense schools, resulting in a decrease in their overall spatial extent. In November and December, herring schools were generally diffuse with localized centers of high abundance, whereas herring distributions were more concentrated during January and February with discrete centers of abundance concentrated within a single strata (Figs. 3 and 4). Although the spatial extents vary across months and between winters, the centers of greatest abundance occur in similar locations and with similar magnitudes (Figs. 3 and 4). Inverse distance weighted estimates of monthly herring biomass distributions suggest that the center of biomass is concentrated along the eastern margin of Lynn Canal, typically characterized by water depths ranging from 50-150 m. The areal extent of the upper 50<sup>th</sup> percentile distribution of herring biomasses (Figs. 3 and 4; orange contour) generally increased throughout the winter season, increasing by more than a factor of two as winter progressed (2.3 and 5.5) for 2007-2008 and 2008-2009, respectively.

As herring coalesced into increasingly dense schools over winter, they descended to greater water depths. Schools distribution in the water column was variable across months, with more diffuse schools higher in the water column during November and December ( $P < 0.001$ ; Fig. 5; Table 2). As winter progressed, herring schools became more consolidated and concentrated along the trench floors at deeper depths (100-150 m). Changes in depth distribution were similar for both years ( $P = 0.89$ ; Table 2). Herring lengths varied significantly across strata ( $P < 0.001$ ;  $F_{4,250} = 6.26$ ) though the mean range was relatively small among all strata and catches were composed of individuals ranging from 15-21 cm in length. Length-at-age relationships constructed from scale analysis for herring in Lynn Canal indicate that fish within this size range are age 2 to age 8 and are thus predominantly adults.

### *Whales*

Whale survey efforts varied between both study years, largely as a function of logistical constraints (e.g., weather), though cumulative survey effort was extensive regionally (Fig. 2)

with a total of 197.3 hours (2007-2008: 117.2hr; 2008-2009: 80.1 hr) being committed to survey efforts. Based on the regional historical whale distribution in Lynn Canal, most effort was concentrated in the eastern portion of the study region, with peaks in effort representing areas with greatest whale abundance within each 2 km<sup>2</sup> cell (Fig. 2).

During the course of this study, we identified 48 individual whales using the waters of Lynn Canal during the fall and winter months. Seasonal peaks in abundance occurred before the acoustic survey period and before herring moved into the study area (Moran et al. Chapter 1; Sigler and Csepp 2007). Monthly estimates of 'whale days' decreased over both winters as whales left the area, though the magnitude of whale days and the rate of departure was different. In the winter of 2008-2009, 'whale days' were nearly double that of 2007-2008 (Tables 3 and 4). Though whales were more numerous in 2008-2009, they had completely left the area by February. In contrast, whales lingered into February during 2007-2008. Additional details on whale attendance patterns and seasonal distribution can be found in Moran et al. (Chapter 1).

### *Herring and whales*

Humpback whales were found in close association with herring schools during all winter months, both herring and whales occupying a greater spatial extent in November and December than January and February (Figs. 3 and 4). As whale days declined, normalized school area increased considerably, illustrative of herring schools coalescing (Fig. 6). This relationship was not gradual but occurred as an abrupt shift potentially suggestive of a threshold foraging response (see Piatt and Methven 1992). Once whale days diminished to approximately 150 whales, the release in whale predation pressure may allow herring to form their overwintering schools. A strong and significant spatial association was observed between whales and herring in November and December of 2007, with significant associations among congregating whales at 400 m distance (November) and 3200 m (December), as indicated by  $L(d)$  exceeding the confidence interval in both months (Fig. 7). Observations of humpback whale foraging behavior and efforts to identify prey indicate that whale associations with herring were predominantly a result of foraging on herring (Straley et al. Chapter 2).

As 'whale days' declined and whales departed the study area each winter, herring schools became increasingly characteristic of overwinter behavior. Seasonal decreases in 'whale days' were associated with increasing mean depth of herring schools ( $P < 0.001$ ; Fig. 8). Seasonal trends in historical counts of Steller sea lions showed similar seasonal trends (Womble et al. 2009; Fig. 8). Thus, all indications of herring schooling behavior suggest that they are free to form their deep, dense, overwintering schools when whale predation is gone.

Changes in herring schooling behavior were unrelated to water column characteristics. Though monthly temperature and salinity profiles of the water column reveal intermittent thermoclines and haloclines at 100 m depth, the timing is misaligned with herring behavior (Fig. 9). Thermoclines at 100 m are evident by December and may persist through the winter, however the herring do not move to these depths until January. Furthermore, water at 100 m depth is warmer than shallower water for the majority of the winter, which is contrary to the energetic savings hypothesis. It is not until April that deeper water offers a cold refuge. Thus we conclude

that humpback whale foraging delays herring from assuming their desired overwintering school formation.

### Discussion

Humpback whale predation appears to delay the formation of overwinter schools that is characteristic behavior of Pacific herring. Early in the winter in the presence of humpback whales, Pacific herring formed diffuse, pelagic schools spread over a relatively large geographic area. The progressive departure of humpback whales from the study area corresponded to herring behavior that was increasingly characteristic of overwintering schools. As whale predation decreased, more herring moved into the area, and schools became increasingly dense and descended to greater water depths at 100 m. We discount other mechanisms that often structure fish behavior, including herring foraging and temperature refugia.

Similar to other forage species, herring schooling behavior is known to vary with the type of predatory attack (Pitcher et al. 1996). For example, the anti-predatory behavior of Atlantic herring to fin whales in offshore areas in the Norwegian Sea is to form large, dense schools at depth in close proximity to neighboring schools (Nottestad et al. 2002). Though seemingly in contrast to the results of our study, the depths occupied by the Atlantic herring were considerably greater at 300-400 m, which were presumably outside the dive range for fin whales. All fin-whale foraging was limited to night when herring schools were less than 200 m (Nottestad et al. 2002). In lower Lynn Canal, the bathymetry is such that herring cannot reside below humpback whale foraging depths which can dive to 300 (Herman et al. 2007). Unable to flee humpback whales, remaining relatively dispersed appears to be a good predator avoidance technique against whales which can engulf a large number of herring in a single attack. In comparison, dense schools would be an antipredator defense against predators that consume a single fish at a time such as Steller sea lions, sea-birds and piscivorous fish. Similarly, herring schools in the coastal waters of the Norwegian Sea retained their risk-dilution advantages of dense schooling and did not disperse during attacks by individual cod and haddock predators (Pitcher et al. 1996). In contrast, when predatory attacks occurred by fast-moving schooling predators such as saithe, the consolidated schools broke apart temporarily. Repeated foraging may prolong the dispersed behavior (Pitcher et al. 1996). Thus in the presence of foraging humpback whales, herring form diffuse, pelagic schools.

We believe the preferred configuration for herring schools in the winter is the formation of deep, dense schools which confer energetic advantages during limited prey availability as well as offering safety against surface-oriented predators. During winter when prey is scarce, herring coincidentally incur large energetic demands in preparation for spring spawning. In the winter, herring lose up to 66% of their lipid and 50% of their total energy content due to the cessation of feeding and concurrent energetic demands of maturation (Vollenweider et al. 2011; Slotte 1999; Heintz and Vollenweider *In Prep.*). Cold refugia are not found at depth during winter months in Lynn Canal, thus energy savings are likely derived from hydrodynamic advantages of large schools (Landa 1998) and reduced swimming costs attained by neutral buoyancy at depth (Huse and Ona 1996; Radakov and Solovjev 1959). Interestingly, the herring don't form these presumed beneficial tight schools in the trenches until after the whales have moved out of the



area. We hypothesize that herring would assume their overwintering school behavior earlier in the winter in the absence of foraging humpback whales. In these overwinter configurations, however, herring are more susceptible to humpback whale predation. Therefore whale presence delays the formation of overwintering schools.

It is unknown why herring select specific locations for overwintering. We observed the herring in the same location in both years after the whales departed. This is the same location noted in the early 2000's by Sigler and Csepp (2007). This selection is unrelated to water column characteristics or food availability. As observed in Norwegian over-wintering herring (Slotte 1999), Pacific herring rarely feed during over-wintering periods and thus likely benefit from decreased intraspecific competition (Nottestad and Axelsen 1999). Similarly, limited gut content analysis from Lynn Canal indicates that herring feeding is largely negligible between the winter months of November to February (n=44; Vollenweider unpub. data). Nevertheless Lynn Canal attracts wintering herring from a wide area. The local spawning stock is estimated at approximately 1,000 tonnes (ADFG). However, spawn deposition surveys conducted in northern southeast Alaska during the spring of 2009 indicated a total spawner biomass of 31,500 tonnes (Hebert 2009) excepting Sitka Sound, remarkably similar to our peak biomass in February 2009 of 39,500 tonnes.

We hypothesize that the disruption of herring's formation of overwinter schools by foraging humpback whales facilitates foraging from Steller sea lions, sea birds, and other pelagic predators for which the deep overwintering herring schools would otherwise be relatively inaccessible. Glaucous-winged gulls (*Larus glaucescens*), herring gulls (*Larus argentatus*) and mew gulls (*Larus canus*) forage on or just below the surface of Lynn Canal in the winter (Moran pers. comm.). Similarly, recent tagging studies of adult female Steller sea lions in Lynn Canal in the winter indicate that though these animals are capable of dives greater than 250 m, more than 80% of their dives (> 4m) are to depths less than 100 m (Fadely and Lander, pers. comm.). Furthermore, the tagging studies show a strong mode in dives to depths of 50-74 m in November and December (2009), which is coincident with herring depths observed during whale disruptions. Previous studies of juvenile sea lion diving behavior also indicate relatively few dives beyond 100 m (Pitcher et al. 2005). Womble et al. (2006) report herring as the most frequently occurring prey item identified in collected scat samples in Lynn Canal during wintering periods. Further, sea lion presence was positively correlated to presence of large herring schools, particularly during peak overwintering months (January and February) (Womble and Sigler 2006; Sigler and Csepp 2007; Womble et al. 2009). Thus we hypothesize that there is a commensal relationship among humpback whales, seabirds and Steller sea lions which is ultimately a function of whale foraging activity. Therefore we believe humpback whale foraging on Pacific herring facilitates the transfer of energy through the food web during winter.

It is difficult to quantify the importance of herring as a food source to marine mammals and seabirds in the winter. Certainly, winter is a period of high energetic demands for these predators. In winter, humpback whales prepare to embark on their 9,000 km seasonal migration to Hawaii to mate, give birth, and suckle their young before returning to their feeding grounds in the Northern Gulf of Alaska (Baker 1986). Similarly, immediately following winter, the energetic requirements of adult Steller sea lions reaches a seasonal peak as they reduce their

feeding while mating, giving birth, and suckling their young (Winship et al. 2002) and energy demand peaks in February (Winship et al. 2002). In general, herring are one of the more energy-rich prey sources in Lynn Canal, particularly in early winter when they reach maximum lipid content (Vollenweider et al. 2011). Thus, the opportunity for humpback whales to forage on herring in winter and the foraging opportunities provided by humpback whales could be an important energy source for many species.

Marine mammals are significant predators in many marine ecosystems and have the potential to impose strong top-down pressure on the forage base, thus strongly regulating the food web (Tjelmeland and Lindstrøm 2005). Recent estimates suggest that humpback whales, in particular, can consume on average 0.4 tons of biomass per whale per day (Witteveen 2003) and have the potential of depleting the local forage base at similar rates to commercial fisheries (Heintz et al. Chapter 4). Given this notion and the recent expansion of humpback whale abundance in Southeast Alaska (SEAK) at approximately 5% per year (Calambokidis et al. 2008), there is growing awareness of the potential for humpback whales to regulate the forage base, namely the Pacific herring. In addition to increasing whale abundance and foraging pressure in SEAK, Steller sea lion abundance has increased and studies have demonstrated their affinity for over-wintering herring as a preferred food source (Womble et al. 2009). Increasing prey removals by humpback whales and those afforded to commensal foragers may have top-down influence prey populations including herring. How this affects depleted populations such as the herring populations in Lynn Canal and Prince William Sound is unknown.

### *Conclusion*

Our acoustic surveys identified Lynn Canal as an important wintering ground for Pacific herring in southeastern Alaska that is attractive to humpback whales. Moreover we found the presence of foraging whales interfered with the herring's preferred schooling behavior. Whale foraging dispersed herring into the water column and made them available to other surface oriented consumers. Biomass removals by these other predators represent an indirect effect of whales on herring that adds to the direct effects resulting from consumption.

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### Tables

Table 1. Strata surveyed during acoustic transects conducted in Lynn Canal with corresponding area (km<sup>2</sup>) and total transect length (km) used for calculating herring biomass.

Strata	Area (km <sup>2</sup> )	Transect Length (km)
Aaron Island Trench	1.8	5.9
Amalga Trench	22.9	16.1
Auke Bay	7.0	28.3
Benjamin Island Trench	6.2	11.7
Eagle Beach	8.1	9.6
East Portland Island	14.8	9.1
Favorite Channel	23.0	23.3
Fritz Cove	4.5	12.6
Halibut Cove	2.3	2.6
Lena Point	11.0	11.5
Mansfield Peninsula	20.1	21.5
Portland Island Trench	16.9	20.7
Saginaw Channel	22.4	24.4
Total	161.0	197.4



Table 2. Analysis of Variance statistics of mean herring school depth (SAS 9.2; PROC GLM).

Effect	Num DF	Den DF	Type III SS	<i>F</i>	<i>P</i>
Month	3	331	48008.52	36.73	<0.001
Strata (Month)	13	331	7711.77	13.77	<0.001
Whale Days (Month)	4	331	4986.36	4.45	<0.001

Table 3. Winter Pacific herring biomass (tons) and ‘whale days’, a cumulative index of humpback whale abundance in Lynn Canal (November 2007 – February 2008). During January 2008, herring were only observed in one stratum, therefore error estimates are not available.

Month	Tons	S.E.	C.V.	Whale Days
November	9,043.3	1268.4	206.4	393.5
December	41,334.5	2891.3	227.6	242.1
January	58,887.9	-	-	150.9
February	91,459.6	14286.1	229.5	57.8

Table 4. Winter Pacific herring biomass (tons) and ‘whale days’, a cumulative index of humpback whale abundance in Lynn Canal (November 2008 – February 2009).

Month	Tons	S.E.	C.V.	Whale Days
November	14,559.6	513.2	95.2	690.0
December	34,671.2	1712.4	156.2	696.9
January	16,828.7	1473.4	276.9	133.6
February	39,599.4	3329.1	306.7	0.0

# Figures

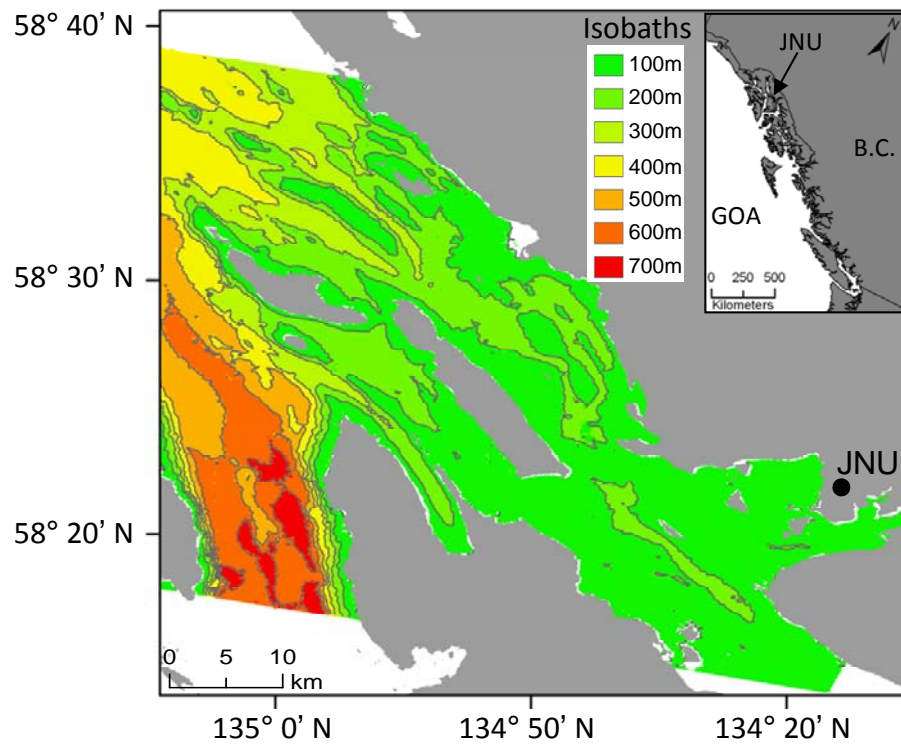


Figure 1. Bathymetry of Lynn Canal region, near Juneau, AK (JNU). Isobaths are displayed at 100m intervals and correspond to color map. Note- inset map is rotated from North.

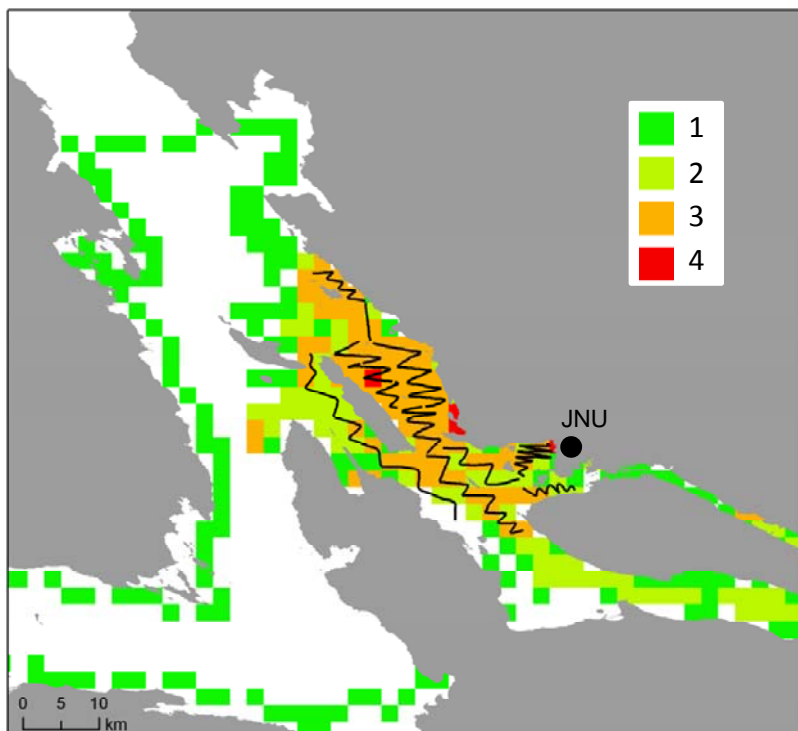


Figure 2. Cumulative maximum search effort (log min) for humpback whales in Lynn Canal, near Juneau, AK (JNU) during the 2007-2008 and 2008-2009 winter months (Nov-Feb). Monthly acoustic survey transect is represented by solid line.

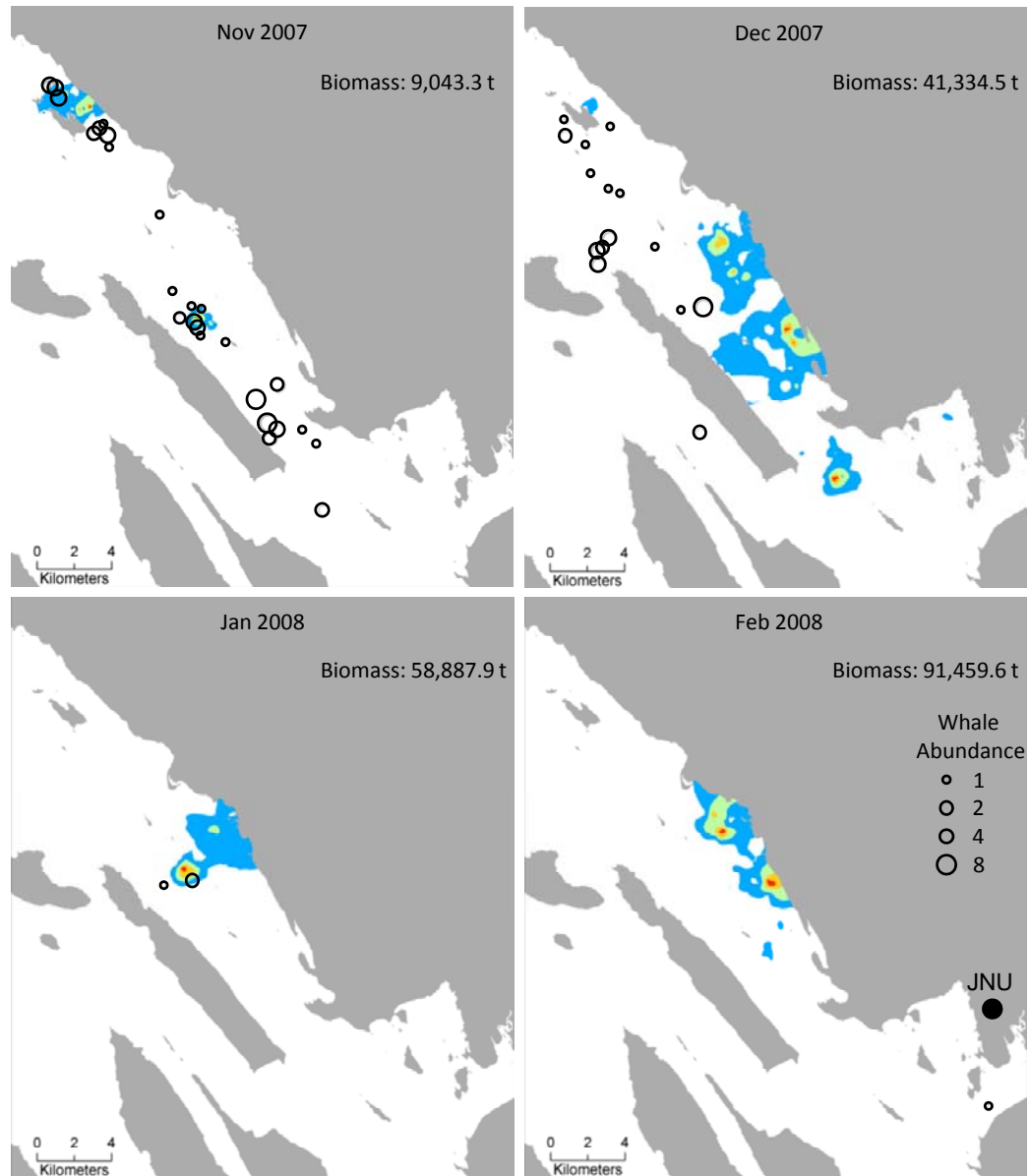


Figure 3. Winter distribution of humpback whales (circles) and Pacific herring (colormap) in Lynn Canal near Juneau, AK (JNU) over the winter of 2007-2008. Spatial distribution of herring density derived from IDW analysis. Colormap represents the spatial distribution of herring coded by the acoustic estimates of school density (blue = area occupied by densities within the first quartile, green = second quartile, orange = third quartile and red=fourth quartile). Whale abundance from visual surveys is represented by graduated open circles. Total monthly biomass (tons) of herring estimated from acoustic surveys is provided for each month.

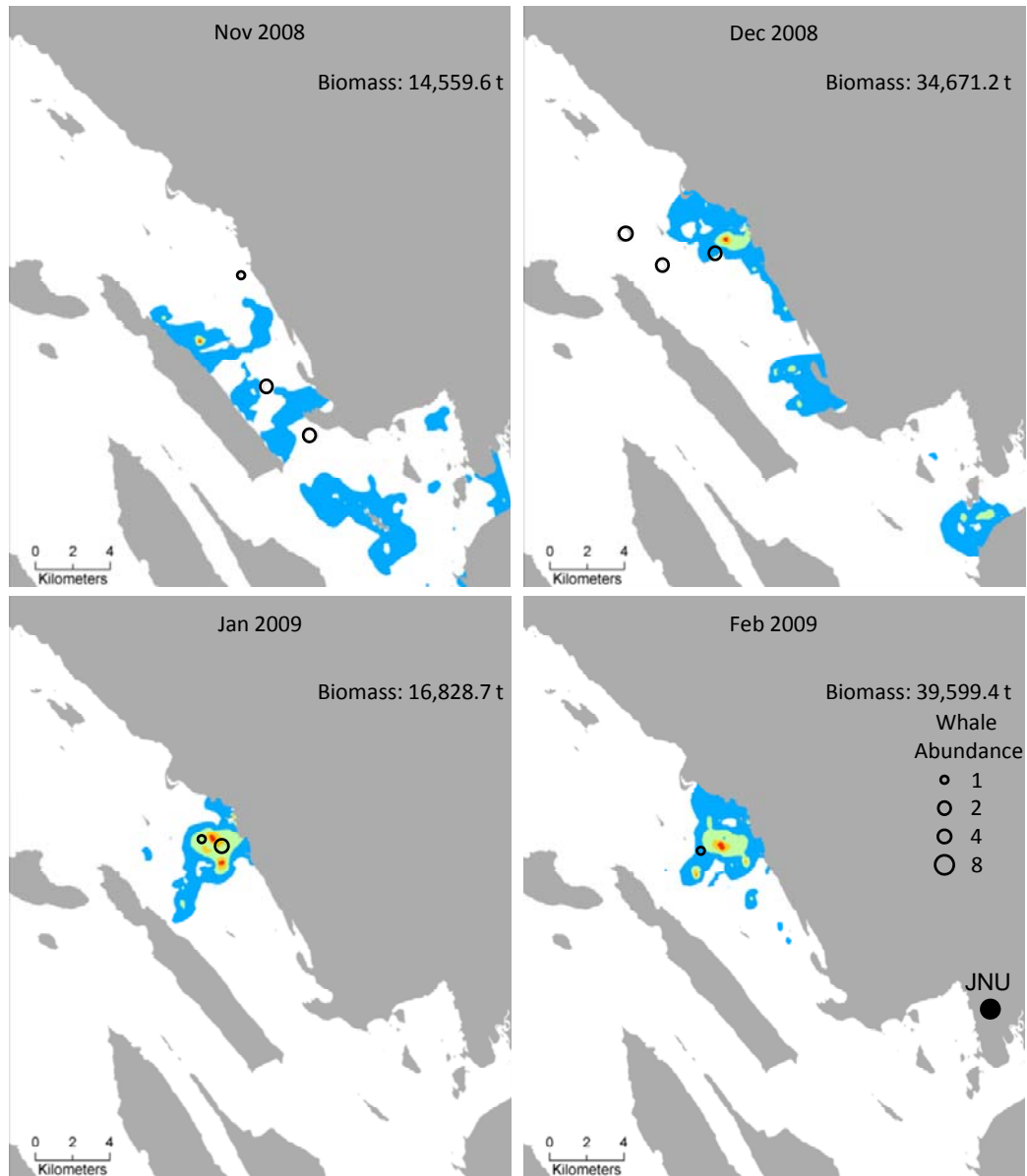


Figure 4. Winter distribution of humpback whales (circles) and Pacific herring (colormap) in Lynn Canal near Juneau, AK (JNU) over the winter of 2008-2009. Spatial distribution of herring density derived from IDW analysis as in Figure 3. Whale abundance from visual surveys are represented by graduated open circles. Total monthly biomass (tons) of herring estimated from acoustic surveys is provided for each month.

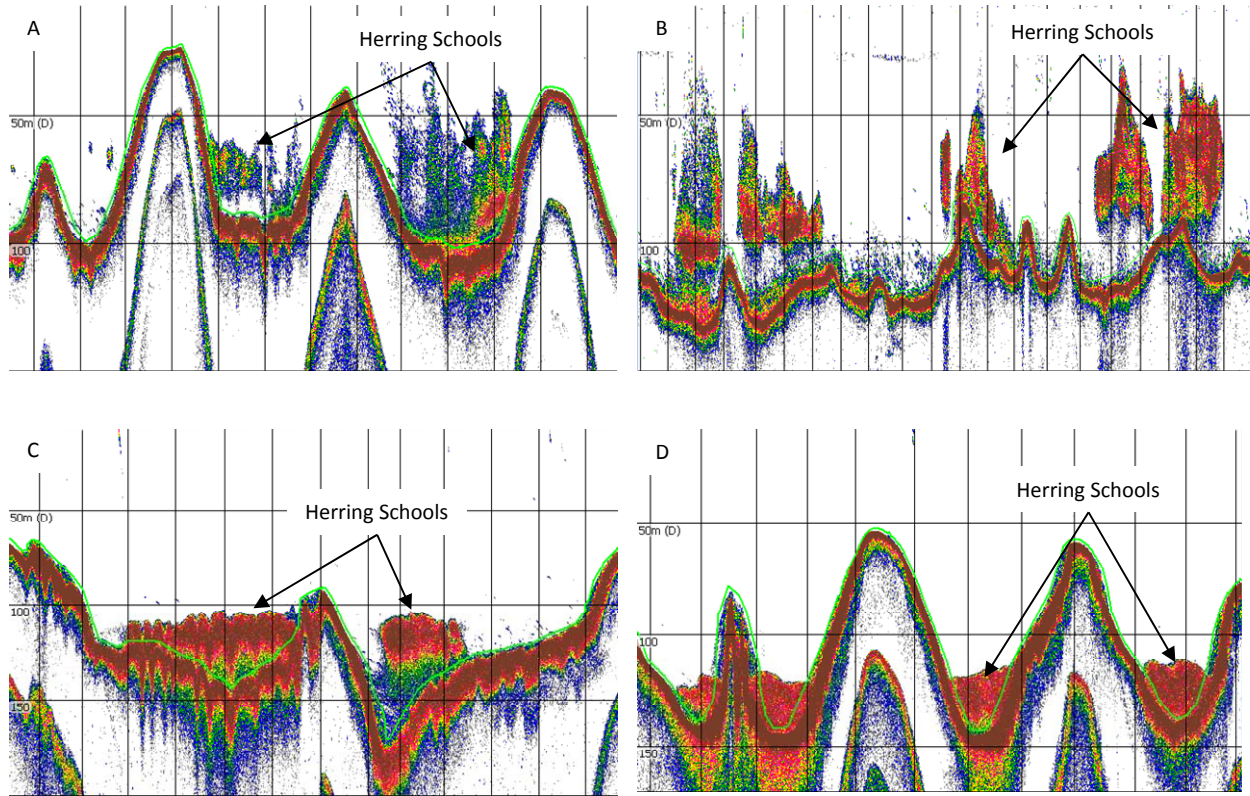


Figure 5. Example echograms of herring distributions observed at 38 kHz during winter months (November-A and B; February-C and D) in Lynn Canal, AK. Depth intervals are displayed at 50 m increments, and horizontal cells are separated by 0.1 nmi. Herring schools are clearly visible during November, whereas herring form dense schools in the deep trenches during February. The green line represents the bottom detection.

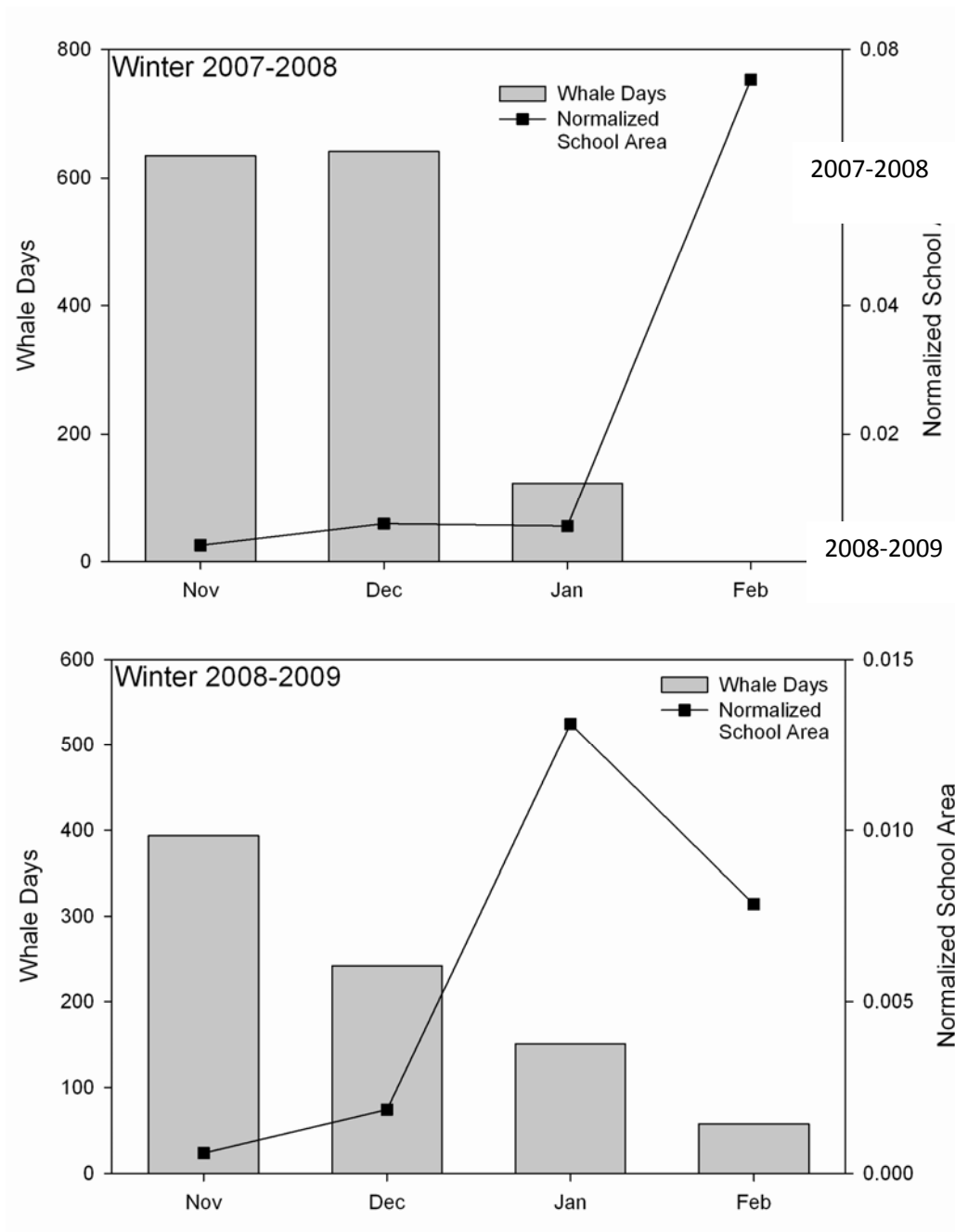


Figure 6. Effect of humpback whale presence on the spatial extent of herring schools, where normalized school area is the ratio of the area occupied by the fourth quartile (most dense herring) divided by the area occupied by the first quartile (least dense herring).

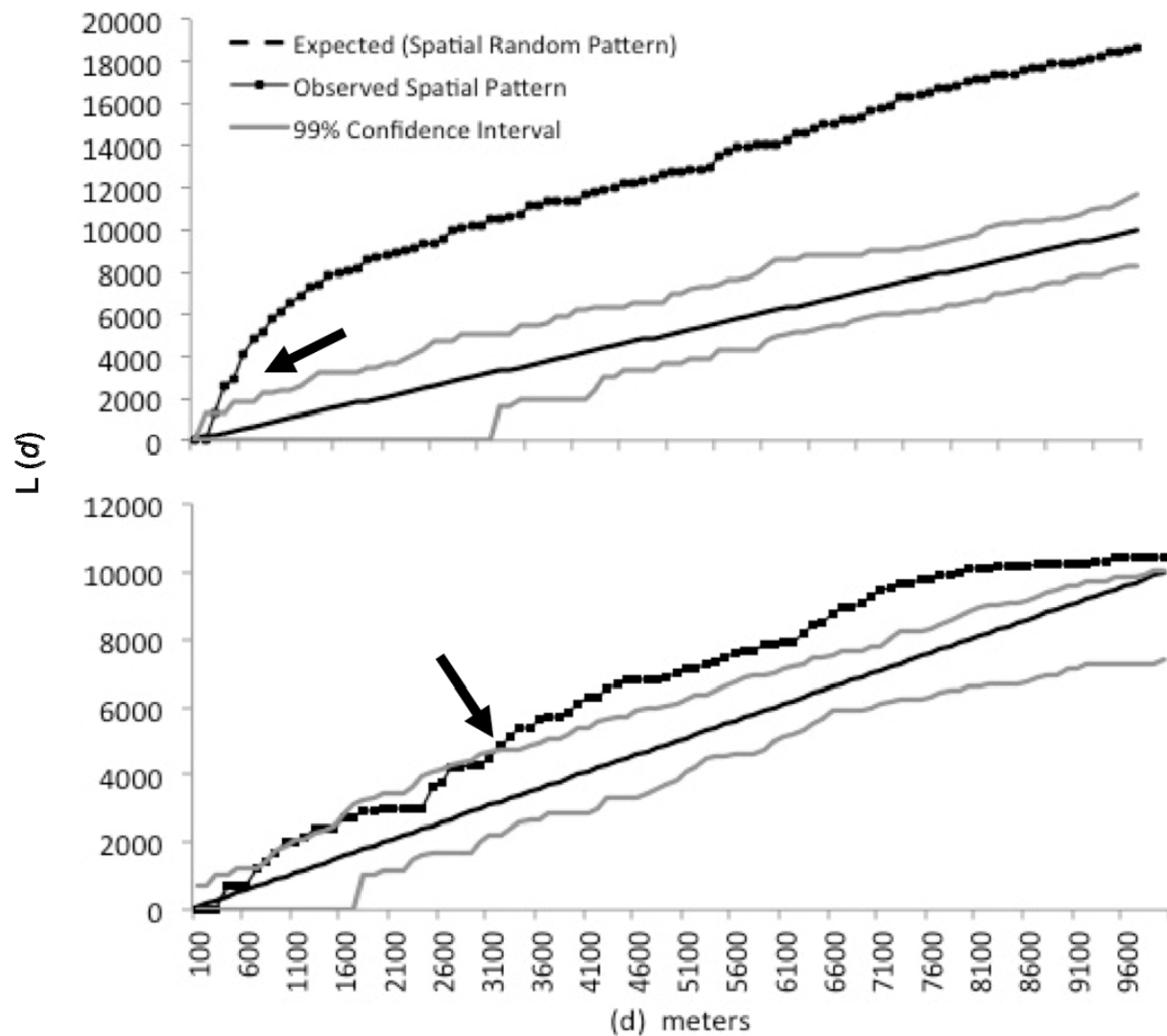


Figure 7. Spatial association among whales in November (upper panel) and December (lower panel) 2007 based on Ripley's K statistic, where significant clustering at spatial scales is observed when the observed spatial pattern line exceeds the bounds of the confidence interval (identified with arrows).



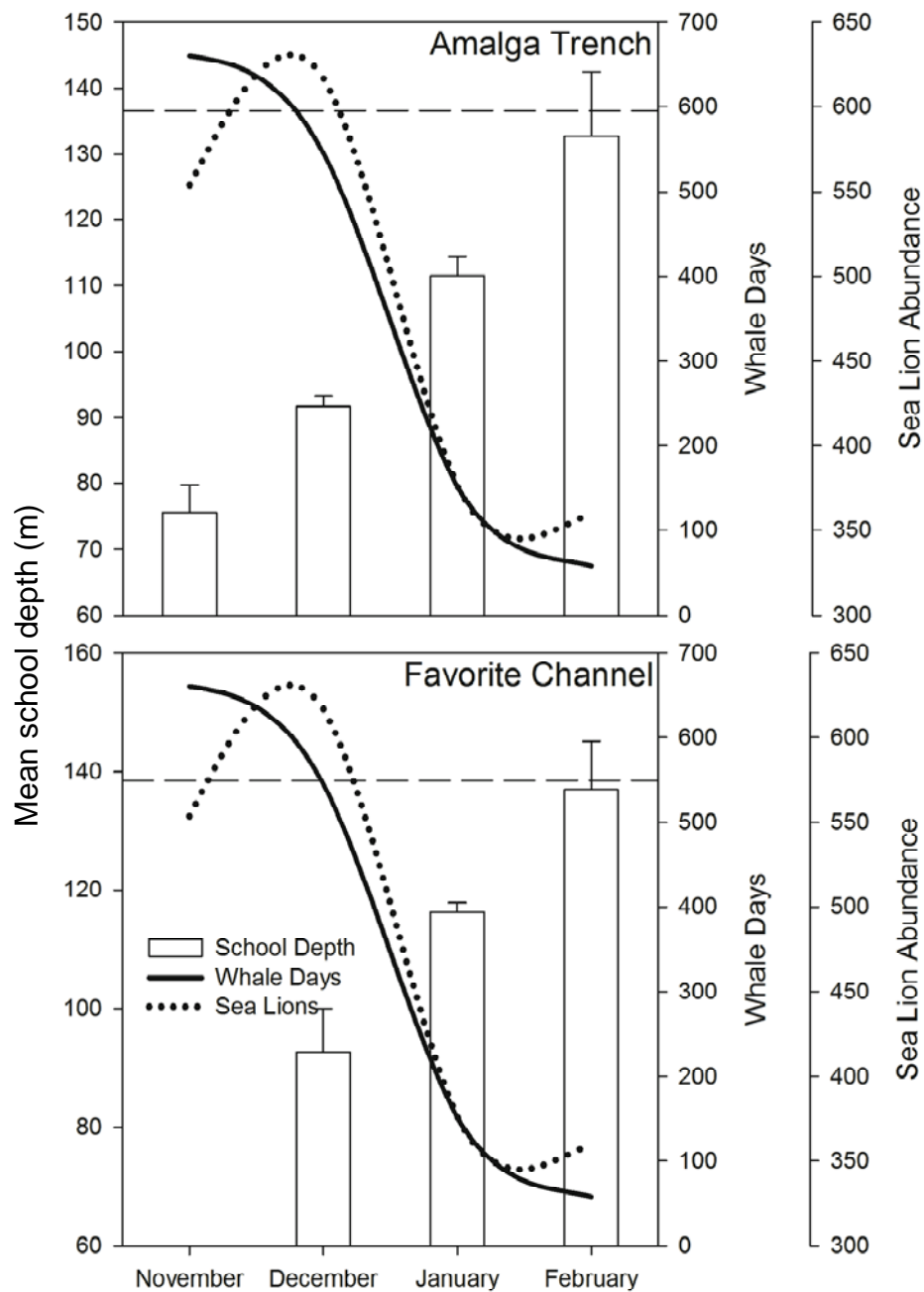


Figure 8. Monthly vertical distribution of Pacific herring schools relative to estimated whale days combined from 2007-2008 and 2008-2009 winter months (Nov-Feb), and historical sea lion abundance data reconstructed from Womble et al. (2009). Broken line on each plot represents mean water depth where herring schools were observed in both substrata. Error bars represent standard error.

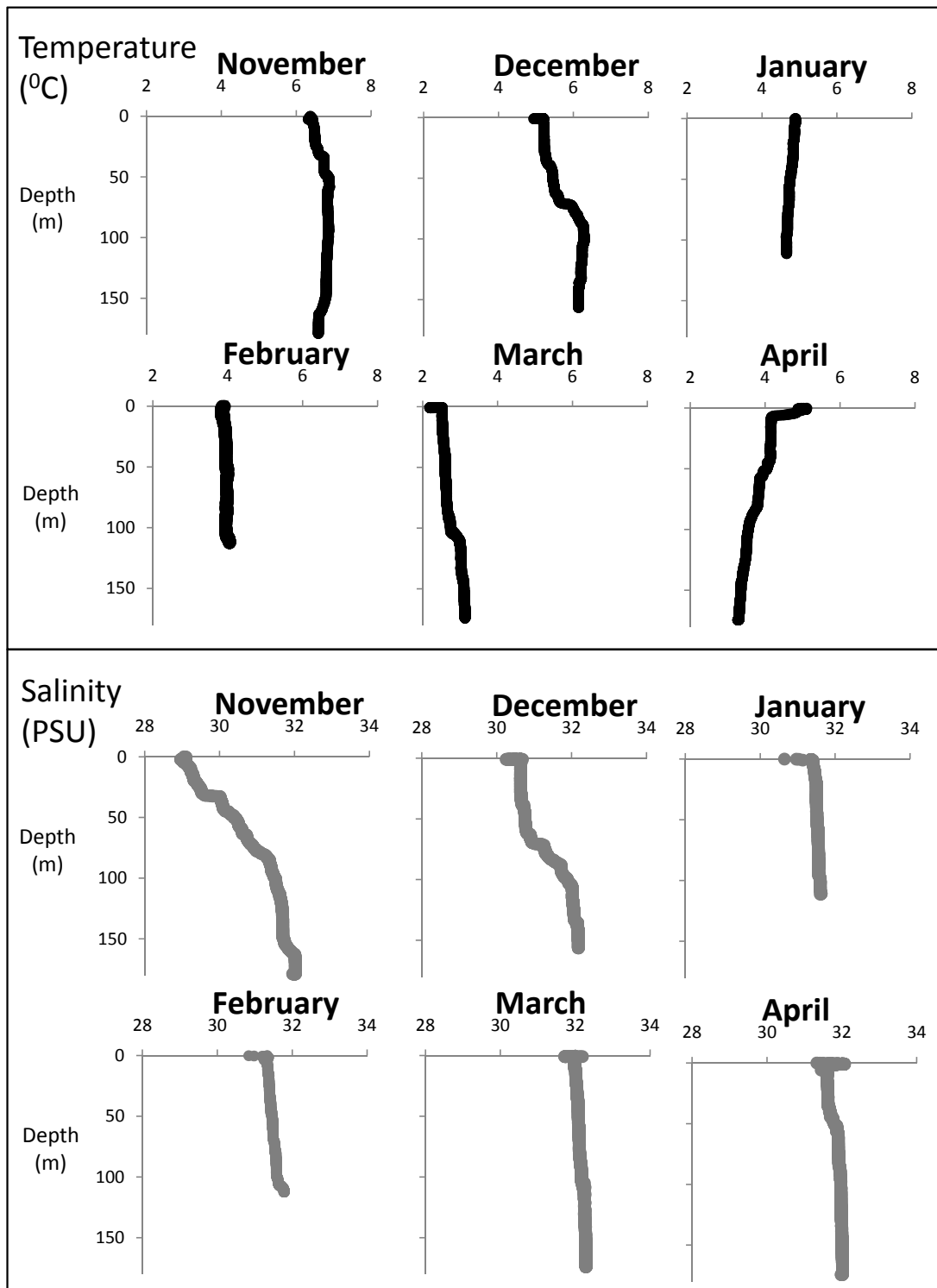


Figure 9. Monthly temperature ( $^{\circ}\text{C}$ ) and salinity (PSU) profiles of overwintering herring habitat.

## **Chapter IV: The Impact of Humpback Whales on Wintering Herring.**

Manuscript title: Regional Variation in the Intensity of Humpback Whale Predation on Pacific Herring in the Gulf of Alaska.

Ron A. Heintz, John Moran, Janice Straley, Johanna J. Vollenweider, Kevin Boswell,  
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### ***ABSTRACT***

The potential impact of humpback whale predation on three Alaskan herring populations was significant, but varied considerably between the three herring populations. The herring populations in Lynn Canal and Prince William Sound were commercially exploited but are currently depressed and have been closed to fishing for more than a decade. Increasing humpback whale predation has been cited a possible cause for the failure to recover. In contrast, the population in Sitka Sound is commercially exploited, also has whales present, but abundance is near historic highs. We modeled the potential herring biomass consumed in each location over two winters by combining observations of whale abundance through the fall/winter period when herring are aggregated, prey selection by the whales, and prey energy content with published data on whale size and metabolic rate. Estimates of the potential biomass removed were compared with independently derived estimates of herring abundance. Whales potentially removed a greater proportion of the total biomass of herring available in the depressed locations than in Sitka Sound. Biomass removals were greatest in Prince William Sound where we observed the largest number of whales. These whales foraged on herring over the entire sampling period. Whales were less abundant in Lynn Canal and only focused their foraging on herring in fall resulting in lower estimated consumption rates. Whales in Sitka Sound were more abundant than Lynn Canal but they foraged predominately on krill so their potential removals were similar to those of Lynn Canal. In addition, more herring were available in Sitka Sound making the potential impact of whale predation much lower in Sitka Sound than in Lynn Canal. The herring biomass consumed in Prince William Sound approximated the biomass lost to natural mortality over winter as projected by age structured stock assessments. These data indicate that the focused predation in Prince William Sound can exert top down controlling pressure, but whale populations are not a ubiquitous threat to forage fish populations in other regions at this time.

## INTRODUCTION

Humpback whales (*Megaptera novaengilae*) have the potential to limit the production of local forage fish populations in the North Pacific. In addition to krill, humpback whales prey on herring (*Clupea pallasii*), capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), juvenile pollock (*Theragra chalcogramma*) and sand lance (*Ammodytes hexapterus*) in the Gulf of Alaska (Witteveen 2008). Near Kodiak, Alaska these forage fish species comprised at least a third of humpback whale diets (Witteveen 2008). Isotopic analysis of humpback whales from Prince William Sound indicated even greater dependence on forage fish (Witteveen et al. 2009). As of 2006, there were approximately 20,000 humpback whales foraging in the north Pacific and their population is increasing at about 5% per year (Calambokidis et al. 2008). At approximately 30 tonnes each (Witteveen et al. 2006), humpback whale biomass in the north Pacific is roughly equivalent to that of eight million human beings.

However, the effect humpback whales exert on forage fish populations is likely to be discontinuously distributed in space and time. Humpback whales demonstrate inter-annual fidelity to foraging areas (Calambokidis et al. 2008). If whales return each year to a particular area and focus their foraging on fish, then the increasing numbers of whales in that area may begin to limit the productivity of local populations. This may be particularly true when whales forage on fish that aggregate in relatively small areas, as is typical for overwintering herring (Sigler and Csepp 2007). In Alaska, humpback whales have been observed foraging on overwintering aggregates of herring in Lynn Canal, Sitka and Prince William Sounds (Moran Chapter 1), but the impact of the whales on these populations is currently unknown.

The contrasting population trajectories for herring and presence of whales in these locations presents an opportunity to examine the impact of whale foraging on discrete herring populations in Alaska. The herring populations in Lynn Canal and Prince William Sound are depressed and have been closed to fishing for more than a decade without recovery. Humpback whale predation has been cited as a possible explanation for the failure of these populations to recover. In contrast, the Sitka Sound herring population appears healthy and recent harvest levels are near historic highs.

The objective of this report is to examine the feasibility of the hypothesis that humpback whale predation is limiting the recovery of depressed herring populations. We compare the potential biomass of herring consumed by humpback whales during fall and winter in each location with independent estimates of herring biomass and harvest. Consumption rates of humpback whales are modeled by combining field observations of whale abundance through the fall/winter period when herring are aggregated, prey choice and seasonal changes in the quality of herring with allometric models describing metabolic rates of marine mammals. These consumption estimates are compared with independent assessments of the herring stock biomass in each location to determine the relative intensity of whale predation on these populations. The exact allometric relation between humpback whale size and metabolic cost is unknown although a large number of models have been published (Leaper and Lavigne 2007). In addition, there is error associated with our estimates of whale abundance (Moran et al. this volume). Consequently, we estimated herring consumption for each location and winter using a variety of

scenarios to determine the range of credible estimates. This range sets the bounds to the intensity of humpback whale predation on herring in each location.

## **METHODS**

We estimated the potential biomass removed by humpback whales from Lynn Canal, Sitka and Prince William Sounds (Figure 1) for the winters of 2007-2008 and 2008-2009. Their large size prevents direct measurement of ingestion rates, therefore estimates of consumption were derived from the allometry between whale size and metabolic requirements. The core model combines estimates of whale size, metabolic rates, abundance, and diet with estimates of the energy content of overwintering herring to predict consumption. The core model and associated parameters are described below. We estimated the potential biomass removed for each location and winter using four different modeling scenarios because of the uncertainty in whale metabolic costs and the numbers of whale present. The different scenarios represent the range of possible estimates. Dividing the total biomass consumed under a given scenario with estimates of herring abundance yields a measure of the intensity of humpback whale predation. This ratio, referred to here as predation intensity, is not meant to indicate the actual proportion of the biomass consumed by whales, but rather as an indicator of the scale of whale predation in each location and winter under each of the modeling scenarios.

### **Core Model:**

The core model used to estimate biomass removals relies on both published data and data collected in the field. The model is given in equation 1.

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

In equation (1)  $C$  is the total biomass removed by whales over the course of a 182 day winter;  $p_t$  is the proportion of the whales known to be eating herring on the  $t^{\text{th}}$  day of winter,  $n_t$  is the number of whales foraging on the  $t^{\text{th}}$  day,  $w_i$  is the weight of a whale in the  $i^{\text{th}}$  size class,  $k$  and  $\beta$  are allometric parameters describing the metabolic rate of whales in the  $i^{\text{th}}$  size class and  $ED_t$  is the energy density of herring on the  $t^{\text{th}}$  day of winter. Values for  $C$  represent the total biomass of herring consumed during at a given location over a single winter.

The four different modeling scenarios relied on different combinations of  $n_t$ ,  $K$  and  $\beta$ . Winters spanned September 15 to March 15. Each scenario was simulated 50 times and a set of simulations is referred to as an experiment. The locations studied include Lynn Canal, Sitka and Prince William Sounds (Figure 1).

## Parameter estimates

### $w_i$ : The weight of whales in the $i^{\text{th}}$ size class

A simulation was initiated by converting a randomly selected set of 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 between 1924 and 1927 and 1948 and 1965 (Nichol and Heise 1992). Each of the lengths in the distribution ( $L_i$ ) was converted to mass using the relationship

$$w_i = \frac{0.0158L_i^{2.95}}{100} \quad (\text{Equation 2})$$

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

### $K$ and $\beta$ : Daily metabolic cost for whales in the $i^{\text{th}}$ size class

Two different allometric models were used to estimate the daily energy needs of foraging humpback whales. The models encompass the range of published estimates of whale metabolic rates that purport to exceed basal metabolic rate (Nagy et al. 1999; Boyd 2002; Acquarone 2006). The first model, herein referred to as the Perez 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  $3/4$  power. This relationship holds across over several orders of magnitude and offers the promise of extrapolating the metabolic rate for species that cannot be measured directly. The second model, herein referred to as the Acquarone model (Acquarone et al. 2006), is based on doubly labeled water experiments involving otariids and odobaenids weighing up to 1300 kg and estimates field metabolic rates.

Metabolic rate under the Perez model predicts average daily metabolic cost. It estimates metabolic demand (kCal per day) from mass (kg) using values of 192 and 0.75 for  $K$  and  $\beta$ , respectively. The value for  $K$  has been adjusted upwards from Kleiber's model to reflect the additional cost of activity (Wahrenbrock et al. 1974). These estimates may underestimate demand during foraging periods, because humpback whales must secure sufficient energy reserves during foraging to fuel a fast that lasts at least two months (Gabrielle et al. 1996). During this fast, 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 Perez model include migration, late term gestation and lactation.

The Acquarone model estimates the field metabolic rate in MJ per day from mass (kg) using values of 1.1 and 0.83 for  $K$  and  $\beta$ , respectively. Field metabolic rates for otariids and odobaenids may be more consistent with baleopterids because otariids and odobaenids also fast for significant periods during the year. Field metabolic rates measured with doubly labeled water include routine metabolic rates as well as costs associated with foraging, digestion, growth and energy storage. In addition, many of the observations in the Acquarone model included lactating

females. For each simulation, estimates of metabolic demand based on the Acquacone model were randomly selected from the 95% prediction interval. Neither the Perez nor the Acquacone models explicitly estimate costs associated with gestation or lactation. In addition, both models assume 100% of ingested prey are digestible.

**$n_t$  : The number of whales present on the  $t^{\text{th}}$  day**

Two different estimates of  $n_t$  were used in the core model, they are herein referred to as  $n_{t \text{ observed}}$  and  $n_{t \text{ expanded}}$ . These values reflect the number of whales in each location on each day of winter as described in Moran et al. (Chapter 1). Values of  $n_{t \text{ observed}}$  represent the lower estimate for the number of whales present on each day and are derived from the observed numbers of whales during each survey. Values of  $n_{t \text{ expanded}}$  represent the upper estimate for whale abundance. They are derived from the whale attendance patterns (Figure 2) reported by Moran et al. and expanded to account for mark-recapture estimates of whale population size.

**$p_t$ : Proportion of whales eating herring on the  $t^{\text{th}}$  day**

Estimates of the proportion of whales predating on herring relied on visual observations of groups of foraging whales as described in Straley et al. (Chapter 2). Values of  $p_t$  were calculated for each month and location as the number of groups observed foraging on herring divided by the number of groups with positively identified diets. The proportion of groups foraging on herring on a given day of winter was modeled as a step function from the visual observations. The winter was divided into six 30 day periods beginning on September 15. 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. 2010) and were estimated as the proportion of whales eating known prey that were consuming herring.

**$ED_t$ : Energy density of herring on the  $t^{\text{th}}$  day**

$ED_t$  was estimated for each location by sampling adult herring throughout each of the winters and determining their mass specific energy content (energy density). Procedures for collecting adult herring and estimating energy density are outlined in Heintz et al. (In prep). Energy density (kJ/g wet wt) was regressed on the day of sampling for each location and winter. For each simulation the estimated energy content of herring at a given location was randomly selected from the 95% prediction interval for the  $t^{\text{th}}$  day.

**Herring biomass estimates and predation intensity**

Predation intensity was calculated by dividing the estimate for potential herring consumption by the published estimates of the biomass of herring present. The Alaska Department of Fish and Game estimates total biomass of herring for Sitka and Prince William Sounds using age structure models as part of their annual stock assessments. These estimates derive from annual surveys conducted on the spawning grounds each spring and represent the biomass of herring available for consumption after spawning. Predation intensity for a given winter is calculated using the herring biomass from the previous spring. There is no age

structured model for Lynn Canal, so spawning stock biomass estimates based on the amount of spawn are used instead of total biomass.

In Lynn Canal herring biomass in winter greatly exceeds the spawning biomass estimated by up to two orders of magnitude (Sigler and Csepp 2007); Boswell et al. In Prep.). We used estimates of herring abundance derived from acoustic surveys conducted during the winters of 2007-2008 to estimate predation intensity on a monthly basis. We summed the median estimate of daily consumption for each month between November 2007 and March 2008 and divided by the acoustically determined estimate of herring biomass to estimate predation intensity.

### **Sensitivity of the core model**

The use of different values of  $n_t$  and  $K$  and  $\beta$  provided an opportunity to determine how errors in the parameter values influences estimates of consumption. Experiments in which  $K$  and  $\beta$  differed but all other conditions were the same allowed for understanding how the range of metabolic allometries might influence estimates of consumption. Likewise, comparison of models in which  $K$  and  $\beta$  were constant but  $n_t$  varied provided a basis for understanding how whale numbers influenced the estimate. One of the modeling scenarios (Lynn Canal for the winter of 2007-2008 using the Acquarone model) was used to examine the effect of errors in energy density through a series of seven experiments. In each experiment the estimated energy density of the herring was adjusted by 10% so that range of energy densities studied varied between 80 and 120% of the observed values. The effect of errors in  $p_t$  were studied by setting the  $p_t$  equal to 1.0 for all months in one of the scenarios (Prince William Sound in 2008-2009 using the Acquarone model and  $n_t$  expanded) and then re-running the experiment under the same conditions but setting  $p_t$  equal to 0.5.

## **RESULTS**

### **$n_t$ The number of whales present**

Humpback whales were generally most abundant across locations in the first half of winter, but the timing of peak abundance depended on both year and location. Peak abundance in Lynn Canal occurred in September during the first winter (2007-2008) and in October during the second winter (2008-2009). This pattern was reversed in Sitka Sound. The peak abundance of whales occurred in November during the first winter and in October during the second winter (2008-2009) (Figure 2). In contrast, abundance in Prince William Sound whales remained at high abundance throughout the fall of the second winter and only began declining after December (Figure 2). This prolonged attendance of whales in Prince William Sound led to a greater abundance of whales when expressed as the total number summed over each of the 182 days of winter (whale-days). Based on  $n_t$  observed the number of whales-days in Prince William Sound was approximately fourfold that of Sitka and more than sevenfold that of Lynn Canal during the winter of 2008-2009 (Table 2).



### **p<sub>t</sub> The proportion of whales consuming herring**

In Lynn Canal and Prince William Sound whales foraged almost entirely on herring in the first months of winter (Table 1). 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 winter. In contrast, humpback whales in Sitka focused on krill early in the winter. They switched to herring in late winter when the herring began staging in Sitka Sound prior to spawning.

### **ED<sub>t</sub> The energy density of herring on the t<sup>th</sup> day**

Herring energy content was highest in the fall, 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 winters (Figure 3). In Lynn Canal and Prince William Sound herring were available throughout the winter (Figure 3), although their energy declined as time progressed. Losses in energy were expected because food supplies are limited in winter. In contrast to Lynn Canal and Prince William Sound, herring in Sitka were not available to whales until later in the winter because they did not arrive in the Sound until much later in the season.

### **Consumption estimates and predation intensity – Lynn Canal**

In Lynn Canal most of the whale foraging effort on herring was most intense in fall when whales were abundant and herring were relatively scarce (Figure 4). Overall, humpback whales potentially consumed between 650 and 2,626 tonnes of herring in 2007-2008 and 446 and 1,783 tonnes in 2008-2009 (Tables 3 and 4). When compared with the spawning biomass of herring, predation intensity ranged between 44-179% in 2007-2008 and 89-3577% in 2008-2009. The overwinter biomass of herring in Lynn Canal supports multiple spawning populations (Boswell Chapter 3), hence the whales were not foraging on only the local spawning biomass. In fall, when most predation occurred, herring biomass exceeded the spawning biomass at least sixfold. In November 2007, whales consumed approximately one third of the total biomass consumed over winter and predation intensity ranged between 1.7% and 6.6% (Table 5). In December, the potential mass of herring consumed declined (Figure 4) as whales departed, but herring biomass increased and predation intensity dropped to no more than 1%. After Similar, though less extreme, impacts were observed in the winter of 2008-2009 because whales were less abundant (Figure 4).

### **Consumption estimates and predation intensity – Sitka Sound**

In Sitka Sound predation intensity on herring was very low because humpback whales focused their foraging effort on krill in fall (Figure 4). In absolute terms, whales in Sitka Sound potentially consumed about the same tonnage of herring as whales in Lynn Canal (Tables 3 and 4) despite higher whale abundance in Sitka Sound. Humpback whales potentially consumed 301-2,776 and 430-2,168 tonnes of herring 2007-2008 and 2008-2009, respectively (Tables 3 and 4). However, this represented less than 3% of the total biomass of herring available. The potential biomass consumed was far less than the biomass removed in the Sitka Sound sac roe harvest:

14,616 and 15,012 tonnes in 2007 and 2008, respectively (Sherry Dressel, Alaska Department of Fish and Game, personal communication).

### **Consumption estimates and predation intensity – Prince William Sound**

Whales foraged in large numbers over much of the fall and winter in Prince William Sound resulting in significant predation intensity (Figure 4, Tables 3 and 4). In absolute terms, whales potentially consumed between 2,639 and 7,443 tonnes of herring in 2007-2008 this represented a predation intensity of 27% to 77%. In 2008-2009 whales potentially consumed between 2,362 and 12,989 tonnes and predation intensities ranged between 11% and 63% of the total biomass present in spring 2008. For comparison, the last harvest of herring from Prince William Sound was 3,904 tonnes in 1998 approximately 20% of the spawning biomass (ADFG 2010).

### **Model Sensitivity**

Predictions for  $C$  varied linearly with errors in most of the parameters and was least sensitive to variations in  $n_t$ . For a given modeling scenario  $n_{t \text{ observed}}$  and  $n_{t \text{ expanded}}$  differed by a factor of two (Table 2), while estimates of biomass removals for the Acquarone models differed by about 80% between  $n_{t \text{ observed}}$  and  $n_{t \text{ expanded}}$  (Table 3). Similarly, Perez models differed by about 70% when  $n_t$  varied between  $n_{t \text{ observed}}$  and  $n_{t \text{ expanded}}$ . Errors in the estimation of metabolic allometry were also linearly related to consumption estimates. The biomass consumed under the Perez and Acquarone models differed approximately by a factor of 2.57 when all other factors were held constant (Tables 3 and 4). In contrast, the estimated metabolic rates for a 30 tonne whale differ about threefold for the two models: 5.6 and 1.83 MJoules  $\cdot$  day<sup>-1</sup> for the Acquarone and Perez models, respectively. The effects of errors in the estimated energy density were approximately linear so long as errors were plus or minus 20% of the predicted value (Figure 5). The model was most sensitive to errors in  $p_t$ . Errors in  $p_t$  were linear in their effect on consumption. Reducing  $p_t$  by 50% reduced the estimated consumption by approximately 50%.

## **DISCUSSION**

Predation intensity by humpback whales in Prince William Sound was greater than either of the two other locations, ranging between 11 to 77%. At a minimum these values indicate whales are removing a biomass equivalent to a commercial fishery, because the guideline harvest level in Prince William Sound varies between 15% and 20%. These data indicate humpback whales remove a significant proportion of the annual herring production in Prince William Sound. It is more difficult to associate whales with the failed recovery of Lynn Canal herring. Predation intensities based on spawning stock biomass are biased too high because they do not account for the much higher wintering biomass. Predation intensities for November ranged between 0.5% and 6.0 %, In November herring biomass was increasing and whale abundance declining, presumably predation intensity was higher in September and October when herring abundance was lower (Sigler and Csepp 2007) and whale abundance higher.

These predation intensities are presented as an index to the relative intensity of whale predation in each location, and should not be used as estimates of the true proportion taken.

There are several problems with estimating the predation take by whales, starting with estimates on the number of whales, how much they eat. We have dealt with these uncertainties by presenting ranges of values that likely encompass the true value. Another uncertainty in determining the impact of whale predation lies with estimating the number of herring available. Estimates of herring biomass may not necessarily represent biomass fish directly available to whales. While age-structured estimates of total biomass account for adult fish that do not spawn, those fish may not be co-located with the rest of the maturing fish or foraging whales. Similarly, it is not clear how to account for the biomass of fish that are too young to be represented in age-structured stock assessments. These juveniles may be found in areas where whales forage but it is not certain if whales forage on them.

In addition 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 the population's collapse is unknown, but habitat loss and overfishing have been identified as important factors (Carls et al. 2008). The herring population in Prince William Sound crashed following an epizootic involving viral hemorrhagic septicemia virus (Rice and Carls 2008). While the whales did not directly cause the decline, they have varying impact on the recovery of these two populations.

### **Impacts of Whale Predation on Lynn Canal Herring**

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 (Boswell et al. Chapter 3) revealed a pattern of herring abundance consistent with that of Sigler and Csepp (2007). There is a biomass of herring in midwinter (December to February) that swamps the spawning stock biomass. Two distinct models could produce this pattern. First, this pattern could be accounted for by the presence of a small local spawning stock (Carlson 1984) that is inundated with large numbers of overwintering herring from distant locations. Second, the small biomass present at spawning in spring could represent a small component of the larger stock that aggregates in Lynn Canal during winter and spawns in multiple locations.

The effect of whales on the Lynn Canal spawning stock biomass depends on whether that biomass is small or large. Most of the whale foraging occurred early in our sampling period when a relatively small biomass of herring would be present. Between 2001 and 2004 the biomass of herring present in October ranged between 700 and 1,200 tonnes (Sigler and Csepp 2007), approximately equal to the estimated spawning stock biomass (Carls et al. 2008). This suggests movement of herring into Lynn Canal occurs after October. The Perez model estimates approximately 246 tonnes were consumed during October, 2007 and available spawning stock biomass was 1,461 tonnes. Thus whales potentially consumed about somewhere near 15% of the spawning stock biomass in October. Alternately, if the fish present in October were a small fraction of a much larger spawning stock, then predation intensity would be much lower. For example, the potential biomass removed in 2007-2008 (975 tonnes) represents 1% of the peak herring biomass (91,000 tonnes) observed in February 2008 (Boswell et al. In prep.).

The management implications of humpback whale predation depend on the proportion of natural mortality accounted for by humpback whale predation. If whale consumption is in excess

of current estimates of natural mortality then fishery managers will need to revise estimates of natural mortality upward if they are to set sustainable harvest quotas. However, if whales are displacing competitors then whale consumption comprises a significant proportion of the current estimates for natural mortality. In this case it is important for managers to ascertain how competition with humpback whales affects other apex predators, because these other predators include commercially fished and statutorily protected species. In either case, the apparent success of whale conservation measures will force resource managers to alter their strategies with respect to commercially valuable and statutorily protected species.

### **Impacts of Whale Predation on Sitka Sound Herring**

The potential consumption of Sitka Sound herring by humpback whales may be underestimated. Whale predation on herring in Sitka Sound was not significant until late in the winter when herring began staging prior to spawning. It is not known where the herring were located in fall (September – January) 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, suggesting some individuals may have been traveling with the herring. Consequently, some level of predation may have occurred outside out study area. Nevertheless, predation intensity would have to increase tenfold to equal that of the other locations.

### **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, which is between 0 and 20% of the spawning biomass when spawning biomass exceeds 22,000 tons (Alaska 1998). This level of removal is considered sustainable and occurs in addition to natural mortality. Between 2001 and 2006 natural mortality over winter accounted for the loss 1,800 to 5,500 tonnes of adult herring (Marty et al. 2010). The lowest estimates of potential herring consumption by humpback whales over the winters of 2007-2008 and 2008-2009 fell within this range, suggesting that humpback whales might account for the majority of the winter mortality of adult herring in Prince William Sound. While the hypothesis that humpback whale predation might be a factor limiting the recovery of herring is feasible, it is less certain if whale consumption adds significantly to current levels of mortality and if that mortality is sustainable.

### **Identification of the most appropriate modeling scenario - $n_t$**

Whale population sizes were in excess of  $n_{t \text{ observed}}$ , hence the estimates derived from  $n_{t \text{ observed}}$  underestimate the true biomass removed. Values of  $n_{t \text{ observed}}$  reflect only the number unique individuals identified for the mark-recapture estimates and do not account for individuals known to be in the area, but not adequately reflected in the photographic record (Moran et al. 2010). Nor does  $n_{t \text{ observed}}$  account for calves or adult whales that were present but not directly observed.

Conversely, the values obtained for  $n_{t \text{ expanded}}$  may slightly overestimate the number of whales present. Closed mark-recapture methods overestimate population size if there is

immigration or emigration during the surveys (Seber 1982). Our populations were open so estimates of  $\hat{n}_{aw}$  are biased upwards. However, none of our estimates of  $n_{t\text{ expanded}}$  exceed  $\hat{n}_{aw}$  suggesting that the upward bias is limited in our case. Moreover, the total number of different whales observed roughly agrees with  $\hat{n}_{aw}$  in each location (Moran et al. Chapter 1.). This suggests any bias in our estimates is likely to be small. Moreover, the sensitivity analysis indicates that small departures from the true value of  $n_t$  have relatively little effect on model predictions. Hence, models based on  $n_{t\text{ expanded}}$  likely reflects the best set of scenarios for estimating predation intensities.

### Identification of the most appropriate modeling scenario – K and $\beta$

Recently several authors (Boyd 2002; Leaper and Lavigne 2007) have indicated that field metabolic rates for whales should be less than or equal to the basal rates predicted by Kleiber's model ( $K = 293.1$ ,  $\beta = 0.75$ ) (Kleiber 1961). The reasons given for the convergence of field and 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 may be less than basal metabolic rates (Folkow and Blix 1992). Hence, the Perez models based on  $n_{t\text{ expanded}}$  provide the best estimates of biomass removals.

These arguments for reduced metabolic rates in whales contrast sharply with predictions of field metabolic rates generated from doubly labeled water studies. While the Acquarone model relies on doubly labeled water studies conducted specifically on marine mammals including walruses, it does not include observations published in contemporary or more recent publications. Combining the data reported by Acquarone et al. (2006), Boyd (2002) and Nagy et al. (1999) with more recent reports (Sparling et al. 2008) indicates the allometric slope should be 0.79 not 0.82 as reported in Acquarone et al. (2006). Consequently, doubly labeled water studies produce an allometric relation that differs from the Kleiber model by a factor of 1.4, not the factor of 8.0 reported by Acquarone et al. (2006). The Perez model we employed differs from Kleiber's model by a factor of 2.24.

One possible explanation for the higher values predicted by doubly labeled water studies is that the Perez model does not account for the metabolic costs of gestation or lactation. Humpback whales have been estimated to output 2,000 MJ/d as milk during mid-lactation (Oftedal 1997). For a thirty tonne female, this is about 200 MJ more than her average daily metabolic cost as predicted by the Perez model. Thus for lactating females, average daily metabolic demand is about twice that predicted by the Perez model, or 4.5 times that of Kleiber's model. This is still less than the value predicted by the Acquarone model. Costs associated with gestation are somewhat lower than those of lactation (Lockyer 2007). If they are assumed to equal lactation and we further assume that all the females in the population are either gestating or lactating then metabolic demands for the population would be approximately 50% greater than those calculated under the Perez model. Accounting for lactation and gestation conservatively results in predicted consumption rates that range to no more than 1.5 times the consumption estimated under the Perez model using  $n_{t\text{ expanded}}$ .

### Effects of whale predation relative to their competitors

Early in winter 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. With an average weight of 750 kg, sea lions biomass likely never exceeded 800 tonnes. 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. Ectothermic predators likely had even less effect on herring. Walleye pollock (*Theragra chalcogramma*) biomass was estimated at less than 637 tonnes between 2001 and 2004 (Sigler and Csepp 2007).

In Prince William Sound the contrasting population trajectories of humpback whales and other piscivorous endotherms suggest whales may be displacing previously abundant herring predators. Sea lion production rates at rookeries near Prince William Sound declined by 3.5% per year between 1992 and 2005 (Fritz et al. 2008) and harbor seal populations in Prince William Sound declined by 63% between 1984 and 1997 (Frost et al. 1999 in assessment). Populations of both species are considered to be low at the current time (Allen and Angeliss 2010). Other endothermic piscivores are less likely to compete with whales. Combining published weights for sea bird species (Sibley 2000) with estimates of bird numbers (Bishop et al. 2010) puts the piscivorous sea bird biomass in Prince William Sound at less than the weight of two whales. Likewise the biomass of resident killer whales foraging in and around Prince William Sound is approximately a third of the whale biomass (Matkin et al. 2003). Piscivorous fish are potential competitors with whales. The last survey of groundfish put walleye pollock biomass at about 7,500 tonnes (Bechtol 2002) and the current status of other species is unknown.

### CONCLUSION

Predation in Prince William Sound was greater than the other locations, approaching the guideline harvest level for a commercial fishery, 20% of the spawning stock biomass. In Prince William Sound this was due to the persistence of relatively large numbers of whales during winter and their focus on herring. In Lynn Canal potential biomass removals were about equal to those from Sitka, but the small herring biomass resulted in greater predation intensity. Moreover, whales in Lynn Canal focused their foraging on herring in fall while whales in Sitka did not forage on herring until spring, when whale abundance was minimal. While these data indicate that current whale populations are not a ubiquitous threat to fish populations, it is clear they can exert significant impacts on forage fish populations over small spatial scales. Thus any consequent adjustments to forage fish management strategies should occur locally and account for the protected status of humpback whales.

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## Tables

Table 1. Values for  $p_i$  used in equation 1.

Period	$p_i$		
	Lynn Canal	Prince William Sound	Sitka Sound
Sep. 15- Oct. 15	1.0	0.86	0
Oct 16. – Nov. 15	1.0	0.90	0.17
Nov. 16 – Dec. 15	0.80	0.94	0.58
Dec. 16 – Jan. 15	1.0	1.0	0.57
Jan. 16 – Feb. 15	1.0	1.0	1.0
Feb. 15 – Mar. 15	0	1.0	1.0

Table 2. Comparison of the sum of  $n_t$  over each winter (whale-days) for each location and winter. Foraging effort is the product of  $p_t$  and whale-days. Values for  $\alpha$  show the scalar used to adjust  $n_t$  *observed* to account the mark recapture estimates of whale abundance. See equations 4 and 5.

Location	$n_t$	Winter	$\alpha$	Whale-days
Lynn Canal	observed	07-08	-	1711
	expanded	07-08	1.7	2940
	observed	08-09	-	1140
	expanded	08-09	1.8	2019
Sitka Sound	observed	07-08	-	2348
	expanded	07-08	1.7	7190
	observed	08-09	-	2188
	expanded	08-09	2.3	5114
Prince William Sound	observed	07-08	-	-
	expanded	07-08	1.1	8916
	observed	08-09	-	8195
	expanded	08-09	2.3	18719

Table 3. Estimates of herring biomass removed from Lynn Canal, Sitka and Prince William Sounds during the winter of 2007-2008 under different modeling scenarios involving the Acquarone and Perez models combined with  $n_{t \text{ observed}}$  and  $n_{t \text{ expanded}}$ . The tonnes 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 winter.

Location	Allometric model	$n_t$	Tonnes of herring consumed	Total Herring Biomass (Tonnes)	Predation Intensity
Lynn Canal	Acquarone	observed	1688	1461 <sup>2</sup>	155%
		expanded	2626	1461 <sup>2</sup>	180%
	Perez	observed	650	1461 <sup>2</sup>	45%
		expanded	975	1461 <sup>2</sup>	67%
Sitka Sound	Acquarone	observed	792	101,209 <sup>2</sup>	1%
		expanded	2776	101,209 <sup>2</sup>	3%
	Perez	observed	301	101,209 <sup>2</sup>	<1%
		expanded	1018	101,209 <sup>2</sup>	1%
Prince William Sound	Acquarone	expanded	7443	9650 <sup>1</sup>	77%
	Perez	expanded	2639	9650 <sup>1</sup>	27%

1. Steve Moffitt personal communication Alaska Department of Fish and Game
2. Dressel Alaska Department of Fish and Game Personal communication

Table 4. Estimates of herring biomass removed from Lynn Canal, Sitka and Prince William Sounds during the winter of 2008-2009 under different modeling scenarios involving the Acquarone and Perez models combined with  $n_{t \text{ observed}}$  and  $n_{t \text{ expanded}}$ . The tonnes of herring consumed is the median value from 50 simulations. Predation intensity is estimated as the biomass consumed divided by the total herring biomass observed in the spring previous to the modeled winter.

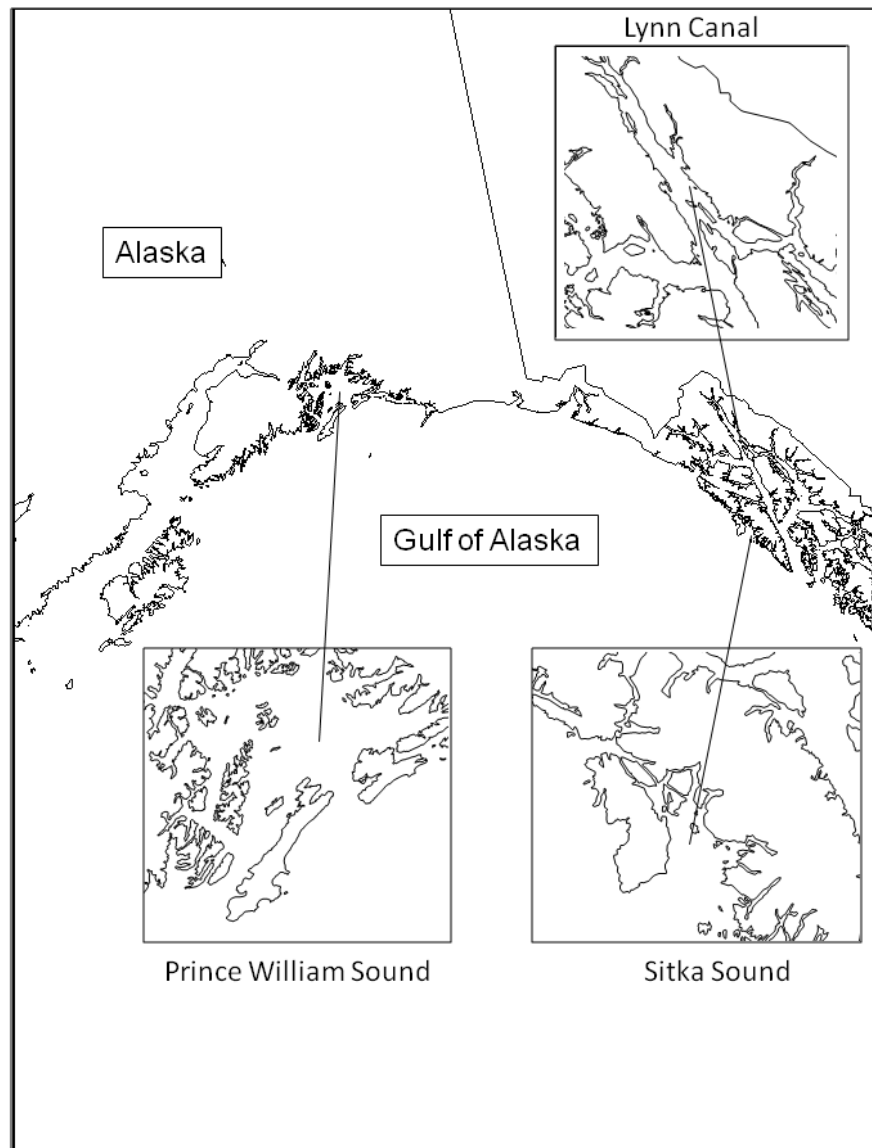
Location	Allometric model	$n_t$	Tonnes of herring consumed	Total Herring Biomass (Tonnes)	Predation Intensity
Lynn Canal	Acquarone	observed	1118	499 <sup>2</sup>	224%
		expanded	1738	499 <sup>2</sup>	357%
	Perez	observed	446	499 <sup>2</sup>	89%
		expanded	501	499 <sup>2</sup>	137%
Sitka Sound	Acquarone	observed	1084	108,192 <sup>2</sup>	1%
		expanded	2168	108,192 <sup>2</sup>	2%
	Perez	observed	417	108,192 <sup>2</sup>	<1%
		expanded	788	108,192 <sup>2</sup>	1%
Prince William Sound	Acquarone	observed	6620	20737 <sup>1</sup>	32%
		expanded	12989	20737 <sup>1</sup>	63%
	Perez	observed	2362	20737 <sup>1</sup>	11%
		expanded	4388	20737 <sup>1</sup>	21%

1. Steve Moffitt personal communication Alaska Department of Fish and Game

2. Amy Dressel Alaska Department of Fish and Game personal communication

Table 5. Monthly predation intensity exerted by humpback whales in Lynn Canal during the winters of 2007-2008 and 2008-2009 as predicted by different model scenarios. Predation intensity is the predicted biomass of herring removed in a given month divided by the estimated biomass of herring present at that time. Herring biomass estimates are taken from Vollenweider and Boswell.

Month	Herring Biomass (Tonnes)	Acquarone		Perez	
		$n_{t \text{ observed}}$	$n_{t \text{ expanded}}$	$n_{t \text{ observed}}$	$n_{t \text{ expanded}}$
November 2007	9,043	386	601	149	224
		(4.2%)	(6.6%)	(1.6%)	(2.5%)
December 2007	41,334	414	644	160	241
		(1.0%)	(1.5%)	(0.4%)	(0.5%)
November 2008	14,559	216	345	86	133
		(1.5%)	(2.4%)	(0.6%)	(0.9%)
December 2008	34,671	155	246	64	99
		(0.4%)	(0.7%)	(0.2%)	(0.3%)



### Figures

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

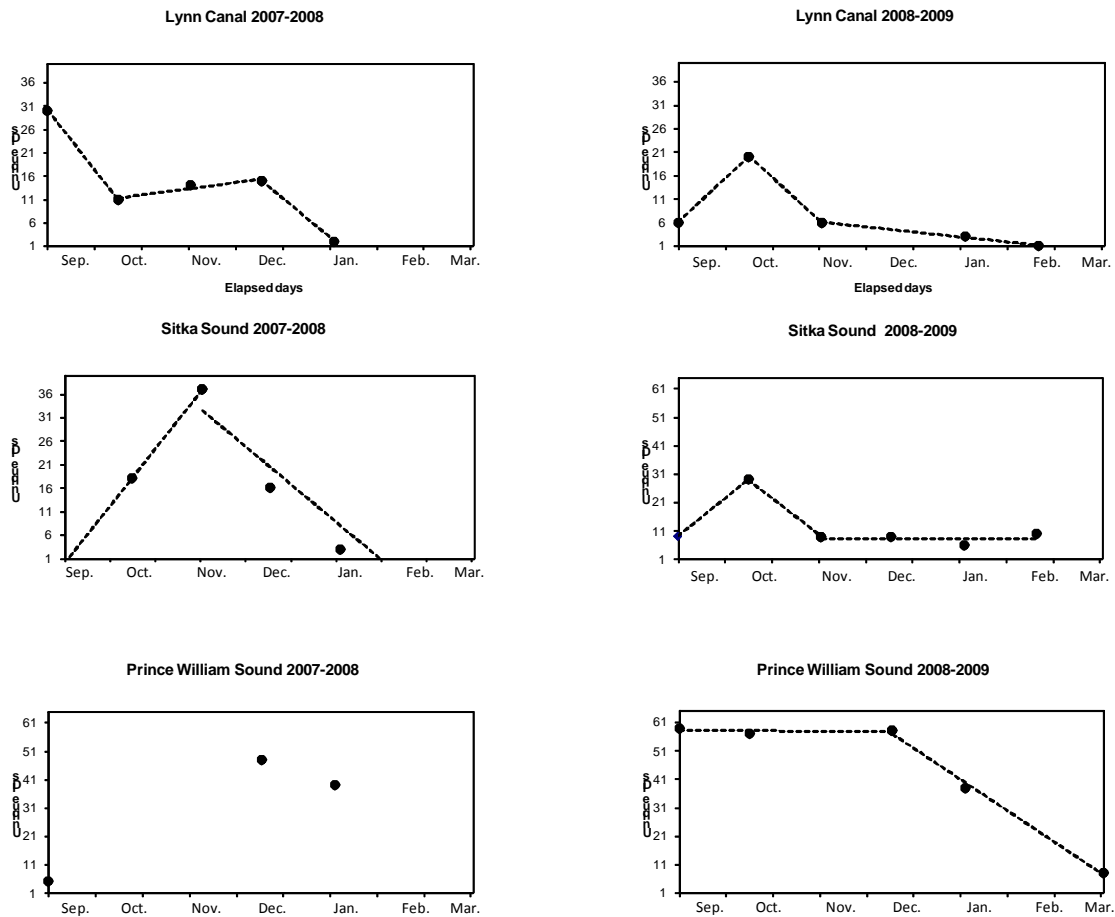


Figure 2. Attendance patterns of humpback whales in Lynn Canal, Sitka and Prince William Sounds. The attendance pattern for Prince William Sound in 2007-2008 was not modeled because only three surveys were conducted over a limited spatial area. Winters spanned between September 15 and March 15.



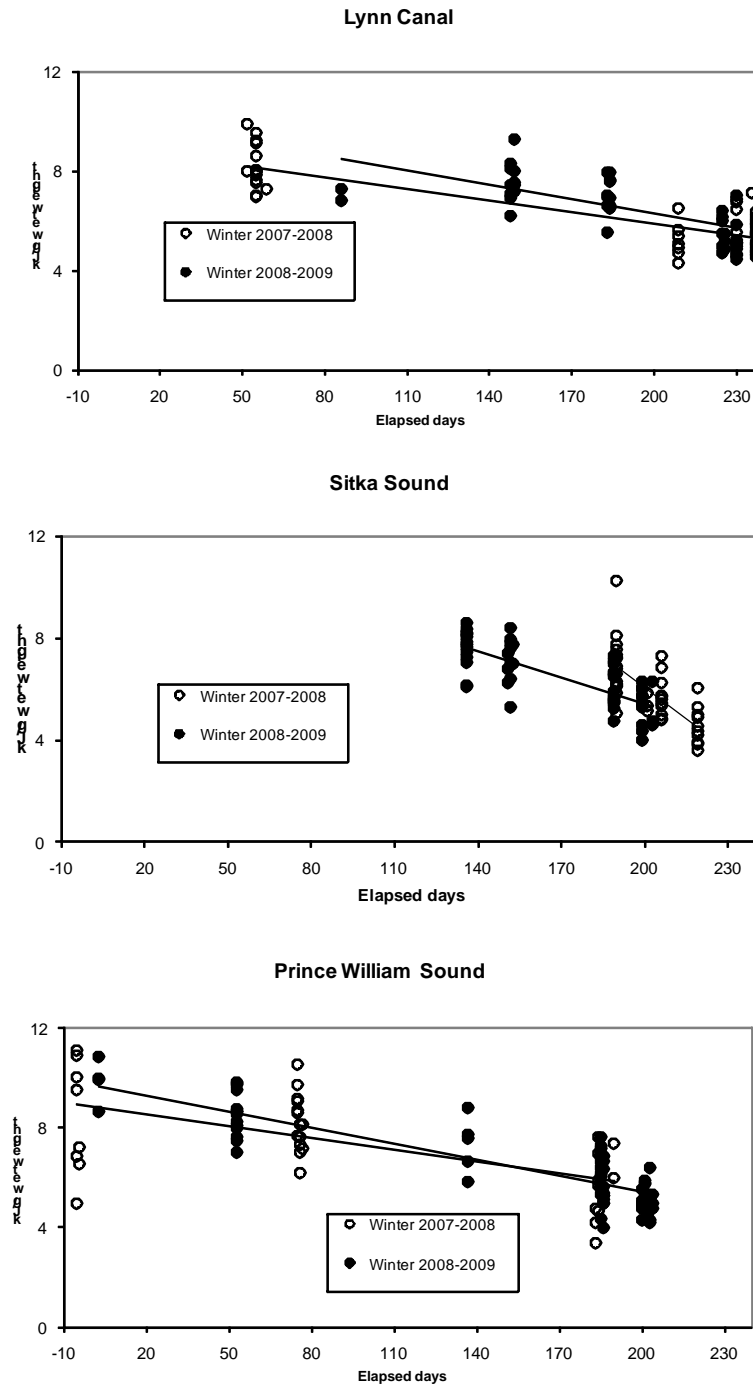


Figure 3. Energy loss in herring from Lynn Canal, Sitka and Prince William Sounds during the winters of 2007-2008 and 2008-009. Abscissa shows the number of days elapsed since September 15, the first day of the study period.

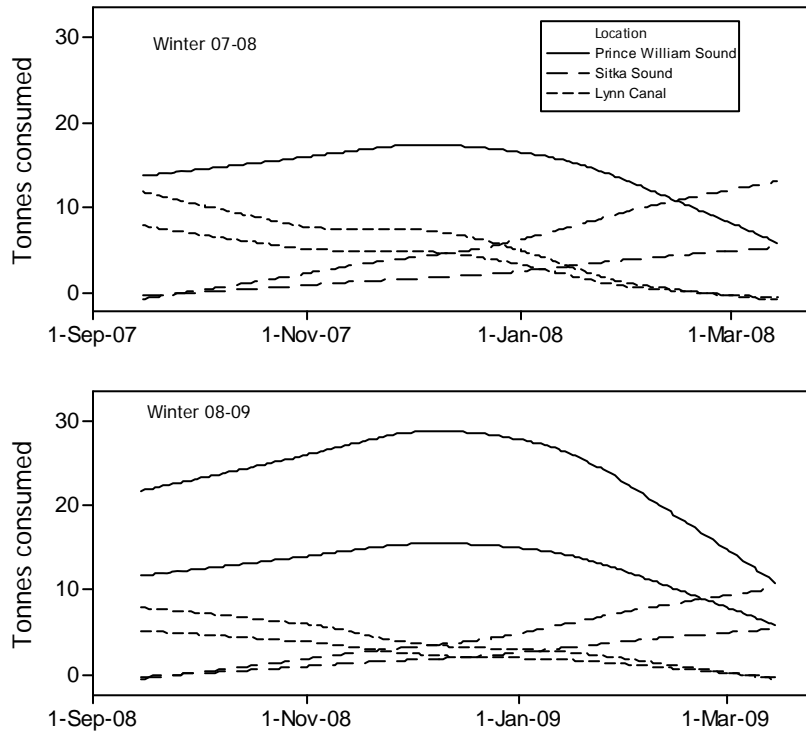


Figure 4. Perez model predictions of the daily consumption of herring by humpback whales over two winters in three locations. The upper line associated with each location shows predictions based on  $n_{t \text{ expanded}}$  and the lower line shows  $n_{t \text{ observed}}$ . A locally weighted smoothing function was applied to daily predictions to derive the curves. A lower limit for 2007-2008 in Prince William Sound was not estimated.

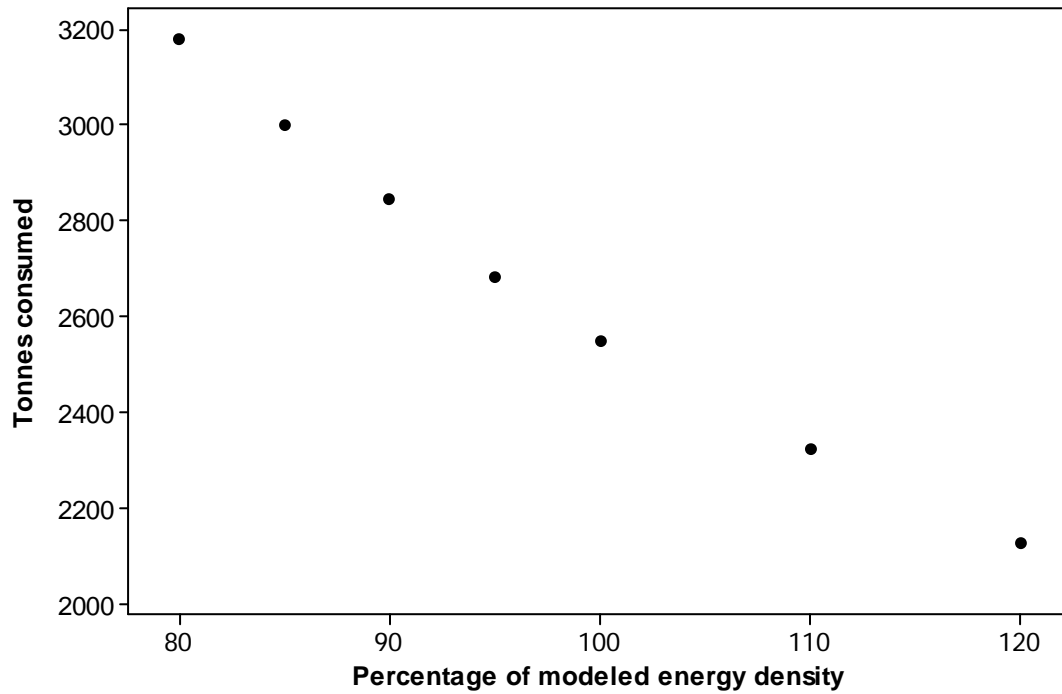


Figure 5. Effect of error in energy density on the estimated number of tonnes herring consumed by humpback whales. The 100% value depicts the model result for whales in Lynn Canal during the winter of 2007-2008 using the Acquarone model and  $n_{t \text{ expanded}}$ .